

FIG. 289.

Mullus surmuletus, L. Nat. size, 29 cm.

CAPROIDÆ

Capros aper, Lacép., 1910, Stations 1, 3, 20, 39 (see Fig. 290).

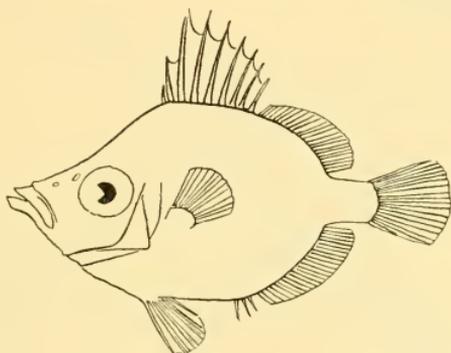


FIG. 290.

Capros aper, Lacép. Nat. size, 9.3 cm.

LABRIDÆ

Coris julis, L., 1910, Station 37 (see Fig. 291).

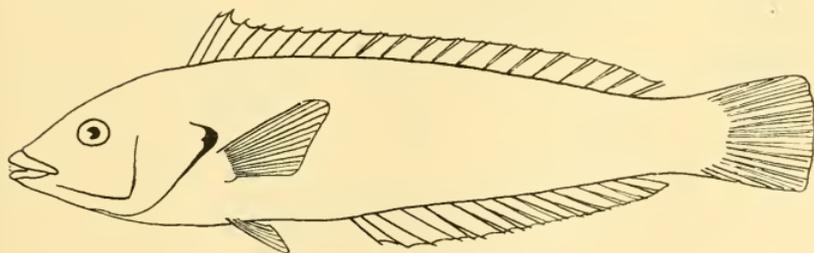


FIG. 291.

Coris julis, L. Nat. size, 18 cm.

Division—SCOMBRIFORMES

CARANGIDÆ

Caranx trachurus, L. (horse-mackerel), 1910, Stations 1, 3, 14, 20, 36, 39 (see Fig. 292).

Temnodon saltator, Cuv. and Val., 1910, Station 36.

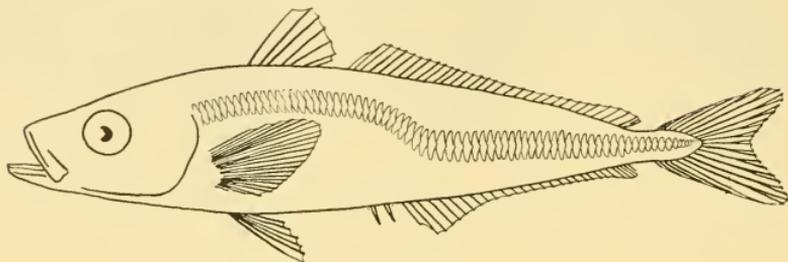


FIG. 292.

Caranx trachurus, L. Nat. size, 11 cm.

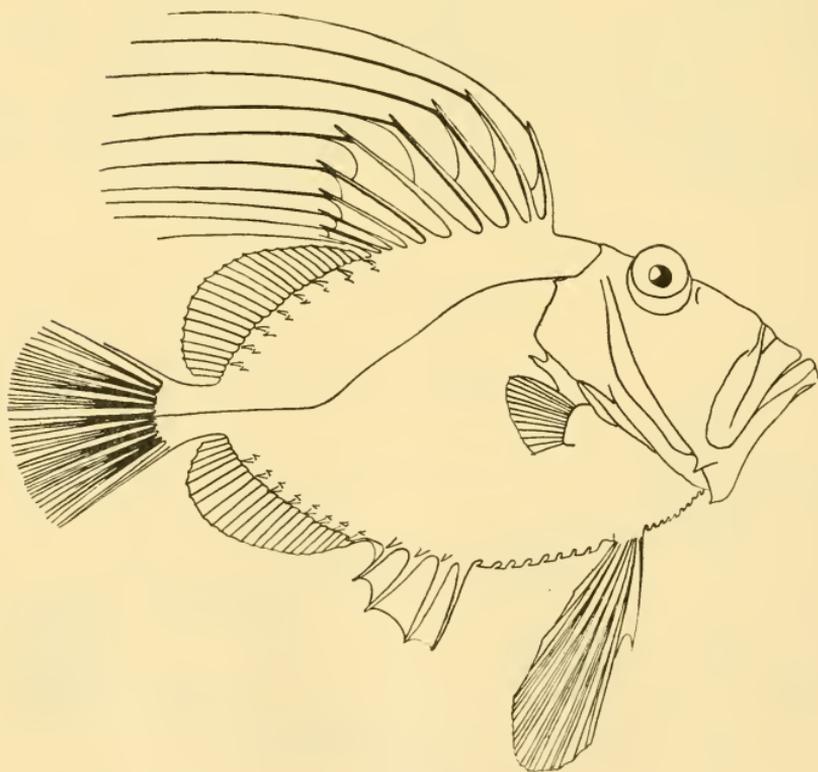


FIG. 293.

Zeus faber, L. Nat. size, 26 cm.

TRICHIURIDÆ

Lepidopus caudatus, Euphr., 1910, Station 43 (Gomera).

Division—ZEORHOMBI

ZEIDÆ

Zeus faber, L. (dory), 1910, Stations 1, 20 (see Fig. 293).

PLEURONECTIDÆ

Hippoglossus vulgaris, Flem. (halibut), 1902, Faroe-Shetland channel; Faroe Bank, 130 to 450 metres (see Fig. 294).

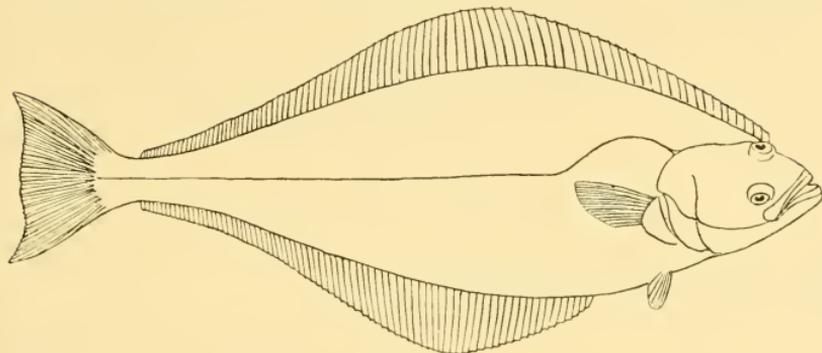


FIG. 294.

Hippoglossus vulgaris, Flem. (After Smitt.)

Pleuronectes limanda, L., 1902, Faroe Bank, 130 metres.

Arnoglossus laterna, Walb., 1910, Station 3.

Arnoglossus lophotes, Günth., 1910, Stations 3, 37, 38.

Arnoglossus grohmanni, Bonap., 1910, Station 38.

Zeugopterus megastoma, Donov. (megrim), 1902, Faroe Bank, 130 metres; 1910, Stations 1, 3, 96 (see Fig. 295).

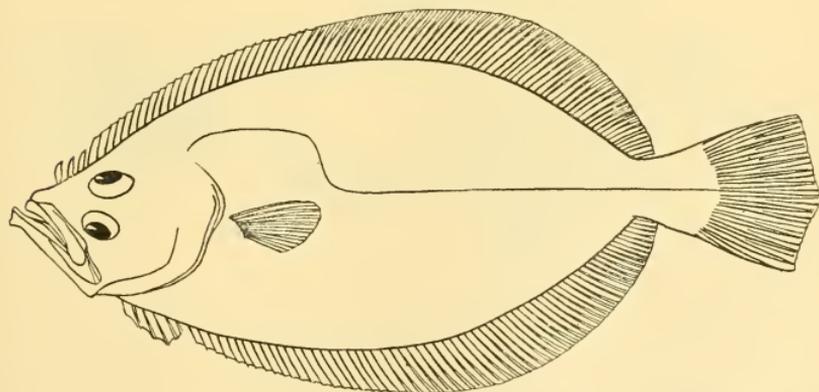


FIG. 295.

Zeugopterus megastoma, Donov. (After Smitt.)

Zeugopterus boscii, Risso, 1910, Station 21.

Solea vulgaris, Quensel (common sole), 1910, Stations 20, 38 (see Fig. 296).

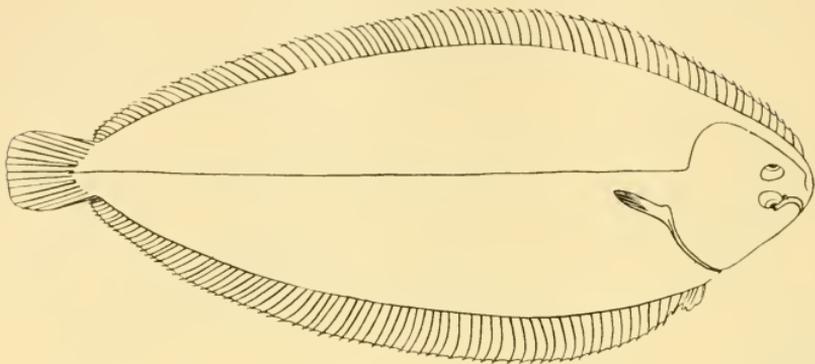


FIG. 296.

Solea vulgaris, Quensel. (After Cunningham.)

Solea lutea, Bonap., 1910, Stations 36, 38.

Solea variegata, Flem., 1910, Station 3.

Division—SCLEROPAREI

SCORPÆNIDÆ

Sebastes dactylopterus, Nilss., 1910, Station 21 (see Fig. 297).

Scorpena scrofa, L., 1910, Stations 37, 38 (see Fig. 298).

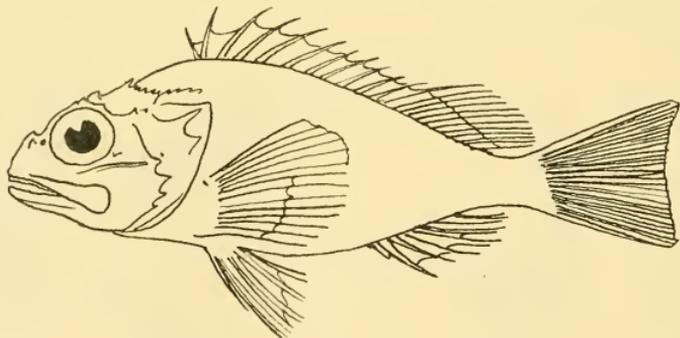


FIG. 297.

Sebastes dactylopterus, Nilss. (After Moreau.)

Scorpena ustulata, Lowe, 1910, Stations 37, 39.

Scorpena cristulata, G. and B., 1910, Station 4.

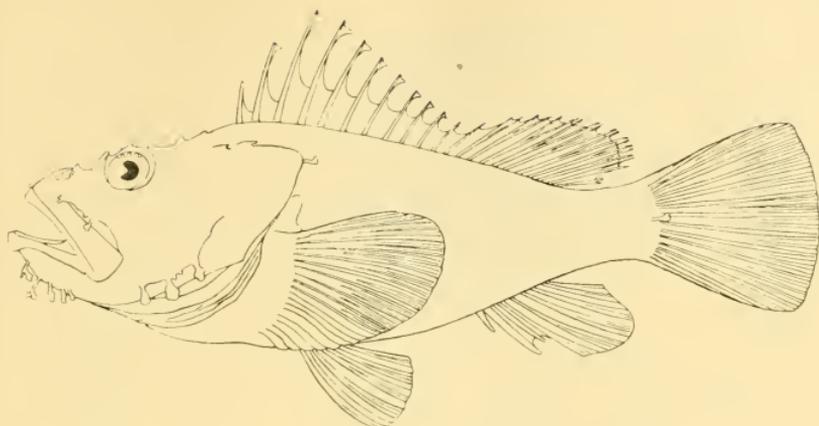


FIG. 298.

Scorpena scrofa, L. Nat. size, 48 cm.

TRIGLIDÆ (Gurnards)

- Trigla pini*, Bl., 1910, Stations 3, 20.
Trigla hirundo, Bl., 1910, Station 20.
Trigla gurnardus, L., 1910, Stations 1, 3.
Trigla cuculus, Bl., 1910, Station 20.
Trigla lyra, L., 1910, Stations 3, 20 (see Fig. 299).
Trigla obscura, L., 1910, Station 38.

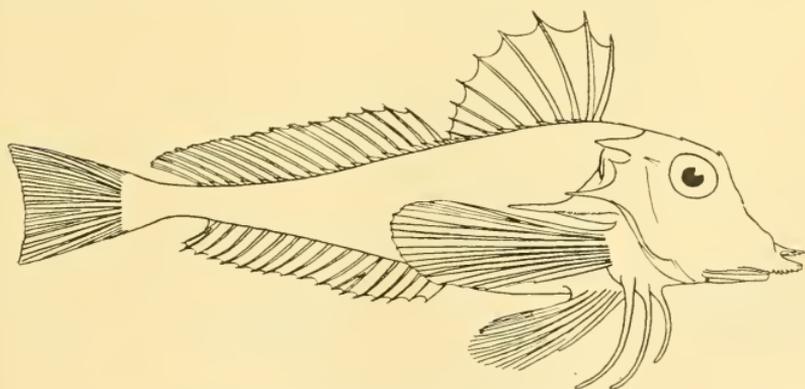


FIG. 299.

Trigla lyra, L. (After Day.)

- Lepidotrigla aspera*, Cuv. and Val. (Günth.), 1910, Stations 20, 39.
Peristedion calaphractum, Cuv. and Val., 1910, Stations 20, 39 (see Fig. 300).

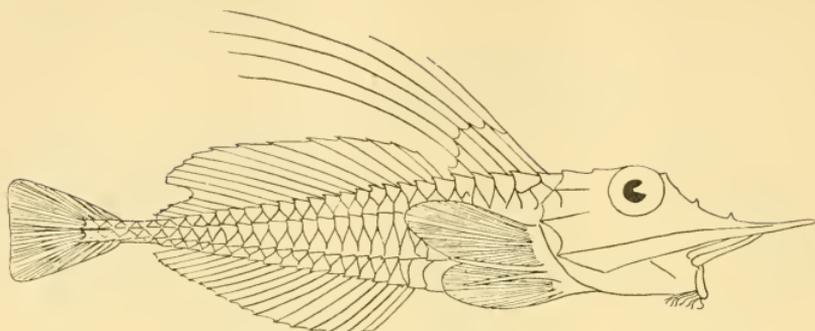


FIG. 300.

Peristedion cataphractum, Cuv. and Val. Nat. size, 30 cm.

Division—JUGULARES

TRACHINIDÆ (Weevers)

Trachinus draco, L., 1910, Station 38.

Trachinus vipera, Cuv. and Val., 1910, Station 14 (see Fig. 301).

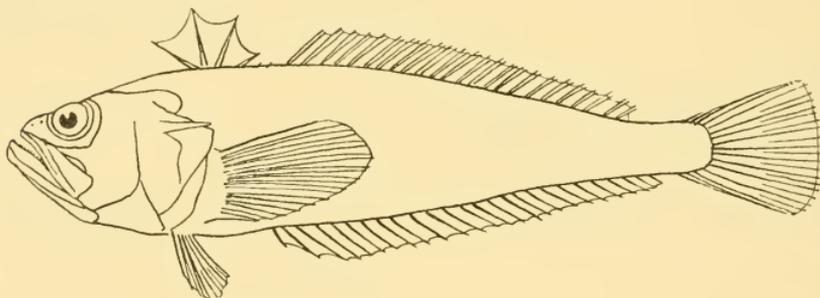


FIG. 301.

Trachinus vipera, Cuv. and Val. (After Cuvier.)

URANOSCOPIDÆ

Uranoscopus scaber, L., 1910, Station 37.

CALLIONYMIDÆ

Callionymus maculatus, Bonap., 1910, Station 3.

ZOARCIDÆ

Lycodes terræ novæ, Coll. (?), 1910, Station 70 (see Fig. 302).

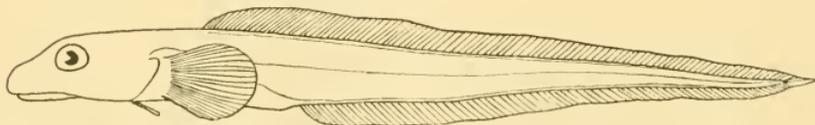


FIG. 302.

Lycodes terræ novæ, Coll. (?) Nat. size, 11 cm.

Sub-Order—**PEDICULATI**

LOPHIIDÆ

Lophius piscatorius, L., 1910, Station 3 (see Fig. 303).

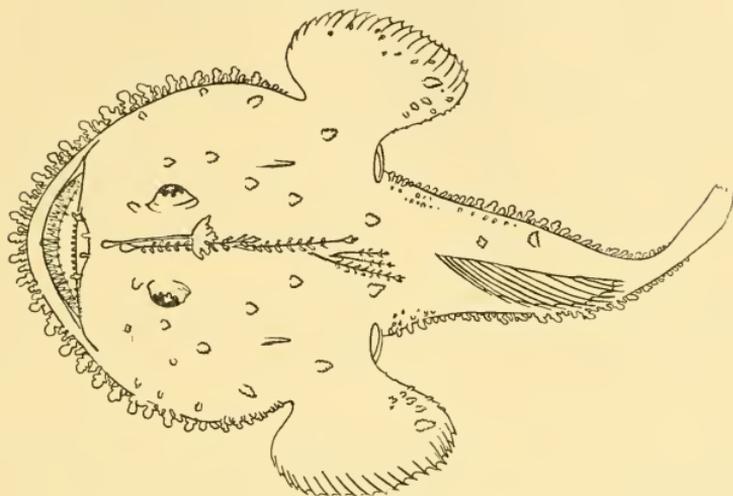


FIG. 303.

Lophius piscatorius, L. (After Smitt.)

MALTHIDÆ

Dibranchus hystrix, Garm., 1910, Station 70.

Sub-Order—**PLECTOGNATHI**

TETRODONTIDÆ

Tetrodon spengleri, Bl., 1910, Station 37 (see Fig. 304).

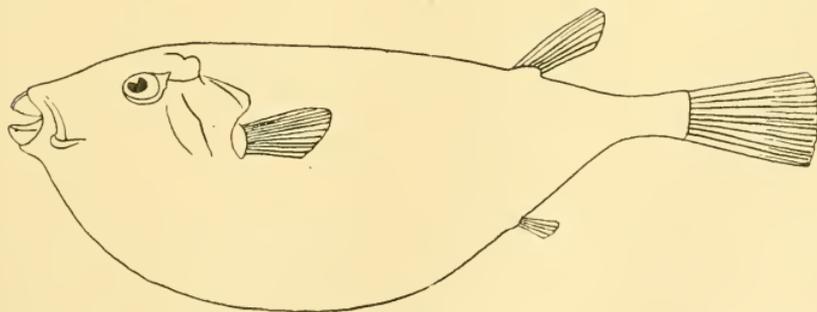


FIG. 304.

Tetrodon spengleri, Bl. (After Valenciennes.)

2. THE GEOGRAPHICAL DISTRIBUTION OF BOTTOM-FISHES IN THE NORTH ATLANTIC

THE FISHES OF THE ABYSSAL PLAIN¹

In Chapter IV. the areas of the ocean-floor at different depths are given, the percentages being as follows:—

Areas shallower than	100 fathoms	=	7.0 %	
„ between 100 and	500	„	= 5.6 %	or 1.4 % per 100 fathoms.
„ „ 500	1000	„	= 3.0 %	or 0.6 % „ 100 „
„ „ 1000	2000	„	= 19.3 %	or 1.9 % „ 100 „
„ „ 2000	3000	„	= 58.4 %	or 5.8 % „ 100 „
„ deeper than	3000	„	= 6.7 %	

About two-thirds of the sea-floor is thus covered by more than 2000 fathoms (or 3600 metres) of water, forming an abyssal plain 90½ millions of square English miles in extent, or nearly half the surface of the earth.

What organisms inhabit this abyssal plain? When studying the literature of deep-sea expeditions, we must remember that all the hauls hitherto made in the abyssal area have been effected by means of trawls or dredges, which function not only while being towed along the bottom, but also while being lowered and raised, filtering the immense column of water from bottom to surface. Therefore only organisms like worms, molluscs, holothurians, starfishes, corals, and all sessile forms may safely be considered as having been captured at the bottom. In the case of crustaceans and fishes, however, it may be doubted whether they were really caught at the bottom or in intermediate waters. Lists recording the catches of deep-sea expeditions at great depths cannot therefore be accepted as representing the animal-life on the ocean-floor, for in such lists we often find forms which are now known to live quite close to the surface. Although we have now a much more precise idea of the vertical distribution of pelagic fishes than was previously possible, some surprising facts are occasionally brought to light. Thus, as mentioned in Chapter III., the “Michael Sars” at Station 48, between the Canaries and the Azores, brought up an *Alepocephalus* in the large trawl towed at the bottom in 5000 metres, just as these fishes have been captured by most deep-sea expeditions; on the trawl-rope a small tow-net was fixed in

¹ The mean sphere level, which lies at a depth of about 1700 fathoms, has hitherto been regarded as the depth at which the abyssal plain of the ocean commences, but it will be seen that Dr. Hjort places this depth at 2000 fathoms.—J. M.

Difficulty in recognising what animals brought up in the trawl really lived at the bottom.

such a way that it was towed about 1000 metres above the bottom, and in this net an *Alepocephalus* was also captured.

Such facts warn us against hasty conclusions. Many fishes may, like the fishes in the Norwegian Sea (*Gadidæ*, *Sebastes*), occur in midwater above considerable depths as well as on the coastal banks and the continental slopes. A single record of a species from intermediate waters does not necessarily entitle us to consider the species as entirely pelagic. As in most biological questions, we have to judge from the available evidence, and, in dealing with the captures of fishes by deep-sea expeditions¹ in depths exceeding 2000 fathoms (3600 metres), I have endeavoured to eliminate all those species which are apparently pelagic, having been frequently captured at intermediate depths. In this way I have attempted to ascertain how many species and individuals have really been captured on the bottom of the abyssal plain of the oceans, and the result is given in the following table, which comprises 35 individuals belonging to 21 species in all:—

Fishes from
the bottom in
depths over
2000 fathoms.

¹ The excellent lists given by Brauer in his Report on the Deep-Sea Fishes of the "Valdivia" Expedition, the list by Vaillant in his Report of the French deep-sea expeditions, Garman's Report of the "Albatross" expeditions, Goode and Bean's *Oceanic Ichthyology*, and Murray's splendid Summary of the "Challenger" Expedition, have greatly facilitated this task.

BOTTOM-FISH TAKEN AT DEPTHS EXCEEDING 2000 FATHOMS (3600 METRES).

Species.	Taken by.	Greatest Depth (Metres).	Number of Individuals.	Locality.	Other Localities.
ALEPOCEPHALIDÆ.					
<i>Aleposomus copei</i>	"Albatross"	5317	1	East of North America	
<i>Alepocephalus rostratus</i>	"Talisman"	3655	1	Between the Azores and France	Morocco, the Azores, the Canaries, Mediterranean.
<i>Bathytroctes attritus</i>	"Talisman"	3655	1		
SCOPELIDÆ.					
<i>Bathysaurus mollis</i>	"Challenger"	4360	1	Mid-Pacific	
" "	"Talisman"	3655	1	Cape Verdes	
<i>Bathytroctis longipes</i>	"Challenger"	4844	2	East of South America	
" "	"Challenger"	3761	1	Mid-Pacific	
<i>Ipnops murrayi</i>	"Challenger"	3931	1	North of Celebes	Brazil, Tristan da Cunha.
HALOSAURIDÆ.					
<i>Halosaurus rostratus</i>	"Challenger"	5027	1	Mid-Atlantic	
MACRURIDÆ.					
<i>Macrurus sclerorhynchus</i>	"Talisman"	3655	3	Cape Verdes	Whole eastern slope of North Atlantic.
" "	"Challenger"	3747	2	Japan, Mid-Pacific	
" "	"Challenger"	4432	4	South and Mid-Pacific, New Zealand	
" "	"Talisman"	4200	2	Between the Azores and France	
" "	"Challenger"	4843	4	East and West of South America, Antarctic	
ZOARCIDÆ.					
<i>Neobythites crassus</i>	"Talisman"	4255	1	Between the Azores and France	
<i>Mixonus laticeps</i>	"Challenger"	4570	1	Mid-Atlantic	
<i>Lycodes albus</i>	"Talisman"	3975	2	Between the Azores and France	
<i>Bassozetus tania</i>	"Challenger"	4570	1	Mid-Atlantic	
<i>Typhlonus nasus</i>	"Challenger"	4460	2	North of Australia and Celebes	
<i>Alcockia rostrata</i>	"Challenger"	3888	1	North of Celebes	
SYNAPHOBRANCHIDÆ.					
<i>Histiobranchus infernalis</i>	"Albatross"	4062	1	East of North America	
" "	"Challenger"	3749	1	Mid-Pacific	Japan.
Number of species	21		35		

It is doubtful whether all these came from the bottom. Thus the three Alepocephalidæ, the six Scopelidæ, the one

Halosaurus, and the two Synphobranchidæ may be suspected of pelagic habitat. Less doubt may be entertained about the 15 Macruridæ and the 8 Zoarcidæ, and the probability is that these (some 20 individuals) constitute the total result of the attempts of all the deep-sea expeditions to capture bottom-fish on the abyssal plain beyond the 2000-fathoms line. Most of these fishes were taken by the "Challenger" in 57 hauls with the dredge or trawl in depths exceeding 2000 fathoms. In these hauls 22 individuals were captured, and the French expeditions caught 11 bottom-fish in eight hauls, giving an average of 1 fish to two hauls.

The 35 individual fishes enumerated belong to 21 species, 15 genera, and 6 families. On the average not even two individuals of each species have been captured. The genus *Macrurus* preponderates, 15 of the 35 individuals belonging to this genus, and of deep-sea fishes the Macruridæ may most safely be regarded as bottom-dwellers. The impression of scantiness conveyed by these facts, only one or two individuals of each species of fish being known from the immense area of the abyssal plain, agrees with the scarcity of the lower orders in the same barren region. A perusal of the "Challenger" Reports astonishes us by the fact that large numbers of species of lower animals are known only from a single locality, and often from one solitary specimen.

Scantiness of animal life at great depths.

These facts suggest that the bottom-fishes of the abyssal region are very local in their occurrence, but, considering the small number of individuals recorded, it seems risky to come to that conclusion, as the want of material for comparison tends to weaken our power of discriminating between the species. In certain problems of geographical distribution, the question may be vital whether two individual fishes caught in widely separated parts of the world are to be referred to one species or not. The systematic study of these deep-sea species leaves a strong impression that many of them differ very slightly from one another. Thus, for instance, my collaborator, Mr. E. Koefoed, and myself have not been able to convince ourselves that there is any specific difference between the two species, *Macrurus armatus* and *M. gigas*, mentioned in the above table, and this circumstance alone leads to far-reaching conclusions, *M. armatus* having been caught in the Pacific and *M. gigas* in the North Atlantic (see Fig. 308).

Wide distribution of deep-sea forms.

The collections of the "Michael Sars" throw much new light on these questions. In the following table I give the

distribution of the most important forms taken in the abyssal plain and the bordering intermediate zone. The localities of special importance are the Southern Ocean for *Halosauropsis macrochir*, and the Pacific for *Macrurus armatus*.

Species.	Localities where Captured.	
	By the "Michael Sars."	By other Expeditions.
	Stations.	
<i>Hariotta raleighana</i> .	35, 101	Off the east coast of North America.
<i>Bathypterois longipes</i> .	41, 53	Off the east coast of South America.
<i>Halosauropsis macrochir</i>	35, 53, 88, 95	Between South Africa and Kerguelen, off east coast of North America, Gibraltar, Morocco, the Azores.
<i>Macrurus aequalis</i> .	25, 35, 41	From Faroe Islands to Cape Verdes.
„ <i>simulus</i> .	53, 88	Off the east coast of North America, Denmark Straits.
„ <i>brevibarbis</i>	10, 88	Off the east coast of North America, Denmark Straits.
„ <i>armatus</i> .	10, 35, 53, 88	Pacific.
„ <i>globiceps</i> .	41, 88	Bay of Biscay to the Azores.
<i>Synaphobranchus pinnatus</i>	24, 41, 53, 88, 95, 101	Japan, Philippines, Arabian Sea, off east coast of North America, Faroe Islands to Cape Verdes, off Brazil.

Besides these we caught at Station 48 an *Alepocephalus* and the new form *Bathymicrops regis* (see Fig. 305), which may both be pelagic.

Excepting the *Hariotta*, which has only been taken at somewhat lesser depths (Station 35, 2603 metres), all these species

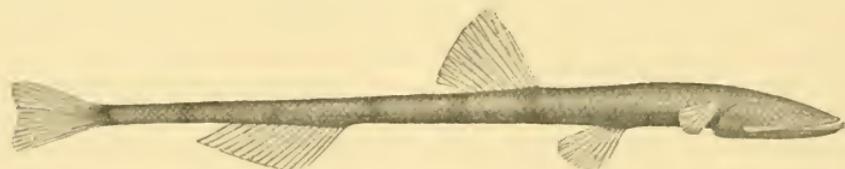


FIG. 305.

Bathymicrops regis, n.g., n.sp. Nat. size, 11 cm.

belong to the genera recorded by previous expeditions from the abyssal plain. Of the nine species, three (*Halosauropsis macrochir*, *Macrurus armatus*, and *Synaphobranchus pinnatus*) have previously been taken in other oceans. Of special interest is the fact that *M. armatus* has been found in so many new

localities, and this species is now known to have the widest distribution on the abyssal plain, and on this only. Another

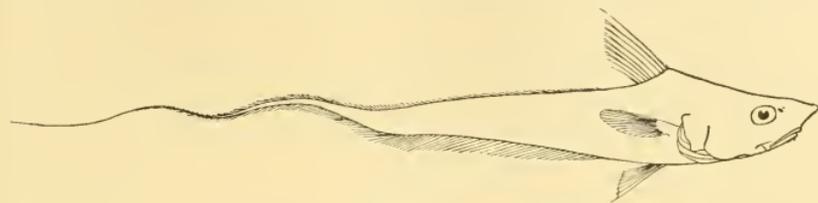


FIG. 306.
Macrurus (Lionurus) filicauda, Günth. (After Günther.)



FIG. 307.
Hariotta raleighana, G. and B. Nat. size, 30 cm.



FIG. 308.
Chart showing the localities where *Macrurus armatus* ● and *M. filicauda* ○ have been taken.
Temperatures in Centigrade.

species, *M. filicauda*, also shares this wide distribution (see Fig. 306, and Chart, Fig. 308).

Highly interesting also is the fact that no less than four of these deep-sea forms, viz. *Hariotta raleighana* (see Fig. 307),

Species found on both sides of the North Atlantic.

Bathypterois longipes, *Macrurus simulus*, and *Macrurus brevibarbis*, are now known from both sides of the Atlantic. The three last-mentioned species were also caught near the Azores, and we must therefore conclude that their habitat stretches right across the Atlantic. *Macrurus æqualis* was previously known only from the eastern side, *Macrurus globiceps* also from the Azores, and during the cruise of the "Michael Sars" it was taken a little north of the latter locality (Station 88). If the above table is compared with the list of "Michael Sars" stations, it will be noticed that these fishes from the abyssal region have a considerable vertical distribution, occurring also on the continental slopes.

Abyssal forms have a considerable vertical distribution.

Sir John Murray has, in his excellent "Summary," given lists recording all the different animals captured at each of the "Challenger" stations, and in a final chapter he endeavours to lay down some of the most important laws governing the distribution of animals in the ocean. At twenty-five stations where the depth exceeded 2500 fathoms the "Challenger" took with dredge and trawl 600 individual animals of all kinds; this gives 24 individuals per haul. Now, firstly, many of these were pelagic (most of the crustaceans and some of the fishes), and secondly, many of them were very small (hydroids, bryozoa). As examples I give a list of the bottom-forms (protozoa excluded) obtained at some of the "Challenger" stations between the Canaries and the West Indies.

"Challenger" hauls in the deep water of the North Atlantic.

- | | | | |
|---------|-----|----------------------|--|
| Station | 5. | Depth, 2740 fathoms. | Three living mussels (<i>Leda</i> , <i>Limopsis</i> , <i>Arca</i>), and some dead shells. |
| " | 13. | Depth, 1900 fathoms. | Some bryozoa and brachiopods (10 <i>Terebratula</i>). |
| " | 14. | Depth, 1950 fathoms. | Some bryozoa. |
| " | 16. | Depth, 2435 fathoms. | Sharks' teeth (<i>Oxyrhina</i> , <i>Lamna</i>), valves of <i>Scalpellum</i> , 2 mussels (<i>Arca</i>). |
| " | 20. | Depth, 2975 fathoms. | Dredge came up half full of clay, containing half a dozen tubes of serpulids, some of these with the worms living. |
| " | 61. | Depth, 2850 fathoms. | Trawl captured some ophiuridæ (<i>Ophioglypha</i>), 2 holothurians, 7 <i>Scalpellum</i> . |
| " | 63. | Depth, 2750 fathoms. | Trawl captured some fragments of worms, 3 <i>Scalpellum</i> , 1 fish (<i>Halosaurus rostratus</i>). |

This list is representative of most deep-sea hauls, and their uniform poverty is only broken by rare exceptions, as in a noteworthy haul taken by the "Challenger" in the Pacific, between Japan and Hawaii, at Station 244, in 2900 fathoms, which gave:—

1 sponge, 1 antipatharian, 6 actinians, 2 corals, 1 hydroid colony, 2 crinoids, 3 starfish, 1 sea-urchin, 5 holothurians, many worms, 7 or 8 mussels, and a brachiopod.

This is, as far as I have been able to ascertain, the richest haul in depths exceeding 2000 fathoms on record, but nevertheless the impression created by the results of the many deep-sea hauls of the "Challenger" is that animal life is poorly developed in the abyssal region.

During the cruise of the "Michael Sars" I therefore considered it an interesting object to ascertain if our large otter trawl could catch more, and possibly larger, animals on the abyssal plain. As stated in Chapter III., technical success attended our attempts at great depths, and the catches were certainly somewhat larger than those previously taken in the North Atlantic, but nevertheless they were very poor, as shown by the following list:—

"Michael Sars" hauls in the deep water of the North Atlantic.

Station 10. Bay of Biscay, 2567 fathoms (4700 metres). Trawl dragged for five hours gave: Some sponges, 3 actinians, some holothurians (*Elpidia*), 2 starfish (*Frugella*, *Dorigona*), a few worms, ascidians, and bryozoa, 1 gasteropod, and 2 fishes, presumably bottom-fish: *Macrurus armatus* (Hector), 1 individual 70 cm. in length, and *M. brevibarbis* (G. and B.), 1 individual 25 cm. in length.

Same Station. Duration of haul, 3½ hours. Cod-end full of ooze, and in the meshes 3 ophiurids (*Ophiopleura*, *Ophioglypha*, *Ophiocten?*); washing the ooze produced 4 actinians (one of them growing on a hermit crab), 1 holothurian (*Elpidia*), worms in clay tubes, and some gasteropods.

Station 48. Between the Canaries and the Azores, over 5000 metres. Duration of haul, 4½ hours. Trawl contained a large quantity of ooze, the washing of which produced: 30 pieces of pumice-stone, 1 shell of *Argonauta*, 1 ear-bone of a whale, 2 sharks' teeth (*Carcharodon* and *Oxyrhina*), 10 large shells of pteropods (*Cavolinia*), 1 umbellularian (*Umbellula guntheri*), 1 sertularian, 2 holothurians (*Latmogone violacea*, *Elpidia* sp.). Besides these there were 3 pelagic fishes (*Malacosteus indicus*, *Argyropelecus* sp., and a *Leptocephalus*), and 3 fishes which may be surmised to have lived at the bottom (*Alepocephalus*, a new genus related to *Ipnops*: *Bathymicrops regis*, see Fig. 305, and a specimen not yet determined).

These hauls of the "Michael Sars" thus entirely confirm the idea of the poverty of the abyssal plain, a confirmation especially valuable on account of the size of the trawl employed and the technical success attending its use in great depths. The proof afforded by these results of the "Michael Sars," like that from all other expeditions, suffers from the inherent weakness attached to all negative proofs. The barrenness of the abyssal plain may be only apparent, owing to imperfections in

the methods of capture, the technical difficulties of operating dredges and trawls at great depths being of considerable moment, but I do not attach great importance to this, because the same appliances, when used in deep water on the continental slope, gave large catches.

If we fix the boundary of the abyssal plain at the 2000-fathoms line, we may consider the area between the 2000- and 1500-fathoms lines as an intermediate zone between the abyssal plain and the continental slope. In this zone the "Challenger" made 25 hauls with trawls and dredges, with the result that three times as many fishes per haul, and twice as many invertebrates, were captured as on the abyssal plain. The "Michael Sars" made 3 hauls with the trawl in such depths, which, compared with our results from the abyssal plain, are very interesting, and invite inspection of their details:—

- Station 35. South of the Canaries, 1424 fathoms (2603 metres). Trawl dragged two hours. Result of haul: Many silicious sponges (including *Hyalonema*), hundreds of holothurians, large prawns (*Benthescyrmus*, n.sp.), 18 bottom-fish (9 Macrurids, 1 *Bathysaurus*, 2 *Halosauropsis*, 5 *Alepocephalus*, 1 *Hariotta*).
- „ 53. South of the Azores, 1430 to 1570 fathoms (2615 to 2865 metres). Trawl dragged three or four hours. Result of haul: 2 large and many small sponges, 3 mussels, 5 cirripeds (*Scalpellum*), 30 large prawns (*Aristeopsis*), 15 hermit crabs, 5 *Pentacheles*, 1 large white decapod (*Munidopsis*, n.sp.), 500 holothurians, 39 bottom-fishes, (17 *Macrurus*, 5 *Halosauropsis*, 2 *Benthosaurus*, 2 *Bathysaurus*, 2 *Bathypterois*, 6 *Alepocephalus*, 5 *Synaphobranchus*).
- „ 88. North of the Azores, 1700 fathoms (3120 metres). Result of haul: a great number of holothurians, sea-urchins, starfish, ophiurids, some crustaceans (*Polycheles*, *Munidopsis*, *Parapagurus*), 21 bottom-fishes (17 *Macrurus*, 1 *Bathysaurus*, 3 *Histiobranchus*).

These hauls plainly show that the appliances of the "Michael Sars" were excellently suited for the capture of bottom organisms, fish as well as invertebrates. Indeed in one single haul (Station 53) we caught nearly as many individual bottom-fishes as the "Challenger" captured in its twenty-five hauls in depths between 1500 and 2000 fathoms. I think we are justified in concluding that the vast difference between our captures on the abyssal plain and these three hauls in 2600 to 3200 metres represents an actual difference in the abundance of animal life in the two regions. The fauna of the abyssal plain must be very poor compared with the more abundant life met with, at all events in the Atlantic, in depths of about 3000 metres and less, where the fauna is infinitely richer in number of species as well as in number of individuals. Perhaps the most striking contrast is

Hauls in
depths of
1500 to 2000
fathoms.

obtained when we consider the enormous difference in the *number* of animals brought up by the trawl from the two regions in question.

THE FISHES OF THE CONTINENTAL SLOPES

The angle of the slopes rising from the abyssal plain towards the coast varies in different parts of the globe, being in some places steeper than in others. The percentages of the ocean-floor given on p. 132 show that the steepest angle occurs between 500 and 1000 fathoms, while the slope between 1000 and 2000 fathoms is much steeper than in the upper 100 fathoms. Between the shore-line and the 100-fathoms line the angle of the slope is low, and this area is regarded as a special region, generally termed the coast-plateau, or the continental shelf or platform (see Fig. 144, p. 198). The fishermen's term for this section of the sea-bottom is "the banks," and the narrow intermediate belt between the coast-plateau and the continental slope is by the fishermen termed "the edge."

One of the objects of the "Michael Sars" Expedition was to make a number of trawlings on the continental slopes of the Atlantic in different latitudes, in order to study the fish-fauna at different depths and under varying conditions. We succeeded in making quite a number of good hauls, and, taken together with the captures of other expeditions (especially those of the French deep-sea expeditions), they give a good representation of the different fish-faunas. Our stations along the slope may be divided into three groups:—

"Michael Sars" hauls on the continental slope.

1. West of Great Britain (including some hauls from localities south of the Faroe Islands in the year 1902).
2. Spanish Bay, west of Morocco.
3. South of the Canaries.

First of all, we will consider the number of fishes caught in these hauls at different depths, as recorded in the following table, and next we will investigate the vertical and horizontal distribution of the species:—

West of Great Britain.			Spanish Bay, west of Morocco.			South of the Canaries.		
Station.	Depth (metres).	Number of Fishes.	Station.	Depth (metres).	Number of Fishes.	Station.	Depth (metres).	Number of Fishes.
1	146	308	20	141	161
3	184	332
Faroe slope	831	300	21	535	117	39	280	about 300
4	923	332
Faroe slope	1060	76
"	1073	127	23	1215	77	41	1365	about 80
95	1797	82	24	1615	32
101	1853	90	25	2055	29	35	2603	18

The French deep-sea expeditions made in all 106 hauls at different depths down to 5000 metres, mostly in the same part of the Atlantic examined by the "Michael Sars," the fishing results being very interesting:—

4 hauls between	0 and	100 metres gave	224 fishes, or	56 per haul.
9	"	100 " 200	"	323 " 36 "
6	"	200 " 500	"	1275 " 212 "
28	"	500 " 1000	"	1044 " 37 "
29	"	1000 " 2000	"	905 " 31 "
20	"	2000 " 2900	"	115 " 6 "
4	"	2995 " 4000	"	61 " 15 "
6	"	4000 " 5000	"	10 " 2 "

Both these tables show clearly that the number of bottom-fish decreases from land towards the abyssal plain. This decrease is, however, far from uniform. Even down to 500 fathoms the "Michael Sars" obtained just as many fishes as on the bank, viz. about 300 fishes in one haul, and these were not small. At the same time the trawl was also crammed with other animals. In depths greater than 500 or 600 fathoms we no longer obtained anything like that number, but even down to 1000 fathoms (1853 metres) we still got as many as 90 fishes in one haul. Beyond 1000 fathoms fishes seem rapidly to decrease in number, for neither the "Michael Sars" nor the French expeditions got more than a score, or exceptionally nearly two score of fishes in depths exceeding 1000 fathoms. The richest haul of fishes known from a great depth is one taken by the "Michael Sars" at Station 53, in 2865 metres, viz. 39 fishes, of which some were large.

If we now consider what *species* of fish we obtain in our trawlings along the continental slopes, we immediately recognise different strata, each characterised by its peculiar fish-community. It will be of interest to define the extent of these communities by means of the species found most abundantly at different depths, though there are no sharp limits between them, as it is difficult to find even two kinds of fish (or other animals) having in every respect the same distribution. It is thus obvious that on the borders of the different communities recognised by us, we shall find species belonging to neighbouring communities.

We have already mentioned that the "Michael Sars" caught some of the abyssal species along the continental slopes, and the French deep-sea expeditions also gathered similar information. We may then first consider the bathymetrical range of some of these peculiar bottom-fish living at the greatest depths:—

Bathymetrical
range of deep-
sea fishes.

	Bathymetrical Range.
<i>Macrurus sclerorhynchus</i>	from 540 to 3655 metres.
" <i>talismani</i> ,	" 460 " 2220 " "
" <i>globiceps</i>	" 1139 " 2995 " "
<i>Alepocephalus rostratus</i>	" 830 " 3655 " "
<i>Halosauropsis macrochir</i>	" 1183 " 2995 " "
<i>Synaphobranchus pinnatus</i> ¹	" 201 " 3250 " "

We see here a group of species which may occur in very deep water as well as along the continental slope; the upper limit seems to be about 800 or 900 metres (about 450 fathoms), although stray individuals have been caught in somewhat shallower water.

The main body of the fishes peculiar to the continental slopes consists, however, of other species, which have not been captured in the abyssal plain, though they have a wide distribution, like the denizens of the abyssal plain, and resemble them also in shape. Such are the following:—

	Bathymetrical Range.
<i>Macrurus aequalis</i>	from 460 to 1319 metres.
" <i>zaniophorus</i>	" 830 " 1590 " "
<i>Bathygadus melanobranchus</i>	" 830 " 1590 " "
" <i>longifilis</i>	" 1374 " 1635 " "
<i>Mora mora</i>	" 614 " 1367 " "
<i>Lepidion lepidion</i>	" 631 " 1097 " "
<i>Chimæra monstrosa</i>	" 535 " 1257 " "
Different species of <i>Centrophorus</i> (sharks)	" 1230 " 1853 " "

¹ The fact that this form has been taken within such wide limits must, in my opinion, give rise to the suspicion that it may really be caught in midwater; perhaps it never actually occurs in the abyssal area.

These appear to be representatives of the fauna peculiar to the steepest part of the slope, from 700 to 1500 metres (400 to 800 fathoms).

The "Michael Sars" captured on the Atlantic slope, in depths between 800 and 2600 metres, over 1200 fishes, the relative abundance of the different forms being as follows:—

569 fishes, or about 47 per cent,	belonged to Macruridæ.			
393	"	33	"	Gadidæ (<i>Mora</i> , <i>Antimora</i> , <i>Lepidion</i> , <i>Halargyreus</i>).
66	"	6	"	Alepocephalidæ.
47	"	4	"	Sharks (<i>Centrophorus</i> , <i>Chimæra</i> , <i>Etmopterus</i>).

The remaining 10 per cent consisted of fish represented by only a few individuals (*Notacanthus*, rays, and others).

In about 400 to 500 fathoms (700 to 900 metres) we meet with forms having their lower limit in this region, which live in greatest abundance at 200 to 300 fathoms. As instances may be mentioned:—

	Bathymetrical Range.
<i>Sebastes dactylopterus</i>	from 75 to 975 metres.
<i>Motella macrophthalmia</i>	" 146 " 987 "
<i>Hoplostethus mediterraneum</i>	" 140 " 1435 "

In about 300 to 350 fathoms (550 to 650 metres) we meet with real representatives of the fauna of the coast banks. The following are some of these species, found in deep water by the French expeditions, with their bathymetrical range:—

	Bathymetrical Range.
<i>Merluccius vulgaris</i> (hake)	from 65 to 640 metres.
<i>Gadiculus argenteus</i>	" 411 " 550 "
<i>Zeugopterus megastoma</i>	" 60 " 560 "
<i>Dentex macrophthalmus</i>	" 120 " 460 "

In these depths we thus find in the same hauls representatives of two entirely different faunas, and we must therefore consider this region as an intermediate belt.

Before attempting to describe the fauna of the coast banks, I wish to discuss some questions of general importance arising from the examination of animal life on the continental slopes.

In his report on the deep-sea fishes of the "Valdivia" Expedition, Brauer gives a very able and interesting review of the general laws governing the geographical distribution of these fish, particularly the Macruridæ. While the genus *Macrurus* is found in all the oceans, he considers most of the species to be local. Of 116 species of Macruridæ he has so far

only found one (*M. parallelus*) which is common to the Indian, Atlantic, and Pacific Oceans. All the 19 species taken at the Sandwich Islands are known only from that locality. Some species, like *M. armatus* and *M. filicauda*, have a wide distribution, but these are exceptions from the rule. Thus, in his opinion, there are no species common to both sides of the Atlantic. The only exceptions then known (*M. simulus*, *M. goodei*, *M. berglax*, and *M. rupestris*) are explained by him as being due to these species following the cold Labrador current from their normal habitat, the eastern side of the ocean.

Brauer attempts to explain the peculiar distribution of the Macruridæ. He considers that the Macruridæ have originated from coast-fishes, and only commenced to migrate towards the abyssal region after a great variety of coast-forms had been developed. "The fact," he observes, "that only a few species have penetrated into the abyssal plain, while the main body of the species still remains on the slope, tends to show that in most cases the migration towards the abyssal plain is still going on, that it is very slow, and that it has not yet reached the borders of the abyss; or else it indicates that the abyssal plain tends to limit further distribution, acting as an almost insurmountable obstacle."

We have seen that all the deep-sea expeditions, prior to the "Michael Sars," captured only 35 individual "bottom-fishes," and that these belonged to twenty-one species. Our present knowledge must therefore be very imperfect. We have not yet learnt to fish to perfection at 2000 or 3000 fathoms, and we have as yet made too few fishing experiments at such depths. The short cruise of the "Michael Sars" in the Atlantic has essentially altered Brauer's ideas of the distribution of *deep-sea* fishes, and it appears desirable to give the interesting question raised by him a fresh trial, in view of the large amount of information which we now possess regarding the migrations of many fishes. When, for instance, we find the cod of the Norwegian Sea at one season spawning near the coasts of Norway, at another season migrating to Spitzbergen, or to the slopes of the coast-plateau, we must conclude that fishes may undertake horizontal as well as vertical migrations of enormous extent in a short space of time. Seeing that *Macrurus sclerorhynchus* has the enormous bathymetrical range of from 540 to 3655 metres, we can hardly suppose that the distribution of deep-sea fishes down the slope and on the abyssal plain could have been prevented by "lack of time." We have

every reason to believe that the physical conditions in these depths have been essentially the same at least for thousands of years.

We possess, of course, no information as to the time required for the distribution of a species into oceanic depths. In shallow waters we know quite well that new physical conditions may permit a species to migrate into new areas and to multiply enormously in a short space of time (as an instance may be mentioned the immigration of cod into the Liimfjord after the North Sea broke through at Thyboroen). At all events it seems reasonable, first of all, to look for factors in operation at the present day, the influence of which may be investigated, before we fall back on the hypothetical conditions prevailing in a previous geological period.

In his "Challenger" Summary, Sir John Murray has attempted an explanation of the quantitative distribution of organisms in different depths, which not only throws much light on these important geographical questions, but also possesses the great advantage of containing in itself a whole programme of future research. He found that many deep-sea animals—the hydroids, for example—had developed special apparatus for catching the minute shells and particles of food that fall from the surface waters, and the holothurians and other echinoderms—the most abundant of deep-sea animals—had their intestines always crammed with the surface layers of the deposit on which they were captured, either Blue mud, Diatom ooze, Globigerina ooze, Pteropod ooze, or Red clay.

We have seen in Chapter IV. that marine deposits may be separated into two main groups: terrigenous deposits and pelagic deposits, the former occurring in deep and shallow water around all continents and islands within an average distance of one hundred or two hundred miles from the coast, and the latter occurring in the deeper water towards the central parts of the great ocean basins.

It is a well-known fact that the detrital matter which is carried into the sea by rivers is rapidly deposited on meeting salt water, but in shallow water, where currents and wave-action produce their maximum effect, these fine detrital matters are not allowed to settle on the bottom, but are moved along till they reach the lower limit of wave-action. In enclosed seas this may be at a depth of only a few fathoms, but along coasts facing the great oceans the waves are so long and so high that to a depth of several hundred fathoms minute particles of sand may be dis-

Murray on the "mud-line" and mud-eating animals.

turbed, as, for instance, off the north of Scotland. Murray has termed the limit of wave-action the *mud-line*, and the average depth in the open ocean at which mud commences to be laid down he places at about 100 fathoms.

Beyond the mud-line the physical conditions become more and more uniform, and for a few hundred fathoms below this limit animal life is exceedingly abundant. This region, according to Murray, is the "great feeding ground" of the ocean, especially around continental shores; the organic particles from the continents and from the shallow waters there slowly come to rest on the bottom and supply food to the wealth of crustaceous forms which are captured in such situations (*Calanus*, *Euchæta*, *Pasiphæa*, *Crangon*, *Calocaris*, *Pandalus*, *Hippolyte*, *Pagurus*, Amphipoda, Isopoda, and Mysida).

The surface layers of the organic deposits which are situated in moderate depths towards the central parts of the ocean basins (Diatom ooze, Globigerina ooze, Pteropod ooze), yield an abundance of food for benthonic animals, but all investigations go to show that where the organic oozes pass with increasing depth into Red clay, the quantity of food for bottom-living animals rapidly diminishes, and the number of animals captured on Red clay bottoms likewise diminishes very greatly. The poorest hauls during the whole of the "Challenger" Expedition were those taken in the stretches through the central Pacific from Japan to Valparaiso, and Alexander Agassiz's investigations on board the "Albatross" gave similar results. He calls the central South Pacific a "barren region."

Decreasing amount of food on proceeding into deep water.

This short statement will make it obvious, that the conditions of life offered to organisms may vary greatly in different depths. Murray's theory on the importance of the deposits to the distribution of animal life is of special value, because it opens up to science the possibility of finding certain definable reasons for the differences observed in the specific composition, and in the abundance, of animal life from place to place.

Relation between the different kinds of deposits and the fauna living on them.

This study has, however, been somewhat neglected as far as the oceans are concerned. Most of the deep-sea expeditions have been so absorbed in faunistic research, that the problems of the economy of the ocean have been very little attended to, and the strong interest taken in theoretical plankton-research peculiar to recent times has drawn attention away from the bottom-life of the ocean and the importance of the deposits as food for the bottom fauna, but Lohmann and C. G. J. Petersen have recently turned attention again to Murray's point of view.

Petersen on organic matter in the uppermost layer of deposits.

During his plankton work in the Liimfjord, Petersen arrived at the conclusion that the plankton played a very unimportant part in the food of bottom-animals (as, for instance, the oyster). He commenced therefore to study the finely granular mass found in the gut of the bottom animals. He discovered that the uppermost layer of mud on the fjord bottom, 2 or 3 mm. in thickness, consisted of detritus containing minute remains of organisms, mainly of decayed plants from the littoral region, and that only this upper layer of the mud has any nutritive value, the deeper blue-black layer not occurring in the gut of the bottom animals. Starting from these researches, Petersen studied the organic (nutritive) constituents of the mud, especially of the upper layer, and investigated the abundance of bottom-animals over different kinds of deposits. For this purpose he constructed an apparatus (see Chapter X.) for cutting away from the sea-bottom a square foot of its surface. When this large "bottom sample" is sifted the animals contained in the mud can be counted, and by comparing the quantities of mud-eating animals thus found per square foot of bottom, the yielding power of different areas may be estimated, much on the same principle as the productive value of agricultural land is estimated.

The "Michael Sars" had, during the Atlantic cruise, some of Petersen's apparatus on board, but owing to difficulties in using them in deep water, we did not succeed in obtaining material of any value, a fact all the more regrettable, as there is no doubt that Petersen's method gives far more exact results as regards the quantities of certain animals living on the bottom in shallow water than hauls with dredges and trawls. Nevertheless, the material at hand may be used to illustrate the question. The most stringent quantitative science is in the first stages of a new study satisfied to dispense with the demand for absolute exactness, and contents itself with relative values—in other words, with a comparison between different localities.

"Challenger" hauls on different deposits.

Sir John Murray long ago attempted to compare the number of animals taken in the dredge or trawl on different deposits, based on the results of the "Challenger" Expedition, and I reproduce some of his figures from the second volume of the "Challenger" Summary:—

	Specimens per Haul.	
	Trawlings.	Dredgings.
<i>On Red Clay—</i>		
In the Atlantic	40.0	4.2
„ Pacific	20.3	...
„ Southern Ocean	50.0	13.3
<i>On Globigerina Ooze—</i>		
In the Atlantic	21.1	5.2
„ Pacific	56.5	7.0
„ Southern Ocean	96.7	5.0
<i>On Terrigenous Deposits—</i>		
In the Atlantic	108.5	55.3
„ Pacific	71.4	59.0
„ Magellan Strait	100.0	...
„ Southern Ocean	93.0

These figures plainly show that animal life was found most abundantly on terrigenous deposits, though the *Globigerina* ooze was also, especially in the Southern Ocean, very rich in organisms.

At the two deepest stations of the "Michael Sars" (Station 10, 4700 metres, and Station 48, over 5000 metres) the trawl was dragged for hours along the bottom, and brought up great quantities of ooze, which on being sifted yielded only a few holothurians (one individual at Station 10 and two at Station 48). Of other mud-eating animals we found none at Station 48; and at Station 10, in two hauls, a gasteropod, two ophiurids, and a few worms.

These hauls are comparable with those made by the "Challenger" between the Canaries and the West Indies (see p. 418), in depths between 2000 and 3000 fathoms.

Different conditions are encountered on the slopes in shallower water, the slopes of both continents and submarine ridges. From the "Michael Sars" journal the following results of trawlings on the continental slope west of the British Islands may be quoted:—

Station 101, 1853 metres (about 1000 fathoms). Besides 90 fishes, great numbers of invertebrates, mainly echinoderms, ophiurids and starfish being especially abundant.

Station 95, 1797 metres (981 fathoms). Besides 82 fishes, 300 holothurians, 800 ophiurids, starfish, *Phormosoma*, etc.

"Michael Sars" trawlings on the continental slope to the west of Britain.

Station 4, 923 metres (547 fathoms). Besides 332 fishes, quantities of starfish, sea-urchins (*Brissoopsis*, *Phormosoma*), etc.

South of the Faroe Islands, 831 metres (460 fathoms). Besides 300 fishes, large numbers of invertebrates.

Abundant fauna on Globigerina ooze on and beyond the continental slope.

In Chapter IV. Sir John Murray has stated that the bottom-samples collected during the cruise of the "Michael Sars" show that Globigerina ooze approaches nearer to the coasts of the British Islands than was previously supposed, having been found at Station 4, 547 fathoms; Station 93, 688 fathoms; Station 95, 981 fathoms; Station 98, 742 fathoms; and Station 100, 835 fathoms.

While the fishes of the continental shelf all live on terrigenous deposits, like Blue mud, the "Michael Sars" results prove that in the eastern Atlantic, at any rate, *most of the fauna of the continental slope live on Globigerina ooze*. Circumstances may be quite different on other slopes, as, for instance, the Atlantic slope off the United States, or off Newfoundland, where terrigenous deposits seem to have a much wider distribution. But the very important question of the limits between the terrigenous and the pelagic deposits requires further careful study by means of series of hauls with the trawl and series of samples of the deposits from shallow water down the slope to the abyssal plain.

The results given above show in any case that the Globigerina ooze in depths of 550 to 1000 fathoms may be a rich ground for animal life, since we got such good hauls at the stations quoted, and this is corroborated by the hauls taken on this type of deposit in deeper water, far from continental land, as at Stations 53 and 88.

At Station 53, south of the Azores, 2615 to 2865 metres (1430 to 1570 fathoms), the trawl captured in one haul, besides 39 fishes, about 500 holothurians, and abundance of different crustaceans, actinians, etc.

At Station 88, in 3120 metres (about 1700 fathoms), the trawl brought up a wealth of animals, especially sea-urchins, starfish, ophiurids, holothurians, etc.

We thus see that *it is not terrigenous deposits alone which harbour an abundant bottom fauna*; in fact, on true pelagic deposits, like Globigerina ooze, we may have the conditions necessary for abundant life. The percentage of carbonate of lime gives no indication of the suitability of the conditions for animal life, for the terrigenous deposits with abundant fauna, as well as the barren Red clay, both contain very little calcium carbonate. The important item is the *organic substance* con-

tained in the deposits, which fertilises the surface layers of the Blue mud as well as of the *Globigerina* ooze.

Importance of organic matter in the deposits.

Petersen has shown that only the uppermost layer of the mud contains organic detritus, but the quantity of organic substance deposited is not always the most important factor. Where the water is in motion at the bottom, a fine cloud of organic matter is swept along, and in such localities the mud-eaters thrive in great quantities. The fishermen have for a long time profited by this fact, for they do not seek those places (as in pits and channels on the bottom) where mud is laid down, but choose rather the spots where the bottom is covered with coarser particles, and where the finest mud cannot settle. In these places the fish find most food, and the fishermen most fish.

Influence of bottom-currents on the distribution of fish.

Perhaps conditions like these prevail on the eastern Atlantic slope, as, according to the current-measurements of the "Michael Sars," considerable currents extend down to great depths. All such conditions call for further examination, especially in the open ocean, and it may be affirmed that studies of this kind will be essential for an understanding of the quantity of life along the bottom.

Returning to the question of the *geographical distribution of different species of fish*, we may now examine some of the conditions which influence that distribution, according to the present state of our knowledge.

We have seen that the species *Macrurus armatus* is known from the abyssal plain in the Pacific as well as in the Antarctic and Atlantic Oceans. The chart (Fig. 308) indicates the localities of capture and also the temperature, and shows at a glance that, notwithstanding the immense geographical range of this species, it is taken only where the range of temperature is very small (1° to 3° C.). The species is not local; it is not limited by distance, but by certain physical conditions, which in this case prevail over an immense geographical area.

Distribution of different species of fish.

Temperatures in abyssal depths are, as we have seen in Chapter V., on the whole very uniform. It is therefore interesting to note that it is especially the abyssal forms that are known from wide areas; thus, for instance, *Macrurus filicauda*, known from the Pacific and Antarctic, has a bathymetrical range from 2515 to 4843 metres. *Macrurus parallelus*, known from New Zealand, Japan, Ceylon, South-west Africa, ranges down to 1300 metres. *Halosauropsis macrochir*, known from the Southern

Ocean, between South Africa and Kerguelen, and from the "Michael Sars" Stations 35, 53, 88, and 95, was taken down to 2995 metres.

As regards the North Atlantic in particular, the distribution of the deep-sea fauna and the hydrographical conditions show in many instances a marked and interesting correspondence. The rule just discussed holds good also in this ocean: the deepest living forms have a wide distribution. Thus three forms (*Macrurus brevibarbis*, *M. simulus*, and *Hariotta raleighana*), previously known from the American side of the Atlantic, were found by us on the eastern side, as well as on the ridge in Mid-Atlantic. These forms were only taken at the deepest stations.

In Fig. 99, p. 115, a section is given from Newfoundland to Ireland, showing the vertical distribution of salinities and temperatures, and we see from this that on the eastern side of the Atlantic high temperatures go far deeper than on the western side, where the isotherms take an upward turn along the slope. In intermediate depths, for instance between 500 and 800 fathoms, it is therefore much colder on the western side, while at depths of 1000 to 2000 fathoms similar temperature conditions prevail on both sides. Special interest thus attaches to the fact that representatives of the deepest living forms were found on both sides of the ocean, while the faunæ of the slopes in 500 to 800 fathoms are, on the whole, distinct. From this latter rule exceptions may be noted, some forms being also at these depths common to both sides, like *Antimora viola*, found first on the eastern side by the "Michael Sars," *Macrurus rupestris*, and *M. cælorhynchus*; these forms, however, appear to be allied to the fauna of the coast banks, and they can hardly be counted among the forms characteristic of the intermediate depths on the slopes.

Among the Macruridæ the following species may perhaps be considered as characteristic of the two sides of the North Atlantic:—

Western Side.	Eastern Side.
<i>Macrurus carminatus</i> .	<i>Macrurus zaniophorus</i> .
„ <i>bairdii</i> .	„ <i>æqualis</i> .
„ <i>goodei</i> .	„ <i>sclerorhynchus</i> .
„ <i>sulcatus</i> .	<i>Bathygadus melanobranchus</i> .
	„ <i>longifilis</i> .

We will here only discuss the fauna of the eastern side, where trawlings as well as hydrographical investigations were made by the "Michael Sars." The most important fish caught

are recorded in the following table, arranged according to the three series of trawlings taken: (1) west of the British Isles, (2) west of Morocco, and (3) south of the Canaries:—

West of the British Isles.	West of Morocco.	South of the Canaries.
<p>SOUTH OF FAROE ISLANDS, 831 metres.</p> <p>73 <i>Lepidion eques</i>. 94 <i>Halargyreus affinis</i>. 74 <i>Macrurus</i> mostly <i>rupestris</i> and <i>aqualis</i>. 1 <i>Trachyrhynchus murrayi</i>. 1 <i>Alepocephalus giardi</i>. 15 <i>Notacanthus bonapartii</i>. 1 <i>Synaphobranchus pinnatus</i>, <i>Centrophorus</i>, <i>Chimera</i> <i>mirabilis</i>, and several others.</p>	<p>STATION 21, 535 metres.</p> <p><i>Merluccius</i>, <i>Gadiculus ar-</i> <i>genteus</i>, <i>Molva</i>, <i>Phycis</i>, <i>Zeugopterus boscii</i>, <i>Sebastes</i> <i>dactylopterus</i>, <i>Chimera mon-</i> <i>strosa</i>, <i>Spinax niger</i>, <i>Hoplos-</i> <i>tethus mediterraneum</i>. 20 <i>Macrurus</i>, mostly <i>levis</i> and <i>calorhynchus</i>.</p>	<p>STATION 39 B, 280 metres.</p> <p>400 to 500 fishes, mostly Sparidae.</p>
<p>STATION 4, 923 metres.</p> <p>1 <i>Antimora viola</i>. 70 <i>Mora mora</i>. 31 <i>Lepidion eques</i>. 200 <i>Macrurus</i>, mostly <i>talismani</i>, <i>aqualis</i>, <i>zaniophorus</i>.</p>	<p>STATION 23, 1215 metres.</p> <p>36 <i>Mora mora</i>. 11 <i>Macrurus</i>, mostly <i>aqualis</i> and <i>Bathygadus longifilis</i>. 5 <i>Alepocephalus</i>. 3 <i>Halosaurus</i>. 1 <i>Bathypterois</i>. 3 <i>Synaphobranchus pinnatus</i>.</p>	<p>STATION 41, 1365 metres.</p> <p>4 <i>Mora mora</i>. 18 <i>Macrurus (talismani, sclero-</i> <i>rhynchus, zaniophorus,</i> <i>aqualis, asperimus;</i> <i>Bathygadus melano-</i> <i>branchus)</i>. 6 <i>Alepocephalus</i>. 12 <i>Bathypterois</i>. 15 <i>Synaphobranchus pinnatus</i>.</p>
<p>STATION 95, 1797 metres.</p> <p>16 <i>Antimora viola</i>. 36 <i>Macrurus</i>, mostly <i>sclero-</i> <i>rhynchus, murrayi</i>. 5 <i>Alepocephalus</i>. 2 <i>Bathysaurus</i>. 3 <i>Notacanthus</i>. 2 <i>Synaphobranchus pinnatus</i>. 2 <i>Raia fyllie</i>.</p>	<p>STATION 24, 1615 metres.</p> <p>12 <i>Macrurus</i>, mostly <i>talismani</i>, <i>Bathygadus longifilis</i>. 12 <i>Alepocephalus</i>. 3 <i>Synaphobranchus pinnatus</i>.</p>	<p>STATION 35, 2603 metres.</p> <p>6 <i>Macrurus (armatus and</i> <i>aqualis)</i>. 5 <i>Alepocephalus</i>. 2 <i>Halosauropsis</i>. 1 <i>Hariotta raleighana</i>.</p>
<p>STATION 101, 1853 metres.</p> <p>16 <i>Antimora viola</i>. 66 <i>Macrurus</i>, mostly <i>sclero-</i> <i>rhynchus</i>. 3 <i>Alepocephalus</i>. 3 <i>Synaphobranchus pinnatus</i>. 2 <i>Hariotta raleighana</i>.</p>	<p>STATION 25 B, 2055 metres.</p> <p>9 <i>Macrurus (sclerorhynchus</i> and <i>aqualis)</i>. 16 <i>Alepocephalus</i>. 1 <i>Bathysaurus</i>. 1 <i>Raia fyllie</i>.</p>	

From this list we see that the fish fauna of the slope is very uniform all the way from the Faroe Islands to south of the Canaries; no less than six species are common to the northern

and southern series. The hydrographical conditions prevailing along the east side of the Atlantic at these depths are well seen in the chart for 500 fathoms (see Fig. 202, p. 296), which shows that the temperature at 500 fathoms to the south of the Faroe Islands is above 7.0° C., and south of the Canaries, 8.0° C. Only outside of the Mediterranean do we find a higher temperature. On the western side of the Atlantic the temperature at the same depth is only 4.0° C. These facts seem to me to throw much new light on the geographical distribution of the deep-sea fauna.

The conditions in the deep basin of the Norwegian Sea, which has been described in Chapter IV., are no less interesting. In the little chart (Fig. 309) the contour-lines for 600 and 2000 metres are shown. The 2000 metres isobath encloses the abyssal plain of the Norwegian Sea, the central parts of which are covered by 3000 and 3500 metres of water. The area between the 2000 and the 600 metres isobaths shows the region of the slopes, which are steep all the way from Spitzbergen to the Wyville Thomson Ridge, a deep channel (the Faroe-Shetland channel) running from the deep basin right down to the ridge. The hydrographical conditions in the Norwegian Sea are indicated in the vertical section (Fig. 310), which runs through the points *a*, *b*, *c*, from the east coast of Greenland across Jan Mayen to Vesteraalen in Norway. In this section the "Atlantic water," with a salinity above 35 per thousand, is shaded, and is seen to be limited to the eastern side, the depth of the layer not exceeding 600 to 700 metres (or 350 to 400 fathoms). All the water to the west, and beneath this "Atlantic water," is quite cold, most of it below 0° C., the abyssal plain itself being covered by water having a temperature below -1° C.

The fauna of this cold deep basin has been extensively studied during the Norwegian expeditions on board the "Vöringen" and the "Michael Sars," during the Danish expeditions on board the "Ingolf" and the "Thor," and also by Swedish and French expeditions (Duke of Orleans, etc.). On the chart (Fig. 309) small circles denote localities where Norwegian expeditions have employed dredges or trawls, the captures everywhere being remarkably poor in species.

The abyssal plain and the slopes of the Norwegian Sea do not show a single species in common with the Atlantic. While in the Atlantic the genus *Macrurus* plays an important part in

Fishes of the
Norwegian
Sea.

Abyssal fauna
of the
Norwegian
Sea.

the fauna of the abyssal area, not one species of this genus has been found in the cold water of the Norwegian Sea, where the genus *Lycodes* (of the family Zoarcidæ) predominates. But *Lycodes* is not limited to the Norwegian Sea, being represented in

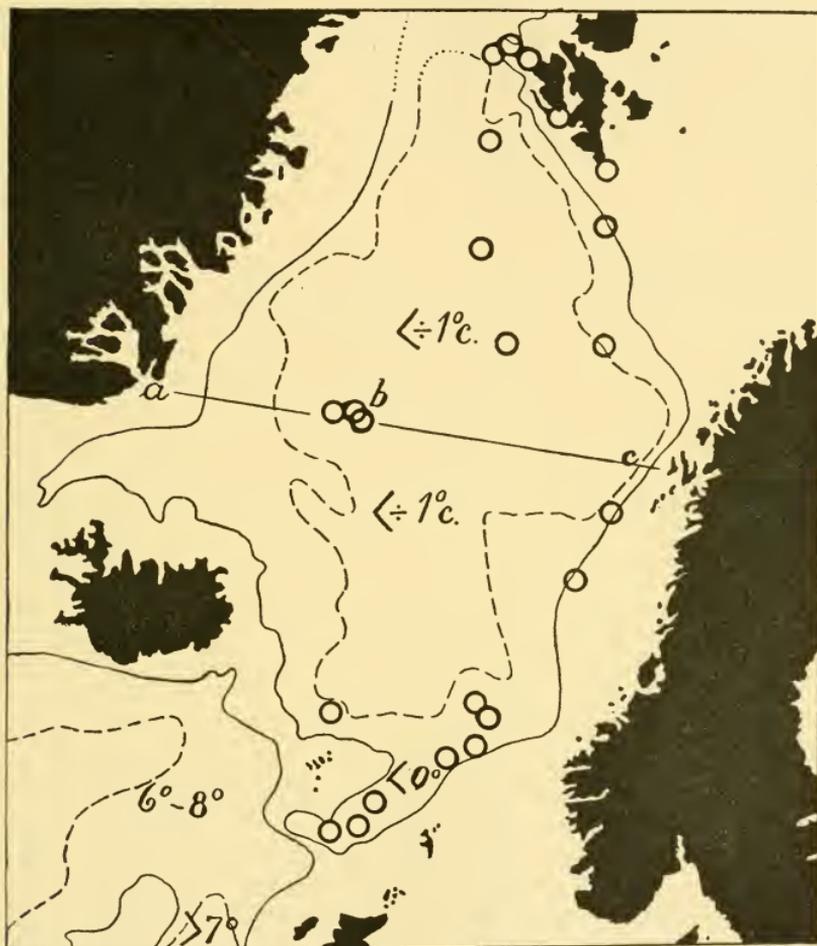


FIG. 309.—THE NORWEGIAN SEA.

Continuous line = 600 metres.

Broken line = 2000 metres.

Section through *a*, *b*, *c*, shown in Fig. 310.

the abyssal depths as well as on the slopes of the Atlantic, though no species has been found common to the Atlantic and the Norwegian Sea. To the Danish scientist Adolf Jensen we owe our knowledge regarding this interesting biological fact.

The principal "cold-water" fish of the deep Norwegian Sea belong to the following species:—

ZOARCIDÆ—*Lycodes muræna*, *L. flagellicauda*, *L. frigidus*, *L. pallidus*, *L. similis*, *L. eudipleurostictus*, *L. seminudus*.

OPHIDIIDÆ—*Rhodichthys regina*.

LIPARIDÆ—*Careproctus reinhardi*, *Paraliparis bathybi*.

COTTIDÆ—*Cottunculus microps*, *C. subspinosus*.

SHARKS—*Somniosus microcephalus* (the Greenland shark).

RAYS—*Raia hyperborea*.

Excepting the Greenland shark these species have been

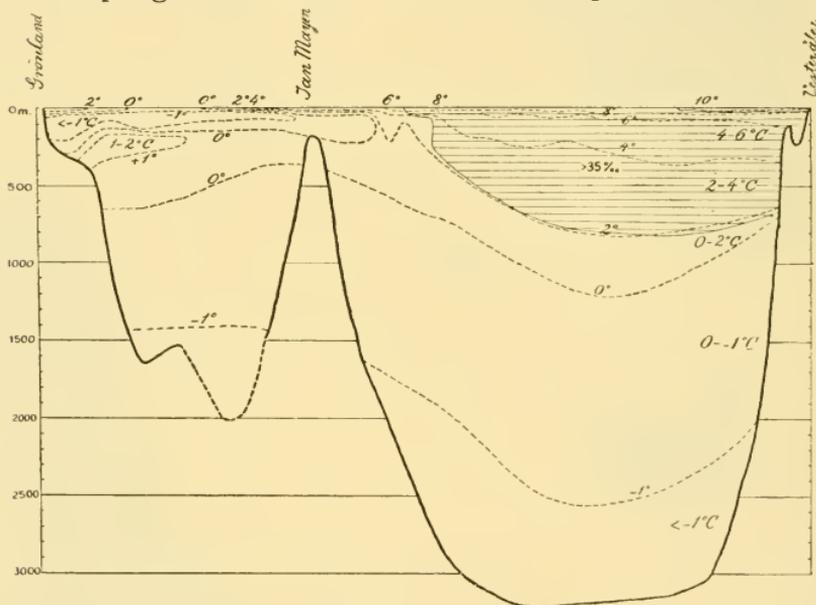


FIG. 310.—SECTION ACROSS THE NORWEGIAN SEA FROM GREENLAND TO NORWAY IN POSITION SHOWN IN FIG. 309. (Drawn by Helland-Hansen.)

taken in cold water only, below 0° C., and mostly in small numbers, though occasionally they are more numerous.

Thus a haul made by the "Michael Sars" to the north of the Faroe Islands, in 975 fathoms, with a trawl similar to the one used in the Atlantic, gave in two hours: 34 *Paraliparis bathybi*, 1 *Rhodichthys regina*, and 17 *Lycodes*. East of Iceland, in 467 fathoms, where the temperature was -0.6° C., the Danish research steamer "Thor," on a line of 225 hooks, obtained 4 *Raia hyperborea*, 1 Greenland shark, and 20 black halibuts (*Hippoglossus hippoglossoides*); the latter two species are not, however, exclusively cold-water fish.

Previously all these fishes of the Norwegian Sea were generally believed to live only along the bottom, but, as mentioned in Chapter III., the "Michael Sars" in May 1911 obtained in a pelagic haul in the cold layers of the Norwegian Sea a specimen of *Paraliparis bathybi*. In the cold water layer there are thus fishes which at least occasionally occur in midwater.

On the coast banks off Greenland, Jan Mayen, and the most northerly coasts of Spitzbergen dwells a genuine Arctic fauna. Of these shallow cold-water species the following are most important: *Icelus hamatus*, *Triglops pingelii*, *Lumpenus maculatus*, *L. medius*, and *L. lampetrisformis*, besides *Gadus saida* (the polar cod).

Arctic
shallow-water
fauna of the
Norwegian
Sea.

On the east and south side of the Norwegian Sea, from Spitzbergen along the coast of Norway and the North Sea banks, and also at Iceland, the cold water does not occur on the slopes in depths less than 600 or 700 metres, and the change from the cold water to "Atlantic water" is very marked. The deep-sea fauna and the fauna of the coast banks are for this reason much more sharply separated than in the Atlantic. At most seasons the limit is determined by the vertical distribution of the Atlantic water, and this limit may oscillate according to changes in the current, though this point has not yet been thoroughly examined.

The fishing experiments of the "Michael Sars" have sometimes in a very striking way shown how sharp the limit is between the two faunæ. In June 1902, for instance, a long line of 1200 fathoms was shot on the northern slope of the North Sea bank towards the deep water, one end of the line being in 217 fathoms, where the temperature was 6° C., and the other end in 300 fathoms, where the temperature was -0.2° C. In the cold water we obtained cold-water fish (*Raia hyperborea*), while near the upper end of the line (in warmer water) the fish belonged to the coast bank species (*Sebastes*, *Macrurus fabricii*). *Raia hyperborea* has been taken from North Spitzbergen down to the slope of the North Sea plateau; *Macrurus fabricii* is known from the Bay of Biscay, from the ocean off the east coast of North America, and from other localities.

THE FISHES OF THE COAST-BANKS

The "Michael Sars" has now had the opportunity of investigating the coast-banks from Spitzbergen to a little south

of the Canaries, a stretch of more than 40 degrees, or 2400 miles. A survey of the animal life on this long stretch of sea-floor is very interesting. As the temperature gradually falls toward the north the fauna changes. Some species are hardy, and are distributed over a greater part of the area; others can only live under more uniform conditions, and therefore have a more limited area of distribution.

Zoological oceanography has long recognised this, and zoological literature contains much information regarding the distribution of animals within our area of investigation. I will mention only one example, for which purpose I choose the excellent survey of the mollusca of Arctic Norway by G. O. Sars, recording the geographical distribution of 174 species of lamellibranchs and 366 species of gasteropods.

G. O. Sars on
the Mollusca
of Norway.

Of the 174 lamellibranchs no less than 128 or 74 per cent were known also from Great Britain; 119 or 70 per cent from the Mediterranean, and 56 or 32 per cent from boreal North America.

Of 366 gasteropods found in Norway, 225 or 62 per cent were also known from Great Britain; 133 or 36 per cent from the Mediterranean, and 77 or 23 per cent from the coasts of boreal North America. A great many species of molluscs have been taken in the Mediterranean as well as in Norway, and quite a number of forms are common to the faunæ of Norway and of North America.

Examining the conditions in various parts of the coast of Norway, we see that the Mediterranean species rapidly decrease in number as we go north from western Norway, for instance, from the latitude of Bergen towards the North Cape. While 119 lamellibranchs and 133 gasteropods are common to the Mediterranean and Southern Norway, Northern Norway and the Mediterranean have only 49 lamellibranchs (28 per cent) and 35 gasteropods (10 per cent) in common. Also south of the Mediterranean we find a similar decrease in the number of species common to both areas; thus only 5 species of lamellibranchs and 4 species of gasteropods are common to Madeira and Northern Norway.

A thorough understanding of the distribution of different animals, or of the different animal-communities, is, however, not obtainable by means of records of this kind, for it makes a world of difference whether a few specimens of a species have been found in a certain locality or whether it lives there in great quantities. A complete knowledge of the distribution of

a species would be based on material containing information as to how many individuals of the species live in different sections of the area, and a complete knowledge of an animal-community would be to have information as to the exact relative occurrence of the animals.

In regard to no species, however, does our present knowledge comply with this ideal demand. As regards the fishes we have



FIG. 311.—STEAM-TRAWLERS LAID UP IN GRIMSBY DURING ENGINEERS' LOCK-OUT.

most information on the species of economic importance, for in recent years many fishing experiments have been made with the object of ascertaining what quantities of fish occur in different waters. In co-operation with the International Council for the study of the sea, the fishery statistics of several countries have also been so far improved, that the quantities of fish landed are now separated in regard to species and areas where caught. The quantities landed are certainly not on the whole repre-

Fishery
statistics.

sentative of the quantities living in the sea. For instance, it is clear that the intensity of fishing is not only determined by the abundance of fish, the prices and the distances to fish markets being (among others) very important points. But notwithstanding these drawbacks, we possess at the present time hardly any better means of judging of the abundance of fish in different areas than the information regarding the capture of edible fish contained in the fishery statistics of recent years. An enormous fleet of modern fishing steamers (see Fig. 311) is now distributed from Cape Kanin, at the mouth of the White Sea, down to Morocco, that is to say, over the area investigated by the "Michael Sars."

From the statistics published by Dr. Kyle of the International Bureau for the Study of the Sea, we have compiled two tables recording the capture of bottom-fish in 1906. One (Table A) shows the catch of each species in each fishing area expressed in percentages of the quantity of the species landed from all areas; the other (Table B) shows the catch of each species expressed in percentages of the aggregate quantity landed from each area. The tables deal with nearly a million tons of fish of all kinds from all waters, the quantities varying greatly in different areas. First of all is the North Sea with nearly 400,000 tons, or nearly 40 per cent of the total quantity; then comes the coast of Norway, north of Stat, with 28 per cent, Iceland with 18 per cent, the Faroe Islands with 4 per cent, the region north-west of the British Isles with 5 per cent, the Bay of Biscay, Portugal, and Morocco with less than $\frac{1}{2}$ per cent each. Among the different bottom-fish the cod plays the most important part with no less than 44 per cent, next comes the haddock with 25 per cent, plaice with $6\frac{1}{2}$ per cent, saithe with $3\frac{1}{2}$ per cent, ling 3 per cent, and hake with a little above 2 per cent, of the total quantity.

Considering now the abundance of each species in each of the nine areas recognised by the fishery statistics, we first observe that most of the species have their maximum abundance in the North Sea. This applies principally to the haddock, the whiting, the species of *Bothus*, the plaice, the lemon sole, and the dab. The intensity of the fishing in the North Sea is, of course, to some extent responsible for this. But nevertheless we find several exceptions. Thus the Norway haddock (*Sebastes*), the cod, the saithe, and the tusk are taken in the greatest quantities off the coast of Norway, the halibut at Iceland. On the other hand, we find in regard to dog-fish,

TABLE A.—CATCH OF EACH SPECIES FROM EACH AREA IN PERCENTAGES OF THE QUANTITY OF THE SPECIES LANDED FROM ALL AREAS.

	Species.	White Sea and Barents Sea.	Norway, north of Stat.	Iceland.	Faroe.	North Sea.	N.W. of British Islands.	S.W. of British Islands.	Bay of Biscay.	Portugal and Morocco.	Sum.
1	Dogfish	2.0	...	16.3	3.0	77.8	0.6	0.3	100.0
2	Skates	3.6	2.2	48.3	15.6	26.5	2.3	1.5	100.1
3	Dory	0.6	...	76.5	12.9	10.0	100.0
4	Norw. Haddock	...	70.4	28.9	0.2	0.5	100.0
5	Bream	0.1	6.5	73.5	8.1	11.9	100.1
6	Monk	1.8	2.4	70.8	5.1	18.1	1.5	0.3	100.0
7	Gurnard	0.1	54.3	16.3	...	2.7	0.4	100.0
8	Catfish .	1.0	1.2	33.0	11.9	52.2	0.8	100.1
9	Cod .	100.0	100.0
10	Coalfish .	0.7	51.5	24.7	4.1	16.9	1.6	0.5	100.0
11	Haddock	...	49.3	21.2	3.4	15.4	9.7	0.8	...	0.1	99.9
12	Pollack .	0.7	3.3	15.2	4.5	71.8	3.3	1.1	99.9
13	Whiting	13.9	7.5	9.0	68.2	1.2	0.1	99.9
14	Hake	0.5	1.8	0.2	82.5	3.7	11.3	100.0
15	Ling	0.1	...	8.4	4.1	73.4	11.1	3.0	100.1
16	Moltva	30.3	15.0	3.0	34.6	11.7	5.5	0.1	...	100.1
17	Tusk	81.5	1.3	2.7	11.9	2.6	100.0
18	Sole	68.5	0.2	23.4	1.9	6.0	100.0
19	Brill	77.9	1.1	20.6	0.2	0.2	100.0
20	Turbot	89.3	1.9	8.4	0.2	0.2	100.0
21	Plaice .	3.3	0.8	16.3	0.4	73.5	1.3	4.5	100.1
22	Lemon Sole	6.4	8.9	77.5	2.0	5.2	100.0
23	Dab	5.2	1.1	85.0	0.5	8.2	100.0
24	Witch	13.7	2.4	62.4	15.8	5.7	100.0
25	Halibut	37.5	14.1	15.0	8.2	0.2	100.0
26	Megrim	24.9	3.2	0.4	28.4	28.0	38.6	1.2	0.1	99.9
27	Salmon, Trout	35.8	31.9	17.8	...	14.4	99.9
28	Conger Eel	7.3	23.4	67.8	1.2	0.3	100.0
	All Species, per cent	1.0	28.1	18.3	3.9	30.8	3.5	5.1	0.4	0.2	99.9
	All Species, Tons .	9525	272,750	177,851	36,930	387,345	33,908	49,748	3663	1704	973,484

TABLE B.—CATCH OF EACH SPECIES IN PERCENTAGES OF THE AGGREGATE QUANTITY LANDED FROM EACH AREA.

	Species.	White Sea and Barents Sea.	Norway, north of Stat.	Iceland.	Faroe.	North Sea.	N.W. of British Islands.	S.W. of British Islands.	Bay of Biscay.	Portugal and Morocco.	All Areas, per cent.	All Areas, Tons.
1	Dogfish	0.1	0.1	1.9	0.2	0.1	0.1	1,198
2	Skates	0.5	1.5	3.1	11.5	13.3	15.4	20.5	2.6	24,954
3	Dory	0.3	0.6	170
4	Norw. Haddock	0.4	0.2	0.1	0.4	0.1	1,422
5	Bream	0.2	...	0.2	1.8	2.7	8.2	0.1	1,216
6	Monk	0.2	0.5	0.4	0.9	1.0	0.5	0.3	2,506
7	Gurnard	0.9	3.2	3.5	4.9	1.6	0.7	6,637
8	Catfish . . .	0.4	...	0.8	1.3	0.6	0.1	0.1	0.4	4,105
9	<i>Gadus naevaga</i> . . .	21.9	0.2	2,088
10	<i>callarias</i> . . .	29.4	81.1	59.6	47.7	18.8	...	4.4	44.1	429,031
11	<i>virens</i>	6.0	3.9	3.0	1.3	9.5	0.6	...	1.4	3.3	32,972
12	Haddock . . .	17.7	2.9	20.8	29.9	45.1	23.0	5.4	0.8	4.1	25.0	243,375
13	Pollack	0.2	1.0	0.2	0.1	0.1	720
14	Whiting	2.5	5.2	0.2	0.3	2.4	23,000
15	Hake	2.2	2.5	9.7	3.1	0.7	0.5	2.9	28,054
16	Ling	3.1	2.4	...	0.3	0.7	1.0	9,780
17	Tusk	2.9	0.1	0.7	0.8	...	2.2	2.4	15.7	0.5	4,603
18	Sole	0.3	0.1	0.6	0.1	0.2	0.2	1,479
19	Brill	1.1	0.3	0.8	0.3	0.6	0.5	4,606
20	Turbot	0.2	11.7	2.5	5.6	0.1	0.5	6.3	61,535
21	Platee . . .	22.2	...	5.5	0.7	0.9	0.3	0.5	0.1	0.1	0.5	4,432
22	Lemon Sole	0.3	0.3	2.0	0.1	1.5	0.9	9,206
23	Dab	0.2	0.2	0.4	1.2	0.3	0.3	2,557
24	<i>cinoglossus</i>
25	<i>hippoglossus vulgaris</i> . . .	0.2	1.3	3.1	5.5	0.6	3.5	0.1	...	0.1	1.5	14,467
26	Hallbut	0.1	...	0.3	2.9	2.7	1.1	0.2	0.3	3,470
27	Megrim . . .	7.8	0.2	0.2	...	0.1	0.2	2,067
28	Salmon, Trout	0.2	0.1	0.2	3,199
	Conger Eel	0.1	2.2	4.4	1.0	0.5	0.3	3,199
	Other Species . . .	0.4	1.8	1.9	5.7	3.4	2.9	8.5	2.7	2.4	3.0	28,962
	Various . . .	100.0	99.9	100.0	100.0	99.8	100.0	100.0	99.9	100.2	100.0	973,484

bream (*Pagellus*), pollack, hake, megrim (*Zeugopterus*), and conger-eel, that the greatest quantities are taken south-west of the British Isles in the Atlantic.

We can thus distinguish *northern species* which are mainly taken north of the North Sea and in the North Sea, and *southern species*, which are chiefly derived from the Atlantic, notwithstanding the fact that comparatively little fishing is carried on in this area. The percentages of each species in the aggregate quantities landed from each area confirm these facts.

Northern and southern species in the eastern Atlantic.

In the area between the mouth of the White Sea and the west coast of the British Isles we find the cod constituting at least 20 per cent of all the fish caught, on the coast of Norway even 81 per cent, at Iceland 60 per cent, and at the Faroe Islands 48 per cent. South-west of the British Isles the quantity of cod dwindles to $4\frac{1}{2}$ per cent, and farther south it disappears. The haddock also constitutes a large proportion of the quantities landed from the area between the White Sea and the north-west of the British Isles (excepting off Norway, where the bottom is unsuitable for haddock-fishing); in the North Sea even 45 per cent of all the fish caught are haddock. The quantities of this fish also dwindle and finally disappear south-west of the British Isles. The same applies to plaice, halibut, ling, and tusk.

The percentages of southern fish, on the other hand, increase west of the British Isles. The hake (*Merluccius*) practically does not occur north of the North Sea, where it constitutes only about $\frac{1}{2}$ per cent of the total quantity; south-west of the British Isles it reaches 32 per cent, in the Bay of Biscay even 65 per cent, and all the way southward it constitutes at least 30 per cent of the total quantity. Similar conditions apply to the pollack, sole, sea-bream (*Pagellus*), the monk or angler, the gurnards, and others.

On the coast banks of the western side of the Atlantic we meet with similar groups of northern and southern forms, the change between these groups occurring about the New England states. We give some instances of quantities of fish landed in the New England states, the middle Atlantic states, and the south Atlantic states, taken from the fishery statistics for the year 1906, the figures signifying tons :—

Northern and southern species in the western Atlantic.

	Northern States.	Middle States.	Southern States.
Cod	40,000	1,400	...
Haddock	21,000	200	...
Saithe	7,900	50	...
Flounder	2,150	1,400	350
Halibut	5,500
Hake	15,000	200	...
Mullet	150	18,500
Sciænidaë	3,300	11,400	4,300
Sparidaë	30	...	6,100

The northern forms—cod, haddock, saithe, flounder, and halibut—disappear along the coast of the southern states, as does also the hake. On the other hand mullet, Sciænidaë, and Sparidaë, *i.e.* the southern forms, increase as we go south, just as they do on the eastern side from the Bay of Biscay towards the coast of Morocco.

If, with these facts in mind, we look at the chart (Fig. 312) recording the temperature at a depth of 100 metres (about 50 fathoms), we shall be astonished at the fact that the distribution of different species curiously coincides with certain temperatures. The southern limit of northern boreal species everywhere coincides with the isotherm for 10° C. On the west side this isotherm just reaches the border between the northern and middle states of North America, while on the east side, on the coast of Ireland, this isotherm just separates the two areas termed respectively areas north-west and south-west of the British Islands.

The areas of the northern species correspond on both sides of the ocean to the area between 2° and 10° C., the maximum frequency of the species occurring between 6° and 8° C. These latter temperatures are found on the Newfoundland banks, on the southern and western banks of Iceland, in the North Sea, and along the entire coast of Norway. The uniformity of the fauna peculiar to all these localities compares well with the uniform conditions of temperature. South of the 10° isotherm we have on both sides of the ocean belts with temperatures between 10° and 18° C.; that on the west side ranges from Cape Cod to Florida, and that on the east side from Iceland to south of the Canaries.

A peculiar feature is that all the isotherms on the west side are quite close together, the water layers being squeezed

between the oceanic sub-tropical waters from the south and the arctic Labrador current from the north. All changes in temperature are therefore on the western side very sharp. On the eastern side the layers are spread out fan-wise, and as a consequence we may at a depth of 100 metres find the same temperature prevailing from north to south over wide areas, as,

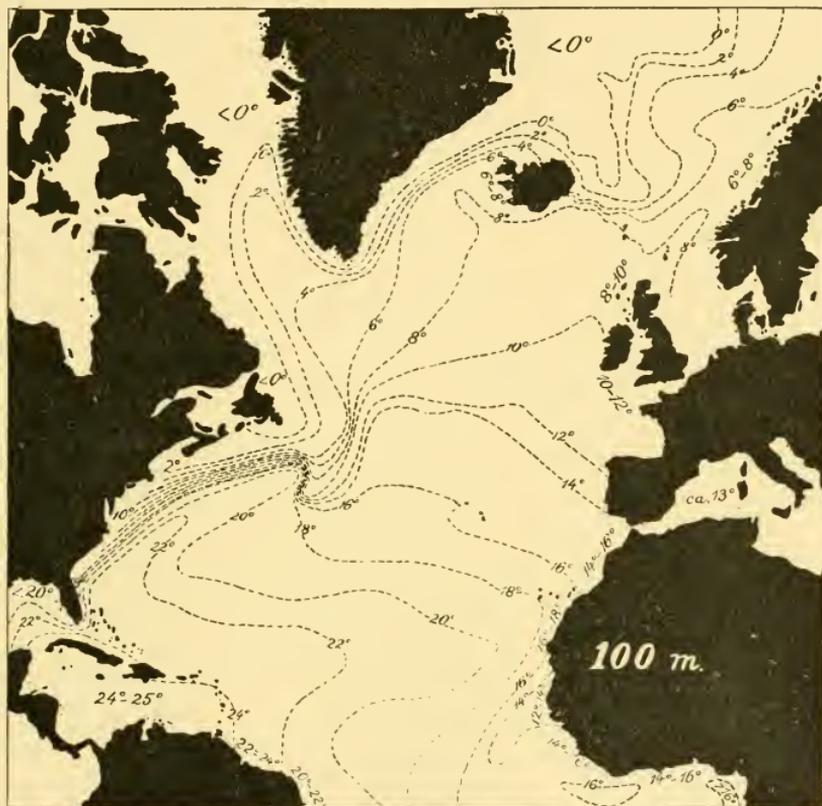


FIG. 312.—DISTRIBUTION OF TEMPERATURE IN THE NORTH ATLANTIC AT A DEPTH OF 100 METRES. (Drawn by Helland-Hansen.)

for instance, along the coast of Norway from the North Sea to the North Cape.

We may now discuss the distribution of the southern and northern species.

Comparing the percentages of the different species noted in the quantities landed from different geographical areas (see The southern species.)

Table B), we observe that northern (boreal) forms decrease enormously to the west of the British Isles. We may say that there is a sharp southern limit to the distribution of these species west of the Channel; the cod, saithe, tusk, and halibut here quite cease to play any part in the captures.

The northern limit for the southern forms is essentially different. Of the species recorded in the systematic list of bottom-fish captured by the "Michael Sars" in the Atlantic, 63 species were previously known from the Mediterranean, and are found there in abundance. Of these only a few are genuine southern forms; 10 species have their northern limit on the coast of France, 19 on the coasts of the British Isles, and 23 occur in varying numbers even on the coasts of Scandinavia. As we shall show in Chapter X., this wide range of certain species is probably due to the fact that the water-layers in the North Atlantic run north, and transport especially the young stages of certain southern species, which may as a consequence pass their youth very far from the localities where they were born. This is why the boreal fish-fauna is more or less mixed up with southern forms, especially in the southern part of the boreal region, for instance in the southern North Sea, in the areas west of the British Isles, in the Kattegat, and along the coast of the Skagerrack, in which localities high summer temperatures prevail in the upper layers.

To the south-west of the British Isles, from the Bay of Biscay towards Morocco, we enter the real area of the southern fauna. This is shown by the table containing the fishery statistics, as well as by the record of the captures made by the "Michael Sars" in the Atlantic. In the following list the captures made during the cruise down to about 500 metres, or 300 fathoms, are recorded and arranged in three groups: (1) West of the British Isles, (2) West of Morocco, and (3) South of the Canaries.

Fishes taken
by the
"Michael
Sars" down to
300 fathoms.

FISHES FROM THE ATLANTIC COAST BANKS.

West of British Isles.	West of Morocco.	South of Canary Islands.
<p>OFF FAROE ISLANDS, 130 metres (trawl and long-line).</p> <p>2 <i>Gadus aeglefinus</i>. 12 <i>Hippoglossus vulgaris</i>. 6 <i>Pleuronectes limanda</i>. 1 <i>Zeugopterus megastoma</i>. 1 <i>Raia clavata</i>. 9 <i>Raia batis</i>.</p>	<p>OFF THE COAST OF PORTUGAL, STATIONS 13-14, 70-80 metres, (trawl and line).</p> <p>8 <i>Gadus merlangus</i>. 36 " <i>luscus</i>. 22 <i>Merluccius vulgaris</i>. 1 <i>Pagellus centrodontus</i>. 1 <i>Caranx trachurus</i>. 3 <i>Trachinus vipera</i>. 1 <i>Mustelus vulgaris</i>. 1 <i>Scyllium canicula</i>. 1 <i>Centrina salviani</i>. 1 <i>Raia clavata</i>. 1 <i>Raia circularis</i>.</p>	<p>STATION 36, 10 metres.</p> <p>5 <i>Merluccius vulgaris</i>. 1 <i>Solea lutea</i>. Many <i>Sargus annularis</i>. Many <i>Pristipoma bennettii</i>. 2 <i>Sciæna aquila</i>. 2 <i>Umbrina ronchus</i>. 2 <i>Box vulgaris</i>. 32 <i>Atherina</i>. 77 <i>Caranx trachurus</i>. 1 <i>Temnodon saltator</i>. 73 <i>Clupea pilchardus</i>. 1 " <i>alosa</i>. 26 <i>Engraulis encrasicolus</i>. 1 <i>Myliobatis aquila</i>.</p>
<p>STATION 1, 146 metres.</p> <p>2 <i>Gadus esmarkii</i>. 2 " <i>poutasson</i>. 2 <i>Phycis blennioides</i>. 20 <i>Merluccius vulgaris</i>. 4 <i>Zeugopterus megastoma</i>. 184 <i>Caranx trachurus</i>. 1 <i>Zeus faber</i>. 52 <i>Capros aper</i>. 18 <i>Trigla gurnardus</i>. 5 <i>Argentina sphyrena</i>. 20 <i>Acanthias vulgaris</i>. 1 <i>Pristiurus melanostomus</i>. 7 <i>Raia clavata</i>.</p>	<p>STATION 20, 141 metres.</p> <p>52 <i>Merluccius vulgaris</i>. 1 <i>Solea vulgaris</i>. 7 <i>Pagellus centrodontus</i>. 1 " <i>acarne</i>. 3 <i>Dentex maroccanus</i>. 5 " <i>macrophthalmus</i>. 11 <i>Mullus surmuletus</i>. 8 <i>Caranx trachurus</i>. 4 <i>Zeus faber</i>. 30 <i>Capros aper</i>. 1 <i>Trigla hirundo</i>. 16 " <i>lyra</i>. 3 " <i>cuculus</i>. 2 " <i>pini</i>. 20 <i>Lepidotrigla aspera</i>. 1 <i>Peristedion cataphractum</i>. 4 <i>Acanthias vulgaris</i>. 6 <i>Scyllium canicula</i>. 1 <i>Raia clavata</i>.</p>	<p>STATION 37, 39 metres.</p> <p>1 <i>Arnoglossus lophotes</i>. 1 <i>Dentex maroccanus</i>. 2 <i>Cantharus lineatus</i>. 3 <i>Serranus cabrilla</i>. 1 <i>Coris julis</i>. 1 <i>Mullus surmuletus</i>. 2 <i>Scorpena scrofa</i>. 2 " <i>ustulata</i>. 1 <i>Uranoscopus scaber</i>. 2 <i>Tetrodon spengleri</i>. 2 <i>Raia punctata</i>. 2 " <i>microcellata</i>. 1 " <i>alba</i>.</p>
<p>STATION 3, 184 metres.</p> <p>1 <i>Gadus aeglefinus</i>. 8 " <i>poutassou</i>. 40 <i>Gadiculus argenteus</i>. 5 <i>Merluccius vulgaris</i>. 1 <i>Phycis blennioides</i>. 170 <i>Zeugopterus megastoma</i>. 2 <i>Arnoglossus laterna</i>. 2 " <i>lophotes</i>. 3 <i>Solea variegata</i>. 2 <i>Caranx trachurus</i>. 2 <i>Capros aper</i>. 12 <i>Trigla gurnardus</i>. 29 " <i>lyra</i>. 1 " <i>pini</i>. 5 <i>Callionymus maculatus</i>. 4 <i>Lophius piscatorius</i>. 4 <i>Argentina sphyrena</i>. 8 <i>Acanthias vulgaris</i>. 5 <i>Scyllium canicula</i>. 25 <i>Raia clavata</i>. 1 " <i>vomer</i>. 1 " <i>circularis</i>.</p>	<p>STATION 21, 535 metres.</p> <p>14 <i>Gadiculus argenteus</i>. 8 <i>Merluccius vulgaris</i>. 12 <i>Phycis blennioides</i>. 1 <i>Molva elongata</i>. 9 <i>Malacocephalus levis</i>. 9 <i>Calorhynchus calorhynchus</i>. 2 <i>Macrurunger</i>. 6 <i>Zeugopterus boscii</i>. 10 <i>Sebastes dactylopterus</i>. 30 <i>Hoplostethus mediterraneum</i>. 2 <i>Chimæra monstrosa</i>. 11 <i>Pristiurus melanostomus</i>. 2 <i>Spinax niger</i>. 1 <i>Raia fullonica</i>.</p>	<p>STATION 38, 77 metres.</p> <p>2 <i>Solea vulgaris</i>. 2 " <i>lutea</i>. 2 <i>Arnoglossus lophotes</i>. 1 " <i>grohmanni</i>. 1 <i>Pagrus vulgaris</i>. 1 <i>Dentex macrophthalmus</i>. 2 <i>Trigla obscura</i>. 1 <i>Scorpena scrofa</i>. 1 <i>Trachinus draco</i>. 1 <i>Lophius piscatorius</i>. 1 <i>Muræna helena</i>. 2 <i>Raia punctata</i>.</p>
<p>OFF FAROE ISLANDS, 442 metres (long-line).</p> <p>8 <i>Molva molva</i>. 40 <i>Brosmius brosme</i>. 2 <i>Hippoglossus vulgaris</i>. 2 <i>Chimæra monstrosa</i>. 40 <i>Pristiurus melanostomus</i>. 1 <i>Spinax niger</i>. 3 <i>Centrophorus squamosus</i>.</p>	<p>STATION 21, 535 metres.</p> <p>14 <i>Gadiculus argenteus</i>. 8 <i>Merluccius vulgaris</i>. 12 <i>Phycis blennioides</i>. 1 <i>Molva elongata</i>. 9 <i>Malacocephalus levis</i>. 9 <i>Calorhynchus calorhynchus</i>. 2 <i>Macrurunger</i>. 6 <i>Zeugopterus boscii</i>. 10 <i>Sebastes dactylopterus</i>. 30 <i>Hoplostethus mediterraneum</i>. 2 <i>Chimæra monstrosa</i>. 11 <i>Pristiurus melanostomus</i>. 2 <i>Spinax niger</i>. 1 <i>Raia fullonica</i>.</p>	<p>STATION 39 B, 280 metres.</p> <p>10 <i>Merluccius vulgaris</i>. 1 <i>Pagrus vulgaris</i>. 250 <i>Dentex macrophthalmus</i>. 1 <i>Mullus surmuletus</i>. 2 <i>Caranx trachurus</i>. 1 <i>Capros aper</i>. Many <i>Centriscus scolopax</i>. 1 <i>Trigla lyra</i>. Many <i>Lepidotrigla aspera</i>. 1 <i>Peristedion cataphractum</i>. 1 <i>Scorpena ustulata</i>. 5 <i>Argentina silus</i>. 5 <i>Acanthias vulgaris</i>. 1 <i>Scyllium canicula</i>. 2 <i>Rhina squatina</i>. 20 <i>Raia miraletus</i>. 1 " <i>clavata</i>. 4 " <i>punctata</i>. 1 " <i>circularis</i>.</p>

In the lists from the stations west of the British Isles we find the northern forms : haddock, halibut, and tusk, but also forms which never occur in the Norwegian Sea or the North Sea, such as *Capros aper* and *Centrophorus squamosus*. The hake (*Merluccius*), the gurnard (*Trigla*), and southern flatfish (*Arnoglossus lophotes*, *A. laterna*) also occur.

To the west of Morocco the hake and the southern cod (*Gadus luscus*), besides a few whiting, are the only representatives of the cod family. Here we find no less than five species of gurnards in one haul, mullets (*Mullus surmuletus*), and Sparidæ (*Pagellus centrodontus*, *Dentex maroccanus*, and *D. macrophthalmus*). In the deep haul in 535 metres we observe the southern ling (*Molva elongata*), *Sebastes dactylopterus*, and different Macruridæ, along with *Merluccius* (hake), and *Gadiculus argenteus*.

To the south of the Canaries the acanthopterygian fish decidedly predominate. We find Sparidæ (*Dentex*, *Pagrus*, *Sargus*, *Box*, *Serranus*, *Scorpena*, *Mullus*, *Trachinus*, *Trigla*). There are also soles (*Solea*, *Arnoglossus*), hake, and anglers. In shallow water we also meet with the young of different herrings, such as pilchards, *Clupea alosa*, and anchovy.

Thus the three series of hauls show the changes encountered in the fauna, from the mingled community of boreal and southern forms west of the British Isles to the entirely southern fauna on the west coast of Africa.

These records also serve to illustrate the catches of fishing vessels on the European and African banks of the Atlantic. As is well known, the trawling industry was developed in the North Sea. When it was carried farther south along the Bay of Biscay, along the coast of Portugal, and along the coast of Morocco, the hake and the sole were first and foremost the main objects of capture. These two species are still of first importance to the trawlers. From Table B, page 442, we learn that in the Bay of Biscay the hake constitutes 65 per cent, and farther south 36 per cent, of all the fish caught. The valuable sole constitutes no less than 16 per cent of the weight of all the fish caught in the most southerly areas. The rays play an important part (in the Bay of Biscay 15 per cent, farther south 21 per cent), but also the acanthopterygians (*Pagellus*, *Mullus*, *Dentex*, etc.) are of great importance. I have obtained some information on their catches off the Moroccan coast-banks from trawlers, who tell me that the hake constitutes two-thirds of the catch. The acanthopterygians very often make up one-fourth,

and farther south, near the Canaries, off Agadir, they may even amount to two-thirds of the total catch. Soles are also numerous. South of the Canaries we saw during our cruise (see Chapter III.) a considerable handline fishery for acanthopterygian fish (*Dentex*, *Diagramma*, etc.) carried out on hard stony and gravelly bottom. The trawl cannot be worked there, where the acanthopterygians were present in enormous shoals, outnumbering all other species. We had there a fauna entirely different from the boreal fauna, lacking all the northern forms.

All the way from western Ireland to the coast banks of Morocco, fishing is carried on down to deep water, at least to 300 fathoms (500 to 600 metres). West of Ireland the trawlers in April capture two kinds of ling (*Molva molva* and *M. elongata*), hake and breams (*Pagellus*), down to 300 fathoms, and west of Morocco they get large hake down to 200 or 300 fathoms. Fishing thus goes on as deep as *the fauna of the coast banks extends*.

Depth limit
of fishing on
Atlantic slope.

As we have seen already, the Macruridæ peculiar to the fauna of the slopes, commence at about 500 or 600 metres. Will this fauna of the slopes, particularly the Macruridæ, *Mora*, etc., ever be the object of a fishing industry? This question is important, and the possibility of such an industry cannot *a priori* be denied. If we consider that the "Michael Sars" in one haul, with a comparatively small trawl, at Station 4 took over 300 fishes, some of which, as for instance the *Mora*, seemed just as fit for the market as the tusk, it does not seem improbable that improved technical appliances may render fishing profitable even down to 500 fathoms and more.

It is very interesting to note, as shown in the following table, that the temperature in 300 fathoms (the limit of the coast fish) is 10° C.—a temperature which we have previously referred to as marking the southern limit of the northern forms to the west of Ireland, where the southern forms commenced to increase in abundance:—

Depths in Fathoms.	Station 43, South of the Canaries.	Station 93, West of Ireland.
50	16.8°	10.8°
100	15.7°	10.4°
200	13.1°	10.3°
250	11.7°	10.2°
300	...	10.0°
350	9.5°	...
400	...	9.2°

Vertically as well as horizontally the fauna termed by me the southern one appears to exist within the same limits of temperature. The different species appear to be at liberty to move within these limits and to be independent of depth. Thus there are many observations showing that the southern species occur in deeper water on the Atlantic slope than they do in the North Sea. This is easy to understand, because in the North Sea only the shallow upper layers are affected by high summer temperatures. Nevertheless the records of such species from deeper water available from the results of the "Michael Sars" and other expeditions are quite surprising. Thus the French deep-sea expeditions found :—

<i>Solea vulgaris</i>		in 235 metres.
<i>Solea variegata</i>		" 306 "
<i>Arnoglossus grohmanni</i>		" 175 "
<i>Gobius minutus</i>		" 118 "
<i>Callionymus lyra</i>		" 411 "
<i>Trachinus draco</i>		" 175 "
<i>Lophius piscatorius</i>	between 219 and	668 "
<i>Merluccius vulgaris</i>	" 99 "	640 "
<i>Motella tricirrhata</i>	" 112 "	640 "
<i>Phycis albidus</i>	" 40 "	460 "

These instances are quite sufficient to show that in the southern part of our area the fishes tend to migrate vertically within considerable bathymetrical ranges. Evidently temperature here plays a dominant part, and perhaps also other factors come into play, above all the deeper penetration of light in southern waters.

We have previously seen that the northern species in North European waters range from the Barents Sea in the north to west of the British Isles in the south. But within this wide area we meet with many variations in detail, even though the fish fauna of the whole area in a broad sense may be said to be homogeneous. Thus some species belong mainly to the most northerly part of the area, while others are taken in quantities worth mentioning only in the far south of the region. The abundance of a species does not alone depend on latitude or conditions of temperature, but the extent of the area of bottom suitable to the species is also of great importance.

An analysis of this question cannot, however, be restricted to a search for the geographical limits of the species. As regards the northern forms, information as to their bathymetrical distribution is very important. The English fishery statistics

flounder, and dab—are the most characteristic, but young stages of cod, rays, and dog-fish (*Acanthias*) also occur plentifully.

In medium depths, from 40 to 100 metres (25 to 50 fathoms), the gadidæ—haddock, large cod, pollack, and whiting—predominate, but we also meet with flat-fish, turbot, lemon sole (*Pleuronectes microcephalus*), and young halibut, and with some southern forms: hake, gurnards, anglers, and conger eels.

Below 100 metres (50 fathoms) we meet with the saithe, ling, tusk (see Fig. 313), large hake, besides witch, megrim, and large halibut.



FIG. 313.—THE "MICHAEL SARS" FISHING LING AND TUSK IN THE DEEP PART OF THE NORTH SEA.

Different physical conditions accompany these characteristic differences in the distribution of the fish; for instance, the depths from 0 to 40 metres are the ones mainly influenced by summer temperatures; on the shallow coast banks and on the Dogger Bank the temperature at the bottom rises to at least 12°C . in the summer season. The sole may thus find here temperatures similar to those off the Atlantic coast of Europe, though in somewhat shallower water. Below 40 metres the summer temperature is not much higher than the temperature during winter, viz. between 6° and 7°C .

The species inhabiting the deeper areas of the plateau extend out towards the deep basin of the Norwegian Sea until

the cold bottom water with a temperature below 0° C. is reached, where they are gradually replaced by the cold water fauna previously described.

The same laws which regulate the distribution of different species in the North Sea apply also in the main to other boreal waters where these species live. Scientific fishing experiments, and above all the mass of information gathered from the fishing industry, have in recent years vastly contributed to our knowledge on these points. If on the basis of this knowledge we want to compare the actual conditions in different boreal waters, we must compare areas of corresponding depth. In this way we may possibly form an idea as to the part played by the extent of the sea-bottom, and by physical conditions, in regard to the distribution of our northern species. Some examples may illustrate this point.

In the North Sea the shallow banks in depths less than 40 metres cover large areas, while off the coast of Norway there are hardly any such banks, the coast sloping steeply into greater depths. Shallow banks occur off the south and west coast of Iceland, and far north and east in the Barents Sea, as well as round Cape Kanin. Of the fish inhabiting the shallow areas of the North Sea, only the plaice and the cod occur in great quantities on these northern banks of Iceland and Cape Kanin. Sole, brill, and other flat-fish might also find suitable conditions of depth here, but the temperature is too low. Off the coast of Norway none of these flat-fish, neither the plaice nor the sole, occur abundantly. Thus we plainly see the important parts played by depth as well as by temperature in respect of the occurrence of various species.

While the haddock in the North Sea constitutes nearly half of the total weight of bottom-fish landed, the same species constitutes only 3 per cent off the coast of Norway. This is not because Norway is too far to the north, nor because the temperature of the water is too low, since at Iceland and in the Barents Sea, where conditions are similar, haddock amounts to 20 per cent of the catch, but because off the coast of Norway there are no great areas of suitable depth and with the soft bottom preferred by the haddock. On the contrary we here meet with great areas of "cod-bottom" (sand, stones, shingle, or rocks overgrown with kelp), and therefore the cod makes up over 80 per cent of all the bottom-fish taken off northern Norway.

Thus the extent of the area, and the captures made therein,

Food-fishes
taken in
different parts
of the North
Atlantic.

are closely correlated. If we know the area where a vessel fishes, we can predict the nature of the catch, and on the other hand we may judge of the extent and nature of the area from a knowledge of the fish caught in that area. This fact may be illustrated by the following table giving the quantities of important food-fish in millions of kilograms landed from different areas of the North Atlantic:—

	Cod.	Haddock.	Plaice.	Halibut.	Hake.
White Sea, Barents Sea.	3	2	2	...	0
Norway, north of Stat	221	8	$\frac{1}{2}$	$3\frac{1}{2}$	0
Iceland	106	37	10	$5\frac{1}{2}$	0
Faroe Islands	18	11	$\frac{1}{4}$	2	0
North Sea	73	174	45	2	2
Atlantic coast of Europe	9	11	$3\frac{1}{2}$	1	20
Total	430	243	88	14	22

According to this table the North Sea proves to be the richest of all in plaice and haddock, just as it includes the greatest area of shallow sandbanks and flats with muddy bottom. The sea of Norway is richest in cod, just as it represents the greatest stretch of rocky coast with temperatures between 6° and 8° C.

Boreal fishes
on the slope
of the
Norwegian
Sea.

Below 100 metres (50 fathoms) and down to 300 fathoms, we find on the northern slope of the North Sea plateau the following species to be the most important: saithe, ling, tusk, and halibut (see Fig. 314). During the summer we also find the cod in such depths, especially to the north of Lofoten, and on the slopes from the Faroe Islands to Lofoten. A little higher up on the bank these species are mingled with large hake, witch (*Pleuronectes cynoglossus*), and megrim (*Zeugopterus megastoma*). Lower down on the slope below 200 metres we find Norway haddock (*Sebastes*), blue ling, black halibut (*Hippoglossus hippoglossoides*), *Macrurus fabricii*, *Argentina silus*, and Greenland sharks. This latter group of species has been found during the Norwegian fishery investigations along the "edge" of the continental platform all the way from Spitzbergen and Bear Island along the coasts of Norway, the North Sea plateau, the Faroe Islands, and along the Faroe-Iceland ridge.

If we follow the 600 metres line in the chart (Fig. 309) from Spitsbergen and round the southern part of the Norwegian Sea

to Iceland, we shall at the same time trace the limit between the cold-water fauna of the deep basin and the boreal fauna of the slope of the coast plateau. Within this boreal region we may discern different areas of distribution. The ling, for instance, is caught off the coast of Norway in abundance as far north as Lofoten; north of Lofoten, between the Faroe Islands and Iceland, and at Iceland, the ling is only poorly represented,

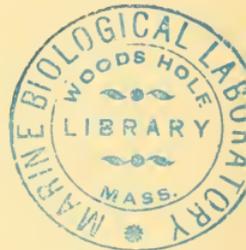
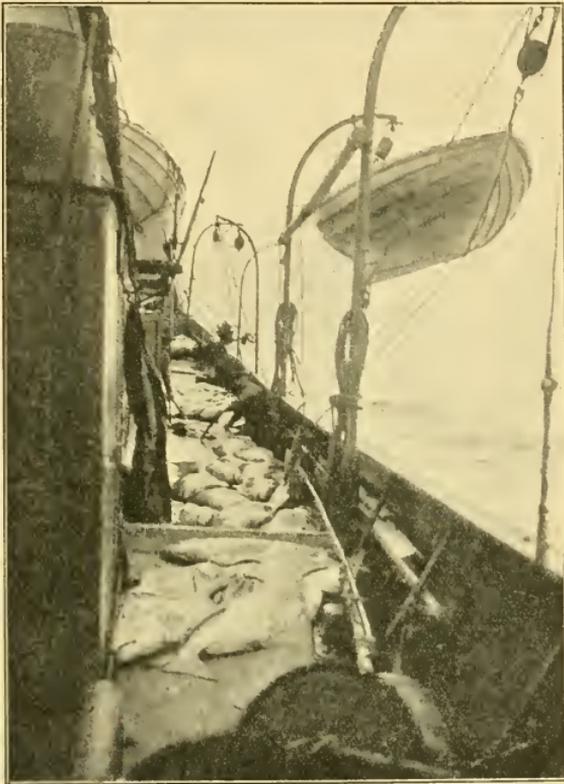


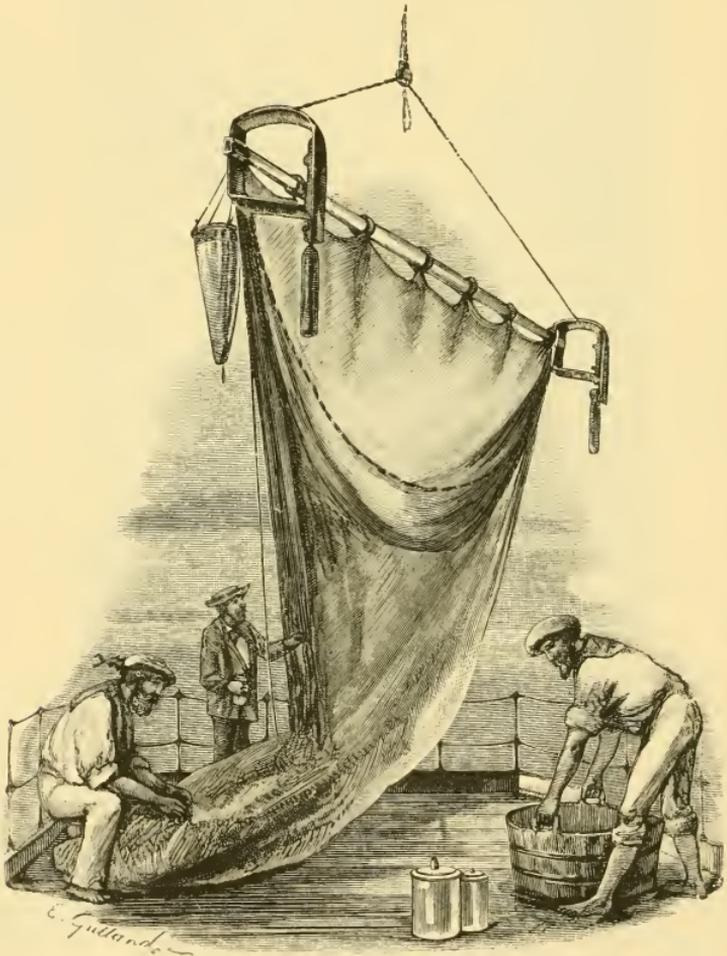
FIG. 314.—THE "MICHAEL SARS" FISHING HALIBUT ON THE SLOPE.

while the cod there plays an important part in the "edge" fishery during the summer. Large halibut, from 50 to 150 kilos in weight, on the other hand, occur on the slope from west of Bear Island, round the North Sea plateau, the Faroe Islands, and on to Iceland. The Norway haddock has a similar distribution to that of the large halibut.

The fauna of the eastern and southern slopes of the Norwegian Sea thus proves to be very uniform for a distance of

1200 or 1500 miles, in accordance with the uniformity of the physical conditions. As we have previously seen, uniform physical conditions of a different character are met with along the slopes of the Atlantic from the Wyville Thomson Ridge down to south of the Canaries, the forms peculiar to this region being entirely different to those inhabiting the slopes of the Norwegian Sea,

J. H.



CHAPTER VIII

INVERTEBRATE BOTTOM FAUNA OF THE NORWEGIAN SEA AND NORTH ATLANTIC

THE topography of the Norwegian Sea has been briefly noticed in Chapter IV. and the hydrography in Chapter V.

The distribution of forms in the Norwegian Sea agrees with the hydrographical conditions, and we can distinguish two great regions, the *boreal* and the *arctic*, each of which has its own appropriate fauna. All those parts of the ocean-floor covered by Gulf Stream water or by coast-water make up the *boreal* region, while the arctic region is covered by water with polar characteristics. The temperature and salinity in boreal areas vary greatly in the different water-layers, and are much affected by the seasons. What chiefly distinguishes the boreal region from the arctic region is the higher temperature, which never falls below 0° C., and over large areas never sinks below 6° C. The uppermost water-layer may form an exception, for the temperature may occasionally at the very surface and for a comparatively short time fall below 0° C. High summer temperatures are characteristic of the upper water-layers, and exercise a considerable effect upon the fauna. The boreal region of the Norwegian Sea includes the North Sea with the Skagerrack and Kattegat, the Norwegian coast plateau as far as the North Cape, the coast plateau of the Faroe Islands, and the south and west coasts of Iceland.

In the *arctic* region the temperature and salinity are much more uniform than in the boreal region: the temperature is usually below 0° C., though in summer the actual surface may show higher temperatures under the influence of the sun, but the sun's heat does not penetrate so deeply as in the boreal region; the salinity varies greatly at the surface, but at the depth of a few metres it is rarely less than 30 per thousand. The arctic region comprises the coast plateaus of Greenland

Boreal region
of the
Norwegian
Sea.

Arctic region
of the
Norwegian
Sea.

north of Denmark Strait, Spitsbergen, Franz-Josef Land, Novaya Zemlya, the coast between the White Sea and the Kara Sea, as well as the plateau of Jan Mayen and the deep central basin of the Norwegian Sea.

Boreo-arctic
region of the
Norwegian
Sea.

In addition to these purely boreal and purely arctic areas there are transitional areas, designated *boreo-arctic*, which may be found wherever boreal and arctic water-masses meet. Such areas occupy more or less extensive tracts, and exercise a distinct influence upon the distribution of the fauna. The temperature is not so high as in the boreal region, except perhaps at the surface, varying between 0° C. and 3° or 4° C., though in the shallower parts a far higher temperature is found in summer, due to the heat of the sun, and as a result there are certain boreal littoral forms that occur also in the boreo-arctic region.

The following are boreo-arctic areas: the south-western portion of the Barents Sea, from the East Finmark and Murman coasts to the White Sea, where a branch of the Gulf Stream, flowing eastwards, is gradually blended with arctic water; the north and east coasts of Iceland, where branches of the Gulf Stream unite with the East Iceland Polar Stream¹; the Iceland-Faroe ridge, where the East Iceland Polar Stream meets the Gulf Stream; the Wyville Thomson Ridge, over which the Gulf Stream passes into the Norwegian Sea, where a mixture of the two waters undoubtedly takes place, but this boreo-arctic area is of small importance compared to the others; and the continental slope on the eastern side of the Norwegian Sea, where there is a narrow area of mixture between Atlantic water and arctic water, resulting in temperatures slightly higher than 0° C. A weak branch of the Gulf Stream flows along the west coast of Spitsbergen, giving rise to a very limited boreo-arctic belt, though, generally speaking, the west side of Spitsbergen must be considered purely arctic. The shallower parts of the coastal waters, as well as the inner portions of the fjords, from Lofoten to the North Cape, are boreo-arctic.

North
Atlantic.

The topographical conditions in the North Atlantic are much like those of the Norwegian Sea, but the hydrographical conditions are dissimilar. On the eastern side the coast banks of both Europe and North-West Africa are bathed by much warmer water than those of corresponding parts of the Nor-

¹ I ought to state, however, that owing to the influence of the East Iceland Polar Stream the north-eastern coast must perhaps be considered a purely arctic area.

wegian Sea, and the littoral fauna naturally accords with its surroundings. This is true also of the archibenthal area (that is to say, the steep continental slopes) and the abyssal region. The temperature at 1000 metres may be as high as 6° or 8° C., and 2° or 3° C. at still greater depths. Here, again, the fauna conforms to its surroundings. In addition to the vast central abyssal plain, the boreal region of the Atlantic includes the coast plateaus off Europe and North-West Africa, and the southern slopes of the ridges extending from the Shetlands to Greenland, that is to say, practically the whole of the eastern portion of the Atlantic. Arctic currents, on the contrary, prevail in the western portion of the Atlantic, and cause hydrographical, and therefore faunal, dissimilarities at different parts of the coast. In the coastal areas south of Cape Cod (about lat. 42° N.) we find Gulf Stream water and a characteristic warm-water fauna; but north of Cape Cod we meet with an icy polar current descending from higher latitudes, so that the stretch of coast from Cape Cod to the north of Newfoundland must be looked upon as boreo-arctic. More genuinely arctic conditions prevail off the coasts of Labrador and Greenland.

BOREAL REGION OF THE NORWEGIAN SEA

The boreal coastal area may be divided into three vertical zones, distinguished by different physical, topographical, and biological conditions. The uppermost is the *littoral zone*, which extends from the shore down to a depth of 30 or 40 metres—that is to say, almost as far down as there are sea-weeds. The physical and topographical conditions characterising the littoral zone are: periodic changes in temperature and salinity (the temperature of the water being directly affected by that of the air), strong light, and a great variety in the materials at the bottom, such as loose stones, solid rock, sand with or without coarse or fine fragments of different kinds of shells, mud, and “mixed mud”—that is to say, sand, mud, and stones all mixed together. Here we find the whole vegetation collected, consisting of fucoids, green and red algæ, *Laminaria*, and *Zostera*, all of which, as a rule, form big interdependent communities that are very often arranged in belts.

The coastal area of the boreal region of the Norwegian Sea.

The lower limit of the *sublittoral zone* on the west coast of the Scandinavian peninsula may be put at about 150 metres. It differs from the preceding in being without vegetation, as well as in having more uniformity in the bottom-

deposits, higher and more constant salinities, and less pronounced differences in temperature. The bottom consists either of solid rock or sandy clay, or else of a rather coarse mixture of shells and sand, which is often found on the slopes of rocky portions in particular, together with large stones and pebbles. On the other hand, we do not get the fine mixture of shells and sand which is so characteristic of the littoral zone out among the skerries. The lower limit of this zone practically coincides with the lower limit of the coastal water, the salinity of which is lower than that of the Atlantic water lying beneath it.¹ The temperature does not vary more than a few degrees in the different seasons, being lowest during the summer in the deeper portions, but it is, for part of the year at any rate, higher than that of the Atlantic water.

Below the sublittoral zone we come to another zone, distinguished by more uniform and more constant topographical and physical conditions, which we may call the *continental deep-sea zone* (ranging from 150 to 1000 metres or more). The bottom consists mainly of rock or a fine mud, which may perhaps be mixed with a little sand in the uppermost portions. In its upper parts, near the borders of the sublittoral zone, temperatures and salinities vary to a slight extent, but in the deeper parts both are constant, the salinity being 35 per thousand or a little over, and the temperature between 6° and 7° C. all the year round.

We propose to discuss the coastal area of the boreal region under three headings: (1) the islands of the Norwegian west coast, where the littoral zone alone is represented; (2) the fjords, where all the zones are represented; and (3) other northern boreal areas.

(1) *Islands of the Norwegian West Coast* ("Skjergaard").— We may divide the littoral zone among the islands of the Norwegian west coast into different areas. There is first a low-tide area, subject to changes of tide, and accordingly dry for certain portions of the twenty-four hours. Here we can distinguish three "facies" with different bottom-conditions, namely (1) rocky, either bare rock or very scantily overgrown; (2) a furoid belt; and (3) sand. Each of these has, as a rule, several forms peculiar to it, though unquestionably a good many species of the littoral fauna are common to all. The dissimilarity in the com-

¹ It must, however, be stated that the limits between the coastal water and Atlantic water vary with the seasons.

position of the fauna of the different "facies" depends to a great extent on the structure of the animal-forms, inasmuch as some forms must have a vegetable or hard solid foundation, while others require loose material. Littoral gasteropods, as a rule, require a solid foundation, and they are therefore generally absent from the sandy bottom; but there are certain burrowing forms which can only live where the bottom is incoherent. Other forms, again, like the crab, are able to live on nearly every kind of bottom.

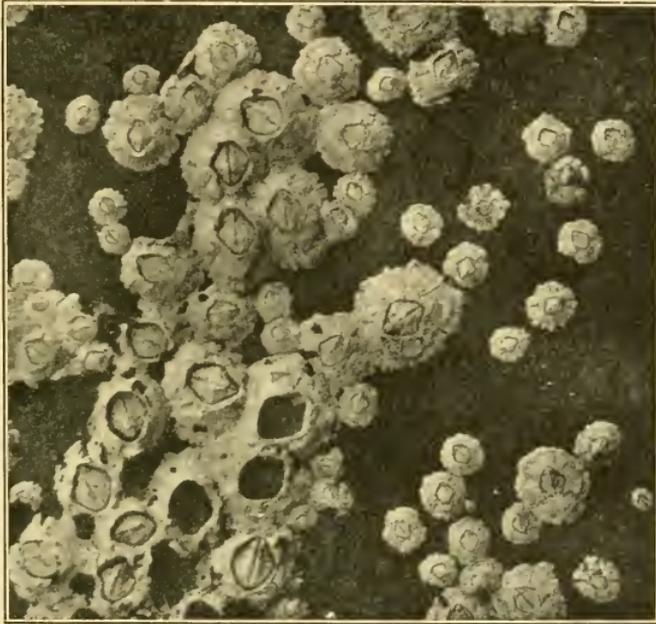


FIG. 315.
Balanus balanoides, L.

Below the low-tide area, with its fucus vegetation, we find on hard bottom a *Laminaria* belt beginning immediately below the fucoïd belt, and always covered by water.¹ We find also a *Zostera* belt, hard bottom, and sandy bottom.

On the bare or scantily overgrown rocks near high-water mark we find a white belt of barnacles (*Balanus balanoides*, see Fig. 315); when examined at high tide we notice these little creatures extending and contracting their lash-like limbs to set

Low-tide
area.

¹ Only at very low ebb-tides and in certain places do we find certain species of *Laminaria* also laid bare.

the water in more rapid motion, and so bring nourishment to their mouths inside their shells, but when exposed at ebb-tide the

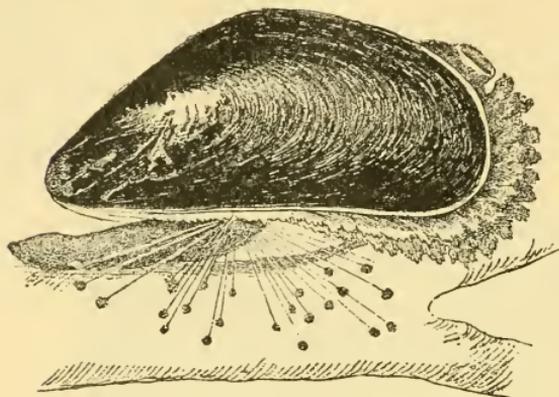


FIG. 316.
Mytilus edulis, L.

shells are closed and the animals remain concealed within them. Immediately below the barnacle-belt we frequently find a belt consisting of dense masses of mussels (*Mytilus edulis*, see Fig. 316), though the individuals in such localities never attain any considerable size. On the rocks we find everywhere

four species of gasteropods, which are very characteristic of this area, namely, the limpet (*Patella vulgata*, see Fig. 317), two periwinkles (*Littorina*

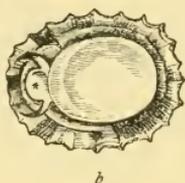


FIG. 317.
Patella vulgata, L. a. From the side; b. from beneath.

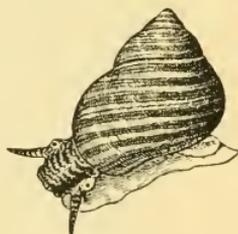


FIG. 318.
Littorina littorea, L.

littorea, see Fig. 318, and *L. rudis*), and the purple snail (*Purpura lapillus*, see Fig. 319), this last being often plentiful in the barnacle-belt, where it feeds on these crustaceans. These forms live chiefly on the naked rock, but, except the limpets, also often on the algæ in the tidal area. But when the belt of fucoids is exposed at ebb-tide, especially in sheltered places where a good current runs, we see that the algæ, the species of *Fucus* in particular, have their special fauna, consisting chiefly of attached forms.



FIG. 319.
Purpura lapillus, L.

The majority of them are hydroids, the commonest species being *Dynamena pumila* (see Fig. 320),

Laomedea flexuosa, and *Clava squamata* (see Fig. 321). There are several bryozoans¹ here too, and the fucoids are often densely thronged by small white spiral-shaped tube-worms (*Spirorbis*).

Amongst the unattached forms associated with the algæ I may mention: *Littorina obtusata*, which keeps mostly to little bays sheltered from the action of the waves; *L. littorea*, which is very common; and our smallest shelled snail *Skenea planorbis*, which is met with in favoured spots under stones and upon algæ of different species.

More local in their occurrence,

though generally numerous where found, are certain species of Actiniæ—the red *Actinia equina* (see Fig. 322), the yellow or brownish *Metridium dianthus* (see Fig. 323), and *Urticina crassicornis* being the commonest forms. The first of these is generally found in quiet bays where the shore is covered with large stones and pebbles, the individuals being sometimes attached to these and sometimes to cracks in the rock. As this species produces its young fully developed, and the newly-born actiniæ are able to attach themselves easily, it is frequently met with in fairly large colonies.

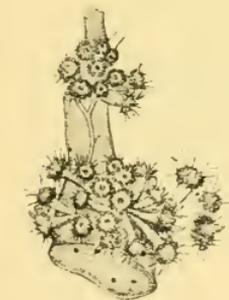


FIG. 321.

Clava squamata, Müll.
(After Hincks.)

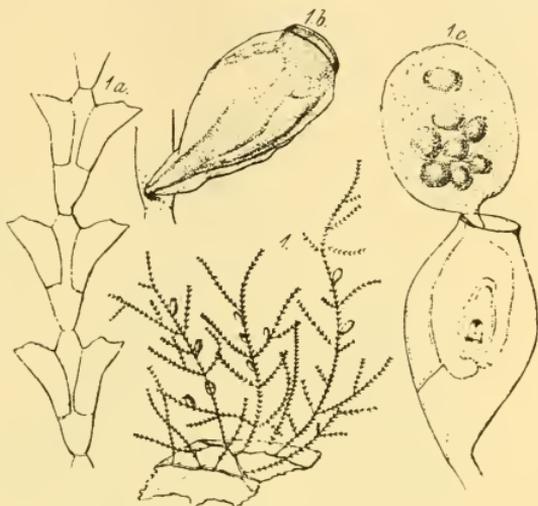


FIG. 320.

Dynamena pumila, L. (After Hincks.)

Another remarkable mode of propagation, namely schizogony, is to be seen in *Metridium dianthus* in its younger stages. From the foot-disc of the animal small pieces unwind and form new organs, such as new tentacles, new mouth, etc. In this way colonies are formed, which may be widely distributed over the rock or the roots of the laminaria.

¹ Chiefly *Alcyonidium hirsutum*, *Flustrella hispida*, *Bowerbankia imbricata*.

The fully developed individuals of *Metridium* are usually found in places where there is a strong current.

Off the coasts of Scandinavia the sandy bottom of the low-tide area is not so extensive as along other coasts of the North Sea, but it is interesting to note that the fauna inhabiting this region is much the same everywhere, and that burrowing forms predominate. There is first the sandgaper (*Mya*

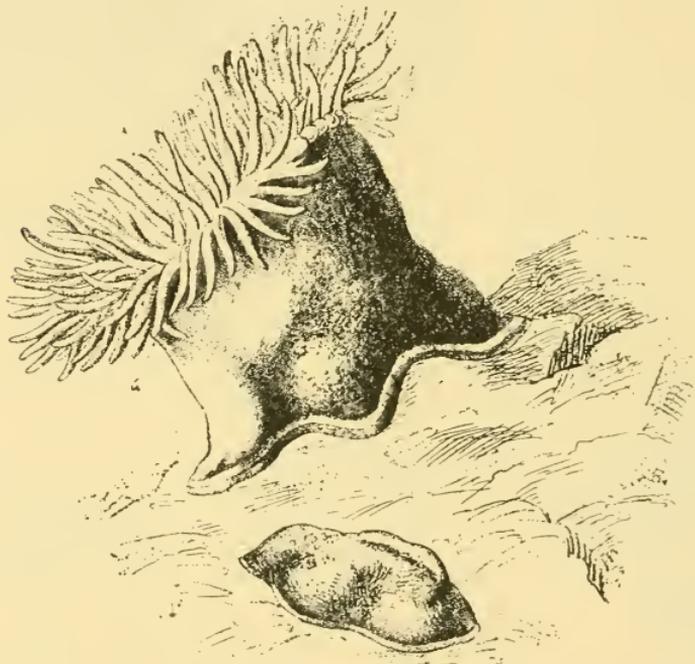


FIG. 322.
Actinia equina, L.

arenaria), and then the cockle (*Cardium edule*, see Fig. 324), and also different species of *Tapes*, though these are not so universally distributed. The lugworm (*Arenicola piscatorum*, see Fig. 325) is another burrowing form, and its presence can easily be detected by little heaps of string-like excrements.

In addition to these forms, which are adapted for life in the low-tide area at those parts of the coast where the ebb-tide recedes a long way, we also get the common shore crab (*Carcinus mænas*), often to be found under fucus that has been left exposed. This is the case also with the common starfish (*Asterias rubens*), and occasionally, too, with the common

sea-urchin (*Echinus esculentus*), the hermit crab (*Pagurus bernhardus*), and a few other forms. Their occurrence is, however, really due to their being surprised by the receding of the tide, and they are not, strictly speaking, adapted to a life in this area.

There are some forms characteristic of the low-tide area



FIG. 323.

Metridium dianthus, Ell. (After Andres.)

which cannot be regarded as belonging solely to any particular facies. Perhaps the commonest are the sandhoppers (Gammarids), which have a wonderful knack of hiding themselves quickly in holes and cracks, when the stone or other object, under which hundreds may be sheltering, is removed. One of the most abundant is *Orchestia littorea*, which, although a true marine form, is able to exist for a long time out of the water. I have found quantities of them during summer living

perfectly happily with true land-animals, such as centipedes and woodlice, in places that were very rarely covered by the sea, so that they had to depend upon the slight moisture retained beneath the stones; individuals found living under these conditions on being

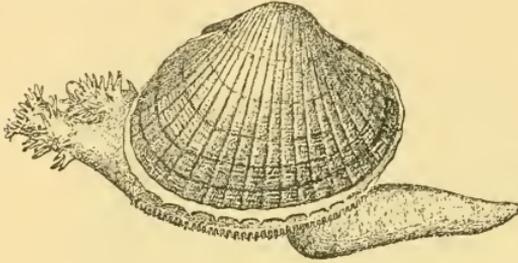


FIG. 324.
Cardium edule, L.

transferred directly to sea-water showed not the least sign of being inconvenienced by the sudden change. Another equally common sandhopper (*Gammarus locusta*, see Fig.

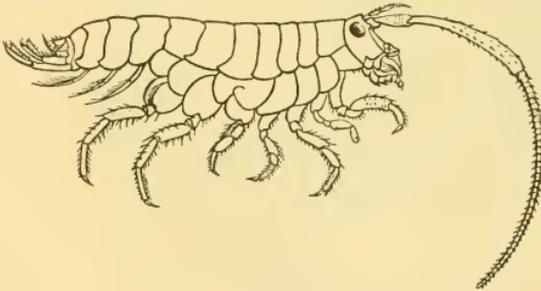


FIG. 326.
Gammarus locusta, L. (After Bate and Westwood.)

326) is also a littoral form, but it never quits the sea for any length of time.

In the unexposed portion of the littoral zone of the skerries we may distinguish four "facies": (1) Laminaria belt, (2) Zostera belt, (3) hard bottom, and (4) sand.

The Laminaria belt begins immediately below the fucoids, and along the west coast of

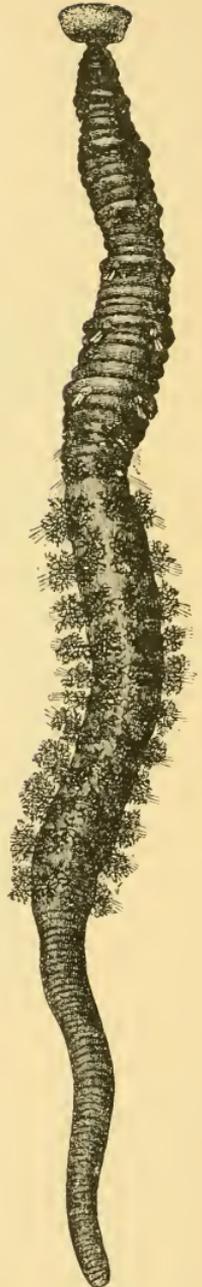


FIG. 325.
Arenicola piscatorum, L.

Unexposed
area.

Laminaria
belt.

Norway there are three common species: *Laminaria hyperborea*, *L. digitata*, and *L. saccharina*. The first of these occurs in great thickets in open bays or places where the play of the waves is felt, whereas the other two grow in more sheltered localities. The fauna varies accordingly. On the stalks of *Laminaria hyperborea* we get numbers of attached forms, chiefly hydroids, bryozoans, synascidians (see Fig. 327), and calcareous sponges. *Halichondria panicea*, one of the few siliceous sponges of the littoral zone, also

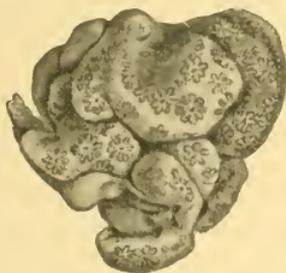


FIG. 327.
Synascidian: *Polycyclus fuscus*,
Huitfeldt Kaas.

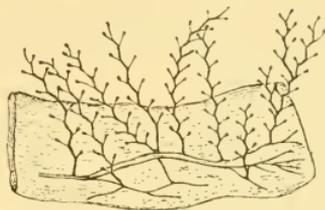


FIG. 328.
Obelia geniculata, L. (After Hincks.)

frequently forms a thick covering over long pieces of the stalks. On the blades of the laminaria two forms are very common, namely the bryozoan *Membranipora membranacea*, which makes a white covering over large portions, and the little hydroid *Obelia geniculata* (see Fig. 328). An unattached form, the gasteropod belonging to the Patellid family (*Nacella pellucida*), is very conspicuous, owing to its handsome blue-striped shell, and lives exclusively on the laminaria.

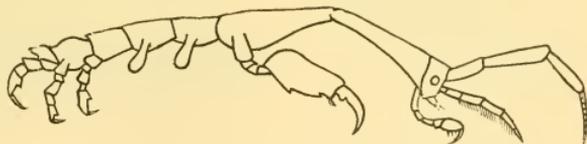


FIG. 329.
Caprella linearis, L.

Besides the attached forms, that often completely cover the lower parts of the laminaria, there are unattached species in great abundance existing upon or among them. The best way of observing them is to shake a thickly overgrown laminaria stalk, placed in a large glass of sea-water, when we may perceive swarms of amphipods, worms,¹ tiny mussels and snails, little starfishes, and other creatures. The most noticeable of the amphipods are the elongated and strangely built caprellids, of which *Caprella linearis* (see Fig. 329)

¹ A species of *Nicolea* is common.

is the commonest. With their prehensile claws they climb about among the hydroids and red algæ, hooking themselves on by their hind limbs, swaying to and fro for a time, and then catching hold of another branch with their front claws and climbing farther. In fairly sheltered localities we often get among the branches of the hydroids and algæ little tube-shaped dwellings constructed out of various materials and inhabited by different species of amphipods,¹ and here, too, we meet with some kinds of pycnogonids.²

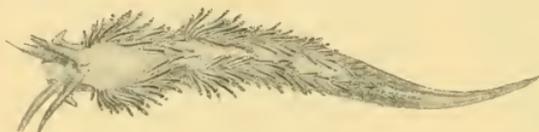


FIG. 330.
Aolis rufobranchialis, Johnst. (After Alder and Hancock.)

Beautifully coloured nudibranchs (usually species of *Aolis*, and especially *Aolis rufobranchialis*, see Fig. 330) crawl slowly about and feed like the pycnogonids upon the hydroids; certain kinds of nudibranchs (especially some species of *Doris*, see Fig. 331, *Polycera*, etc.) occur chiefly in the winter. Animal groups that are very numerous represented in the algæ-vegetation of the littoral zone, though they must be very carefully searched for, are rhabdocœlous turbellaria and several species of Halacarids. There are, in addition, quantities of the young of *Mytilus*, asterids, etc. Among the "roots" of the laminaria we frequently get *Nereis*, *Ophiopholis aculeata*, and borer mussels (*Saxicava*).

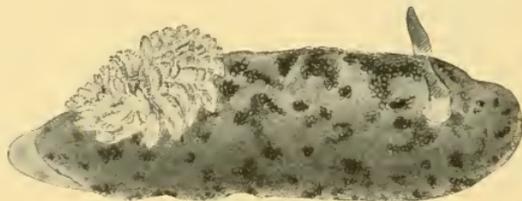


FIG. 331.
Doris tuberculata, Cuv. (After Alder and Hancock.)

In contradistinction to *Laminaria hyper-*

borea, which prefers the most exposed situations, where there are waves or strong currents, as well as hard bottom to which to attach itself, we find the eelgrass (*Zostera marina*) in enclosed sheltered localities (pools, estuaries, etc.) and upon soft muddy bottom. The fauna of the eelgrass is not nearly so rich in species as that of the laminaria, still there are several characteristic forms living mainly, and perhaps exclusively, in its vicinity. There is, for instance, a small whitish semi-trans-

¹ Especially species of the family Podoceridæ, characterised by the extremely hairy antennæ.

² *Nymphon brevirostre*, *Phoxichilidium femoratum*, *Phoxichilus spinosus*, etc.

parent snail (*Rissoa*), which may often be found in enormous quantities; often also there are great numbers of another snail (*Akera bullata*), and in the mud, even where there is no *zostera* vegetation, we frequently find species of *Philine*. A species of attached ascidian (*Ciona intestinalis*, see Fig. 332), which, however, is also found on laminaria, especially when growing in sheltered or rather deep places, is one of the most prominent animal forms of the eelgrass. Hydroids and synascidians are also occasionally met with. Swimming amongst the blades of the eelgrass we further find various crustaceans, of which two species of prawns (*Pandalus annulicornis* and *Palæmon*) are the most noticeable. They are not limited to the eelgrass, however, but occur also in places where *zostera* does not grow. The list of forms to be found here is far from exhausted, for I have mentioned only some of the chief ones. The *zostera* belt is not of so much importance along the Atlantic and North Sea coasts of Scandinavia, as it covers a very limited area in comparison with the other subdivisions of the littoral zone, and it is negligible indeed, when compared with the immense tracts in the Kattegat which are literally overgrown with this plant.

Such in general is a picture of the fauna to be found in the algæ and *zostera* vegetation of the strand-belt; though it must be understood that when speaking of this fauna as associated with the plants I do not imply that these animal-forms can exist only upon them. This is only exceptionally the case. The relationship between them depends on the fact that, as a rule, the algæ afford an excellent foundation for the attached forms, which find favourable conditions of nourishment wherever the algæ flourish. For we must remember that these attached forms are obliged to obtain their nourishment from such organisms as chance to come within their reach, and since currents and waves furnish the necessary assistance, we



FIG. 332.
Ciona intestinalis, L.
(After Alder and Hancock.)

generally find the most abundant animal life among the algæ in localities where wave-action is most effective. Most of the non-attached forms are in no way directly dependent upon the algæ-vegetation.

It will be evident that attachment to fucus and laminaria is not biologically essential, if we bear in mind that the same animal forms which attach themselves to these plants occur also on rocks and stones. The vegetation merely increases the area available for the attached forms. Nor is any particular plant essential for any particular species of animal. No doubt on the Norwegian west coast *Laomedea flexuosa* and *Clava squamata* nearly always attach themselves to *Ascophyllum*, while *Obelia geniculata* and some others prefer laminaria, but this is chiefly owing to the tides. On the Skagerrack coasts, where tides are inconsiderable and irregular, we find even in the fucus belt forms like *Coryne* (see Fig. 333), *Tubularia*, and *Obelia geniculata*, though on the west coast of Norway they grow only among the laminaria and at a lower depth. These forms cannot stand exposure for any length of time, and they are therefore not to be found in places where the ebb regularly goes back a long way.

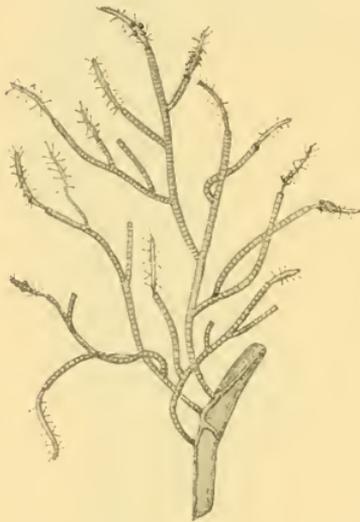


FIG. 333.
Coryne pusilla, Gaertn. (After Hincks.)

The forms met with in the tidal area cannot, however, be in any way dependent upon the ebb-tide for their existence, seeing that they occur numerous also on the coasts of the Skagerrack, where tides are scarcely felt. Instances of this are furnished by *Clava*, *Campanularia flexuosa*, and *Dynamena pumila*, but the fact that these forms are able to withstand exposure for considerable periods of time makes it possible for them to occupy a far more extensive area than would otherwise be the case.

So far as the structure of their organs is concerned, the unattached forms in the algæ-fauna are particularly well equipped for gripping, climbing, or creeping about among the hydroids and the red bushy algæ that usually grow in quantities upon the laminaria. The crustaceans (caprellids and amphipods)

have extremely bent legs and claws, the naked snails have their flexible foot-discs and the planarians their rhabdites, so that these creatures furnish excellent examples of adaptability to external conditions. A bodily structure of this kind is necessary for these forms, or when exposed to the action of the waves or currents they would run the risk of being torn from the objects to which they cling.

The marine algæ are known to be rather particular about the localities they select. Some species grow high up on the

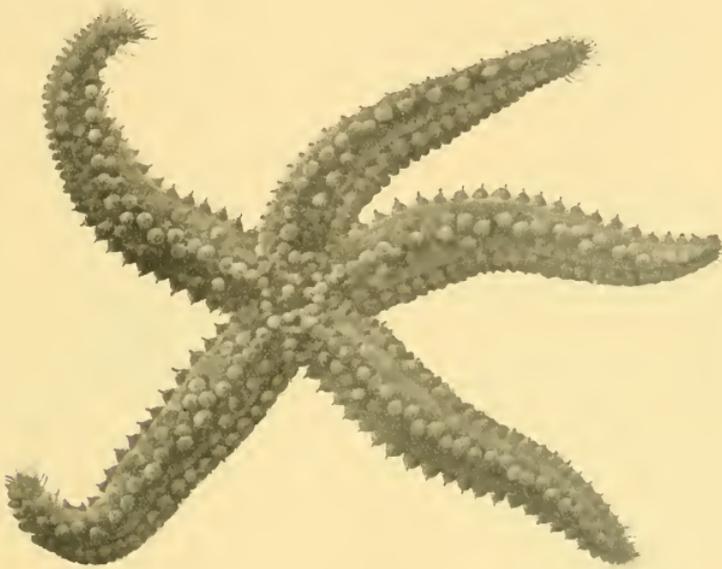


FIG. 334.
Asterias glacialis, L. (After Ludwig.)

rocks so as to be covered only at high tide, while others choose the lowest limit of ebb-tide; some prefer sunlight, while others thrive only away from it; some grow best amidst the waves and breakers, while others need sheltered places. This is, to some extent, true also of the animal forms of the upper littoral zone, many of which prefer the open parts of the coast, while others live in sheltered localities, and others again where the currents are strong. The three bryozoans *Alcyonidium*, *Flustrella*, and *Bowerbankia*, for instance, seem to prefer shelter and a good current, whereas *Membranipora pilosa* flourishes best in the laminaria belt, in exposed places where *Laminaria hyperborea*

grows. *Littorina littorea* and *L. obtusata* again are found in greatest abundance wherever there is shelter, while *Nacella pellucida* generally lives on the blades of *Laminaria hyperborea*. In the sheltered haunts of *Laminaria saccharina* and *L. digitata*, particularly on the first named, we find the brittle-star *Ophiothrix fragilis*, while the localities with *L. hyperborea* have evidently no attractions for it; the blades of *L. saccharina*, too, are much patronised by the bryozoan *Aetea*. *Asterias glacialis* (see Fig. 334) also prefers sheltered localities. Why there should be these apparently capricious affections is as yet unknown, but it may be that in undisturbed waters there are higher temperatures during the summer, and that consequently various influences are brought to bear upon the organisms at one stage or another of their lives.

Hard bottom
in the
unexposed
portion of the
littoral zone.

The most typical localities of this kind are met with as a rule in sounds amongst the skerries, where there is a more or less strong current, which carries away the finer particles of mud that would otherwise settle, and leaves only large fragments of shells and similar debris. On the hard bottom there are usually numbers of both attached and unattached forms, chiefly consisting of bryozoans, hydroids, especially the genus *Tubularia*, and ascidians. The coral *Alcyonium digitatum* too is often plentiful,¹ generally attached to large empty mussel shells or stones. The empty mussel shells are also patronised by big colonies of the serpulid *Pomatoceros triqueter*, which however is just as much at home on the rocks up to the very shore. There are, besides, *Anomia ephippium*, *Chiton cinereus*, *Tectura virginea*, *Buccinum undatum*, and several others, some sedentary, and others, like the chitons and *Tectura*, able to move about from one place to another; as well as *Mytilus modiolus*, though this mussel is far more plentiful inside the fjords, and *Gonactinia prolifera*.

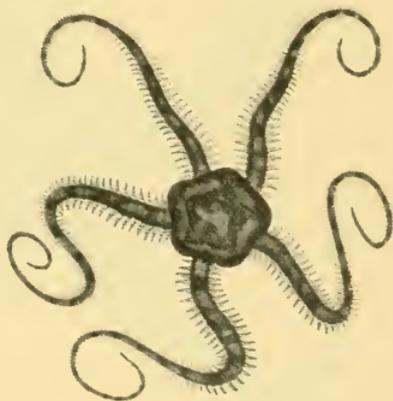


FIG. 335.
Ophiopholis aculeata, L.

¹ This form may even be found up to low-tide mark, where there are strong currents, as for instance in narrow shallow sounds.

Several echinoderms occur numerously wherever there are currents. There are quantities of the brittle-stars: *Ophiopholis aculeata* (see Fig. 335), *Ophiocoma nigra*, and *Ophiura albida*. Two species of sea-urchins that live on the hard bottom in the littoral zone are very common among the skerries on the west coast of Norway, namely *Echinus esculentus* and *Strongylocentrotus dröbachiensis*. On the other hand, *Echinus acutus* and *Parechinus miliaris*¹ have a different local distribution, to which I shall allude later. All four species may be found up to low tide mark. This is true also of the big dark-brown holothurian *Cucumaria frondosa* (see Fig. 336), large numbers of which live on the hard bottom among the skerries, and in the outer parts of the fjords, especially where there is a strong current. They fasten themselves to the rock by means of their suckers, and often have their tentacles stretched out in order to capture pelagic organisms, which are afterwards licked off, the animal sticking one tentacle at a time into its mouth.

Together with the above forms we find a mussel, *Lima hians*, which is very characteristic of these localities. It is of interest biologically, because it lives within a nest constructed with the assistance of its byssus out of bits of empty mollusc shells, fragments of echinids or serpulids, and similar materials; in fact, no loose substances appear to come amiss.

Two starfishes are always present, namely *Asterias rubens* and *A. mülleri*. There are other species as well, of course, such as worms and serpulids, but they cannot be called particularly characteristic.

Here, too, the lobster (*Homarus vulgaris*) is equally at home, and may be met with under rocks and stones, occasionally venturing on to sandy bottom. It is distributed throughout the whole littoral zone from a depth of about one metre downwards, a certain proportion of individuals migrating vertically, descend-

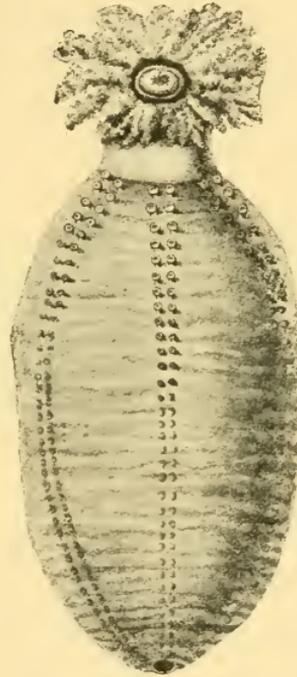


FIG. 336.
Cucumaria frondosa, Gun.

¹ In a few localities all these species may be found together.

ing to greater depths in winter. The spawning females usually repair to shallow places in the summer, the higher temperatures being better suited to the development of the eggs and larvæ.

Several of the strange mask crabs (*Hyas*, see Fig. 337, *Stenorhynchus*, *Inachus*) also inhabit the littoral zone, chiefly where the bottom is overgrown with algæ, bryozoans, and hydroids, being rarely met with upon sandy bottom. They are supplied with small hooks on the carapace and extremities, by which they attach to themselves the algæ or animal-colonies around them. These crabs are extremely sluggish and inactive, and they derive an advantage from this remarkable habit, since they are difficult to distinguish from their surroundings, and consequently they can conceal themselves from their prey as well as from their enemies.



FIG. 337.
Hyas araneus, L.

The bottom here chiefly consists of what has been called shell-sand, made up entirely of shell-fragments of molluscs, echinoderms, balanids and other creatures; it is usual to make a distinction between the coarse and the fine shell-sand. This detritus is practically only met with in the littoral zone of the skerries, and is undoubtedly due to the action of the waves and breakers. Burrowing forms, for the most part mussels, spatangids, clypeastrids, and worms, predominate. The lancelet (*Amphioxus*) also makes this its principal home. The loose formation is burrowed into quite easily, and a lancelet can work its way down in the course of a few seconds.¹ We must also include the sand-eels (*Ammodytes*) amongst the vertebrate forms that burrow in this sandy bottom, though they are somewhat local in their occurrence.

¹ This form burrows in a curving direction beneath the surface of the sand, finally protruding its head very slightly a short distance from where it went in, and remaining stationary in this position.

Sandy bottom
in the unex-
posed littoral
zone.

Several families of burrowing mussels inhabit the shell-sand, the most important being Veneridæ, Tellinidæ, Astartidæ, Cardiidæ, and Solenidæ. The most characteristic species are *Venus casina*, *V. fasciata*, *Timoclea ovata*, the species of *Tellina* and *Psammobia*, *Nicania banksi*, *Solen ensis* and *Cardium fasciatum*. The common cockle, *Cardium edule*, on the other hand, never occurs here. *Solen ensis* is generally so deeply embedded that an ordinary dredge brings up merely fragments instead of the whole animal. The small species of *Lunatia* belonging to the gasteropod family Naticidæ, and particularly *Lunatia intermedia*, also burrow some distance down, as they feed on little mussels, boring through their thin shells to get at the animals within. *Antalis entalis* is often common here.

Spatangids are represented by *Echinocardium flavescens* (see Fig. 338), the commonest of all, *Spatangus purpureus*, and *Echinocyamus pusillus*, the last named being the only clypeastrid in northern seas. Except perhaps *Spatangus purpureus*, they are not confined to the shell-sand of the skerries, but may be found also in the clay of the sublittoral zone. All of them burrow deeply. Another deep-burrowing form is *Astropecten irregularis*, which also lives in the clay bottom of both the skerries and fjords. This creature has conical legs (without suckers) particularly well adapted for digging, though they compel it to procure its food in a different way from *Asterias rubens*, which preys on large mussels by placing its foot-suckers on their shells and pulling the valves apart till the muscles relax and the shell is opened, whereas *Astropecten* swallows whole little worms, mussels, the young of *Echinocardium*, and other small animals.

The worms are chiefly those belonging to the genera *Glycera* and *Nephtys*, and the family Ophelidæ (*Ophelia limacina* and *Travisia forbesi*). They live down in the sand, where they make long passages that are kept open by having the walls lined with a film of slime.

All these animals are variously equipped for living buried in the sand, which naturally forms a splendid protection against their enemies. The burrowing mussels are provided with two more or less elongated movable siphons, the openings of which

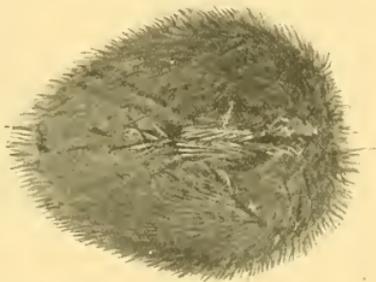


FIG. 338.
Echinocardium flavescens, O. F. Müll.

are always raised above the level of the sea-floor, the one being for supplying food and water, and the other for voiding excrements. The Spatangids get their nourishment down in the sand by means of their remarkably shaped mouth-feet, and through the rapid vibrations of the spines, some of which are specially adapted for the purpose, they keep the water circulating in the holes where they lie, and so obtain oxygen for breathing. *Astropecten* has a row of small spines along its arms, which vibrate in similar fashion, and cause a circulation of water round its body. The tubes of the worms are almost invariably directly connected by an opening with the level of the sea-floor.

Among the higher crustaceans inhabiting the sandy bottom

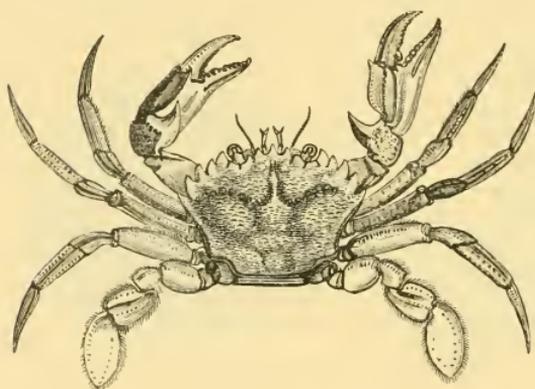


FIG. 339.
Portunus depurator, L. (After Bell.)

we get one or two species of swimming crabs (*Portunus*, see Fig. 339). They harmonise in colour with the variations in the colour of the bottom, and are thus enabled to escape notice when motionless. Their name is derived from the terminal joint of the fifth pair of swimmerets, which is expanded and paddle-

shaped, so that they are able to swim upwards. During the cruises of the "Michael Sars" in the North Sea one of these swimming crabs (*Portunus depurator*) was found hanging in the drift-net, and numbers of young crabs of the same species were captured in the plankton net. These forms must, nevertheless, be regarded as genuine bottom animals; I have observed that they can even burrow down into the sand for a short time, but never remain there long.

One of the most characteristic forms of the littoral zone is the common edible crab, *Cancer pagurus*, which is not so particular as the lobster regarding the nature of the bottom, being as much at home on sand as on rocks. *Cancer pagurus* goes farther up the fjords than the lobster does, but they both are undoubtedly littoral animals, occasionally found close up to low-tide mark, and occurring exceptionally below the lower limit of the littoral zone.

(2) *The Fjords*.—We have seen that the fauna of the littoral zone among the skerries, especially in the tidal area and laminaria belt, is abundant both in species and individuals. There is a diminution, however, as we penetrate farther into the fjords. In the tidal area of the inner fjords, and at greater depths also, we miss the limpet and the purple snail, while the hydroids to be found on the fucus in the skerries become less and less abundant, until even *Dynamena pumila* disappears.¹ This change in the fauna is mainly due to the decrease in salinity, since the surface of the inner fjords, for a great part of the year at any rate, is occupied by a layer of less saline water in which these forms cannot thrive. Far up the fjords, however, in the tidal area, we get the barnacle, the mussel *Mytilus*, and the black periwinkle, which seem to be less affected by a difference in salinity, though even they require a certain percentage of salt, since they disappear, for instance, from the tidal area in the more enclosed parts of the fjords, where, owing to the great accession of fresh water, the salinity is particularly low. The mussel and black periwinkle, it is true, may sometimes occur even here also, but only in fairly deep water. We also find the horse mussel in the fjords. The great thickets of *Laminaria hyperborea*, which are so characteristic of the skerries, are absent from the inner fjords, and so are most of the forms associated with them. In their place, however, we get *Laminaria digitata* and *L. saccharina*, but in comparatively small quantities.

The difference between the inner fjords and the skerries is not so marked when we descend to greater depths, since a good many forms are equally at home in both. Some of the littoral fauna, like the lancelet, appear to avoid the fjords altogether.² Two forms, which rarely ascend far up the fjords of West Norway, are the lobster and the common edible crab; but the common shore crab (*Carcinus maenas*) penetrates to their inmost recesses. The big black sea-slug (*Cucumaria frondosa*) is another form which abounds among the skerries and in the outer parts of the fjords, but very exceptionally penetrates far in. No doubt their absence is due to the feeble currents, or the greater or less accessions of fresh water prevailing in the fjords—local conditions that are bound to affect the distribution of the fauna.

The distribution of the two sea-urchins *Echinus esculentus*

¹ It is interesting to note that *Dynamena pumila* is also found in the estuary of the Elbe as far up as Cuxhaven.

² The reason for this may perhaps be that the lancelet requires pure sand or shell-sand to live in, while the bottom of the fjords generally consists of mud.

and *Echinus acutus* (forma *flemingi*) is curious. The former is very common out among the skerries, while *E. acutus* confines itself to a few localities, but on ascending the fjords *E. esculentus* becomes scarcer, and descends to greater depths, whereas *E. acutus* occurs in the greatest abundance. A similar distribution characterises the sea-urchins *Parechinus miliaris* and *Strongylocentrotus dröbachiensis*, which much resemble one another in outward appearance, and are both exceedingly plentiful in their different localities. *Strongylocentrotus* lives in the more open estuaries and bays of the skerries, whereas *Parechinus miliaris* keeps to sheltered waters, and especially to pools. For instance, in a pool south of Bergen (the Inderø Poll) I found *Parechinus miliaris* literally in thousands, but there was not a single specimen of *Strongylocentrotus*; in the neighbourhood of Bergen again I collected from another pool of a rather less typical character, sixty-three specimens of *Parechinus*, and only three specimens of *Strongylocentrotus*. This difference has not been explained, though most probably the cause is to be found in the difference in temperature. Pools contain water of a much higher temperature than the sea outside, and most likely *Parechinus miliaris* requires for its reproduction warmer water than *Strongylocentrotus*. It is interesting to note that, according to Petersen, there is the same diversity between these two forms in the Kattegat.

The foregoing is not meant to be even an approximately complete account of the forms inhabiting the skerries and the fjords, my sole object having been to show that the dissimilarity in physical conditions (temperature, salinity, etc.) and in the nature of the bottom, between the skerries and the inner parts of the fjords, determines the difference in their biological conditions.

Those areas of the littoral zone which have been called Pools, pools, or "polls" (see p. 225), are salt water basins connected with the sea outside by a shallow channel. The pools vary in depth, the deepest not exceeding 30 metres. One feature which they all have in common is that their channels to the sea are far shallower than their basins. The surface is always covered by a layer of more or less fresh water derived from the land, having a lower temperature than the salt-water layer underneath. About $1\frac{1}{2}$ or 2 metres below the surface the temperature in some summers may rise to 30° C. or even more, while that of the surface-layer does not rise above 18° or 20° C.,

though the conditions vary in different years. Below 2 metres the summer temperature decreases as we approach the bottom, but late in autumn and in winter the temperature is highest at the bottom.

In the intermediate warm salt water layers we get a fauna abounding in individuals that form a distinctive feature of the pools. There is, first of all, the oyster, *Ostrea edulis*, which finds its principal home here, and there are also quantities of *Pecten opercularis* attached to the rocks all round. The ascidian fauna is represented by several species, which are all exceedingly plentiful, the commonest being *Ascidia mentula*, *Asciadiella aspersa*, *Ciona intestinalis*, and *Clavellina lepadiformis*.¹ The most abundant of the bryozoans is *Aetea*, while a species of *Bougainwillia* appears to be the commonest hydroid. The principal sea-anemones are *Metridium dianthus*, *Urticina crassicornis*, and a species of *Sagartia*. *Parechinus miliaris* is the only echinoid, but it occurs in great numbers. *Ostrea*, *Pecten*, and *Parechinus* indicate the decidedly southern character of the fauna, and it may not be out of place to mention that among the plankton forms we get a copepod (*Paracartia grani*) belonging to a genus not met with again till we reach the west coast of Africa.

In addition to the forms having a southern distribution and of southern origin, however, we find eurythermal and euryhaline forms. *Asterias rubens*, *Carcinus maenas*, and *Mytilus edulis* are nearly always present, the last named in particular being in great abundance, frequently attached to the lines stretched across the oyster-pools for carrying the bundles of twigs or the baskets to which the oyster spat attaches itself. Mingled with this assemblage of mussels, ascidians, etc., we get enormous quantities of smaller animal forms, the crustacean family Tanaidæ being invariably represented.

Among the forms described as characteristic of the littoral zone, there are very few that do not occur in all its depths, that is to say, only a few forms are restricted to the actual strand-belt. These few, however, include most of the forms that characterise the tidal area.² No doubt even these may occasionally be met with at a depth of a few fathoms, but

Vertical
distribution of
the littoral
fauna.

¹ In enclosed places, though not actually in pools, *Corella parallelogramma* is also common.

² For instance, *Patella vulgata*, *Purpura lapillus*, *Littorina littorea*, *L. rudis*, and *L. obtusata*; besides *Balanus balanoides*, *Mytilus edulis*, *Orchestia littorea*, *Campanularia flexuosa*, *Clava squamata*, *Actinia equina*, *Alcyonidium hirsutum*; and among the burrowing species *Mya arenaria*, *Cardium edule*, and *Arenicola piscatorum*.

the tidal area is their proper home. On the other hand, those forms which have been described as passing their lives in the vicinity of low-water mark are not limited to this situation, but may be met with throughout the whole littoral zone, sometimes on sand, sometimes on rock, and sometimes impartially on either hard or soft bottom. Furthermore, on the coasts of Norway the majority of the forms which characterise the littoral zone either never, or only to an inconsiderable extent, pass below its lower limit, though there are some that go down to perhaps about 100 metres, and a very few that descend to greater depths. But forms which on the Norwegian west coast are exclusively littoral, may be met with in deeper water in other northern areas, as I shall show later on.

The sub-littoral zone.

It would hardly be possible in a short account like this to give even an approximately complete description of the fauna along the coasts in the sublittoral zone, seeing that this is the abode of most coastal species living below the littoral zone. As a rule, the soft bottom is of a different character from that in the deepest parts of the fjords. Instead of viscous gray clay or mud, a coarser clay, more sandy in character, covers the floor in the medium depths of the sublittoral zone, which in the case of the fjords is near the sides or on submarine banks. Where there are plateaus sloping gradually down from the sides we also get rocks and stones and bits of shells, and there is thus accommodation for forms that naturally live on hard bottom. We often get, for instance, quantities of brachiopods and bryozoans, as well as a certain number of hydroids, ascidians, etc. Generally speaking, the character of the bottom here is more favourable to animal life than in the deep water, for while the mud harbours chiefly burrowing mussels, for instance, the medium depths accommodate, in addition, a large number of creeping snails.

A good many forms which occur in the continental deep-sea zone ascend to the sublittoral, and some even as high as the littoral¹ zone. Still for most of them we may put the upper limit of distribution at 100 to 200 metres. Probably, however, their vertical distribution is affected to some extent by the variations in the vertical distribution of the Atlantic water, which may be higher or lower according to the different seasons

¹ For instance, *Pagurus pubescens*, *Ophiopholis aculeata*, and *Terebellides strömi*.

of the year.¹ Other sublittoral species again are plentiful everywhere throughout the whole sublittoral zone, but rarely descend below its lower limit, so that we find at a depth of 100 to 200 metres a mixed fauna, consisting partly of forms that have here reached their upper or lower limit of vertical distribution, and partly of forms which find here the most favourable conditions of life. The sublittoral zone accordingly ranks first in number of species.

The continental deep-sea zone for all practical purposes coincides with the deeper parts of the fjords, whereas out among the skerries, with their comparatively shallow water, we either do not find it at all or else meet with it merely in very limited areas. A feature of the fjords is their very great depth, usually increasing as we proceed inwards, and in their deepest parts, so far as the nature of the bottom and the physical character of the water are concerned, we get what are practically Atlantic conditions.

The
continental
deep-sea zone

In the fjords the greatest depth is met with along the middle and in the innermost portions, and may be put on an average at 400 to 800 metres.² The sides of the fjords descend in some places practically perpendicularly into deep water, in other places forming more or less extensive submarine plateaus and terraces. At various depths, especially in the seaward portions, there are cross ridges, which frequently consist of hard bottom. The material covering the floor in deep water is almost invariably a soft, viscous, grayish clay or mud. It is the animal life existing upon and in this mud which I shall now describe.

The mud-fauna of the deeper parts of the fjords resembles the sand-fauna in the littoral zone, inasmuch as it consists mainly of burrowing forms, or at any rate of forms which to some extent burrow into the mud to obtain their nourishment. When we sift the mud brought up by the trawl or dredge, we obtain a number of curious little bodies (round, star-shaped, rod-like, conical, etc.), composed of sand or particles of mud. These creatures are rhizopods (foraminifera). By putting out extremely fine thread-like prolongations of their protoplasm through one or more openings in their covering, they attract to themselves small organic particles in the mud which furnish

¹ Thus Helland-Hansen has fixed the summer limit along the coasts at 75 metres, and the winter limit at 150 metres.

² In some fjords, such as the Sogne and Hardanger fjords, the depth is in places 1000 metres or more.

them with nourishment—an operation that under favourable circumstances can actually be observed.¹ Of larger forms, the numbers of which render them characteristic of these depths, two sea-slugs deserve mention: a red one (*Stichopus tremulus*, see Fig. 340), and a gray one (*Mesothuria intestinalis*). They belong, however, to a division different from the sea-slugs found in the littoral zone, the distinction consisting *inter alia* in a different structure of the tentacles.

Other characteristic forms are: the brittle star *Amphiura norvegica*, the sea-slugs *Cucumaria hispida* and *Bathyplores tizardi*. Of higher crustaceans we have the genus *Munida*, with the two species *M. rugosa* and *M. tenuimana*, of which the latter in particular is to be met with in the deepest parts of the fjords, and the prawn *Pontophilus norvegicus*. The mussels come next to the rhizopods in number of species, the forms



FIG. 340.
Stichopus tremulus, Gunn. Reduced. (After O. F. Müller.)

most frequently found being *Malletia obtusa*, *Portlandia lucida*, *P. tenuis*, and *P. frigida*, *Abra longicallis* and *A. nitida*, *Kelliella miliaris*, *Axinus flexuosus* and *A. ferruginosus*, *Nucula tumidula*, and the species of *Neæra*. Scaphopods include three characteristic forms, namely *Antalis striolata*, *Siphonentalis tetragona*, and *Cadulus subfusiformis*, which last becomes more abundant as the depth increases. Worms are represented by the families Maldanidæ and Terebellidæ, of which latter *Terebellides strömi* is very common, and there are also *Lumbrinereis fragilis*, *Nephtys*, *Aricia*, etc.

The cœlenterates are represented on the mud of the deeper parts of the fjords by the group of pennatulids or sea-pens, a kind of unattached coral animal. The commonest forms are *Kophobalenmon stelliferum* (see Fig. 341) and *Funiculina quadrangularis*, though they are not so regularly or abundantly distributed as the two sea-slugs already referred to, which are found practically everywhere. Two species of sea-anemones (*Actinostola callosa* and *Bolocera tuediæ*)² are also universally distributed,

¹ The following are a few forms which are characteristic owing to their numbers and size: the globular *Saccammima spherica*, the rod-like ramifying *Rhabdammina abyssorum*, and the star-shaped *Astrorhiza arenaria*, the test of which consists of particles of sand, the rod-like non-ramifying *Bathysiphon filiformis*, etc. In addition there are other large forms of which I may mention the species of *Cristellaria*, the shells of which are calcareous and consist of several cells.

² Both these forms are found in the deep parts of the fjords, but I am not certain whether they live on the mud or on the patches of harder bottom which occur here and there.

and so is the sponge *Thenea muricata* (see Fig. 342), which adheres to the mud by means of long outgrowths, and the worm-like gephyrean *Sipunculus priapuloides*.

Thus the majority of the mud-fauna in the deep parts of the fjords, owing to the nature of the bottom, consists of unattached animal forms, most of the sponges, corals, hydroids,¹ bryozoans, ascidians (including the unattached molgulids), and brachiopods being absent; in other words, the nature of the bottom gives the fauna its character. Still even here it is possible for certain attached forms to occur normally, and very often abundantly. There are frequently great quantities of the little mussel (*Arca pectunculoides*), which fastens itself by its byssus-filaments sometimes to the larger foraminifera, sometimes to slag from steamers, or any other hard substances which it happens to come across in the mud. There are also numbers of the white semi-transparent *Pecten abyssorum*, which occurs, according to Sars, also in the deepest parts of the Christiania fjord, where it attaches itself to rotten bits of sea-weed.

I shall now turn to the faunal conditions in the fjords where there is hard rocky bottom, *i.e.* the more or less steep sides of the fjords and the submarine ridges or eminences. These latter are sometimes isolated raised portions of the floor surrounded on all sides by softer bottom, and sometimes spurs running out from the walls of the fjord. The slopes of the ridges and eminences are frequently covered with coarse sand and stones, as are also the sides of the fjords where not too steep. In many cases, however, the walls go down so steeply that no loose deposits occur till we reach a depth of several hundred metres.

The fauna here is quite different from that on the muddy bottom, consisting mostly of attached forms of various groups,

¹ Only a little form (*Perigonimus abyssii*) is common here, attached to mussel shells, especially those of *Nucula tumidula*.



FIG. 341.
Kophobolemnou stelliferum,
O. F. Müll. (After
Asbjörnsen.)

especially sponges, cœlenterates, bryozoans, brachiopods, and tube-worms, with a few unattached forms, of which the crustaceans are the most important. Most of the species of attached forms belong to the sponges, cœlenterates, and bryozoans, though the brachiopods and tube-worms exceed the others in number of individuals. The sponges are nearly

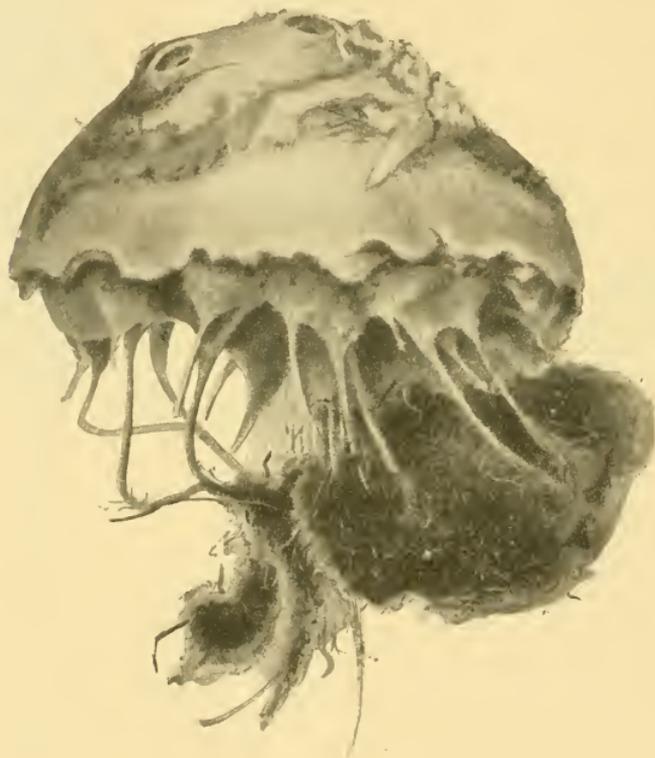


FIG. 342.

Thenea muricata, Bowerbank.

all silicious, whereas in the littoral zone they are chiefly calcareous. The principal cœlenterates are attached coral animals, especially gorgonians,¹ alcyonarians, and hydroids. We commonly get, for instance, one or two species of alcyonaria of the genus *Paraspongodes*, the larger specimens of which resemble cauliflowers; in the same way we find *Alcyonium*

¹ *Paramuricea placomus*, *Primnoa lepadifera*. In the same localities we also find two sea-anemones (*Phellia abyssicola* and *Bolocera medicea*), of which the latter also occurs on muddy bottom in the deep parts of the fjords (see p. 482).

digitatum, belonging to the same group, upon hard bottom in the littoral zone. We must also include among the alcyonaria the sea-tree, *Paragorgia arborea* (see Fig. 343), which is taller than a man and has many branches. Of true corals we may mention *Lophohelia prolifera* and *Amphihelia ramea*, though the coral fauna is not regularly distributed over the hard bottom, but is more or less local ; still

there are often numbers of individuals where hard bottom does occur. Several species of hydroids, such as *Lafocia dumosa*, *Sertularella gayi*, etc., are very common ; and of the bryozoans, *Retepora beaniana*, easily recognisable owing to its trellis-like structure, is both widely distributed and plentiful. So, too, are the brachiopods, *Terebratulina caput-serpentis* and *Waldheimia cranium*, and the two tube-worms, *Placostegus tridentatus*, the tube of which divides into three tooth-like processes, and *Serpula vermicularis* (see Fig. 344). Both these worms, it may be added, have calcareous tubes, in contradistinction to the tube-worms of the mud

which inhabit tubes of mud or sand. There is, besides, a species of barnacle (*Verruca strömi*) on the stones, which is frequently nearly as abundant as *Balanus balanoides* in the tidal area.

It would take too long to give a full description of the unattached fauna associated with the hard bottom. I will therefore merely point out that some free forms occur only upon the attached forms, and seem accordingly to be dependent

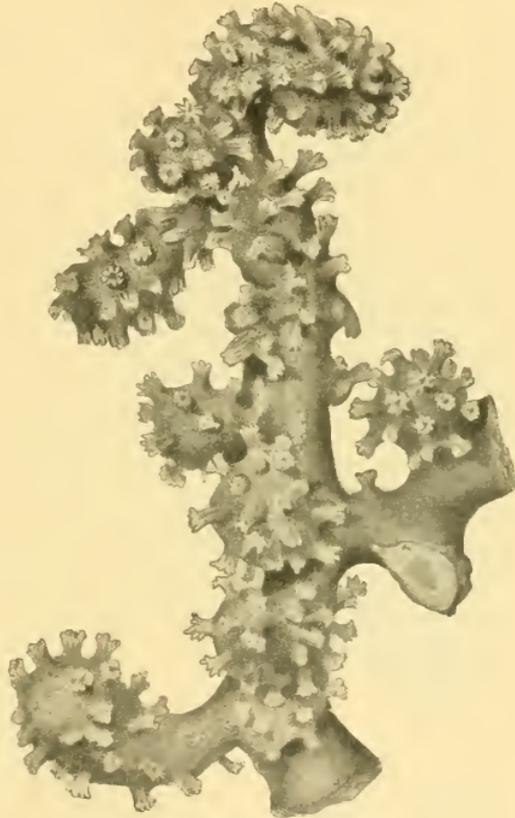


FIG. 343.

Branch of *Paragorgia arborea*, L.

upon them. The most noticeable of these is medusa's head (*Gorgonocephalus linckii*, see Fig. 345), a brittle-star with extremely branching arms that lives upon the larger gorgonians and sea-trees. A crustacean, *Galathodes tridentatus*, appears also to be intimately connected with the corals, and large quantities are occasionally found upon them. As for the remaining higher forms of crustaceans the fauna consists chiefly

of prawns, though they are different from the ones in the littoral zone,¹ but other groups are not entirely wanting.²

The large mussel, *Lima excavata*, is extremely characteristic of the rocky bottom, attaching itself by means of its fine silky byssus-filaments. We may further mention a sea-slug (*Psolus squamatus*, see Fig. 346), easily recognisable owing to its abruptly truncated disc with sucktorial feet, by which it adheres to stones, shells, etc.; a crinoid (*Antedon petasus*) occurring locally, though often in abundance, especially where there are sponges; several star-fishes, *Pentagonaster granularis*, *Porania pulvillus*, *Hippasterias phrygiana (plana)*, which last seems to prefer places where the hard bottom is covered with coarse sand; a brittle-star (*Ophiopholis aculeata*); molluscs, as, for instance, species of *Pecten*; ascidians, particularly of the family

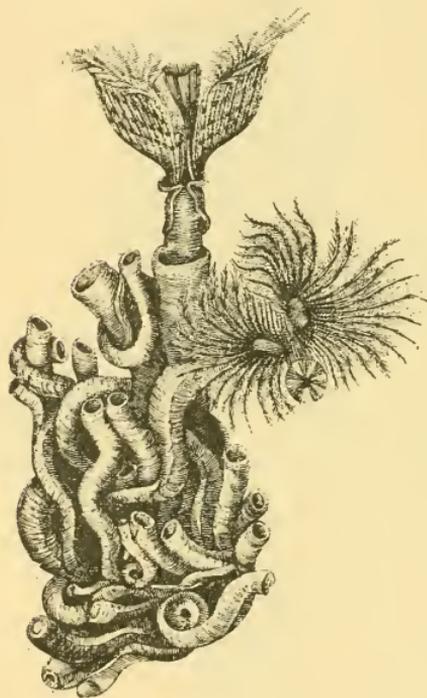


FIG. 344.
Serpula vermicularis, Müll.

Styelidæ; sea-spiders (*Nymphon strömi*), etc. At considerable depths there is also the remarkable starfish *Brisinga endecacnemos*. Some of these are exclusively deep-sea forms, and rarely leave the deeper parts of this zone. *Munida tenuimana*, *Bathyplores tizardi*, *Brisinga endecacnemos*, and *Lima excavata* do not occur in depths less than 300 or 400 metres.

Littoral zone.

(3) *Other Northern Boreal Coastal Areas*.— There are several areas where the littoral zone has been but little studied,

¹ *Pandalus propinquus*, *P. brevirostris*, *Hippolyte polaris*, and *H. securifrons*.

² Thus a hermit-crab (*Pagurus pubescens*), which occurs, too, in the littoral zone, is quite common, and so are *Munida rugosa*, which also inhabits soft bottom, and the stone-crab (*Lithodes maja*).

and the information received from Iceland and the Faroe Islands is not as yet sufficiently comprehensive to enable one to speak with confidence regarding the composition of the littoral fauna there. In Iceland, however, if we may judge from our knowledge of the hydroid fauna in the boreal coast areas, the conditions are very similar to those on the Scandinavian coasts, and the same is true also of the North Sea coasts of Britain.

If we compare the North Sea coasts with the Skagerrack coasts of Scandinavia we find many points of resemblance, the littoral fauna for the most part living under similar natural conditions in both areas. The tides of the Skagerrack, however, are inconsiderable and irregular, and in consequence forms, which on the North Sea coasts belong to the low-tide area, can undoubtedly live here in shallow water and on the same kind of bottom, but they are not left regularly exposed by the ebb. A good instance of this may be seen in the case of the hydroids *Clava squamata* and *Laomedea flexuosa*, which are quite common on the fucoids in spite of the fact that the ebb-tide only on rare occasions leaves them exposed. On the other hand, certain species, which are not met with in the low-tide area of the North Sea, and consequently do not patronise the fucus there, attach themselves to these algæ on the Skagerrack coasts. It is evident from this that it is not the actual foundation but the natural conditions and the ability to adapt themselves to these conditions which determine the distribution of the animals in the strand-belt.



FIG. 345.
Gorgonocephalus linckii, M. and T., var. Reduced.

Although the littoral faunas of these two coastal areas bear a very strong resemblance to each other, there are yet

some differences between them. Thus several forms that abound on the west coast of Norway are absent from the Skagerrack coast, if we may judge from my observations at Risör in Norway compared with the researches of Théel at Kristineberg in Bohuslän.¹ For instance, *Cucumaria frondosa*, a littoral echinoderm common on the North Sea coast, has not been met with in the Skagerrack, and *Ophiocoma nigra* is very rarely found in the latter area. *Echinus acutus* occurs in enormous quantities on the North Sea coast, but is extremely

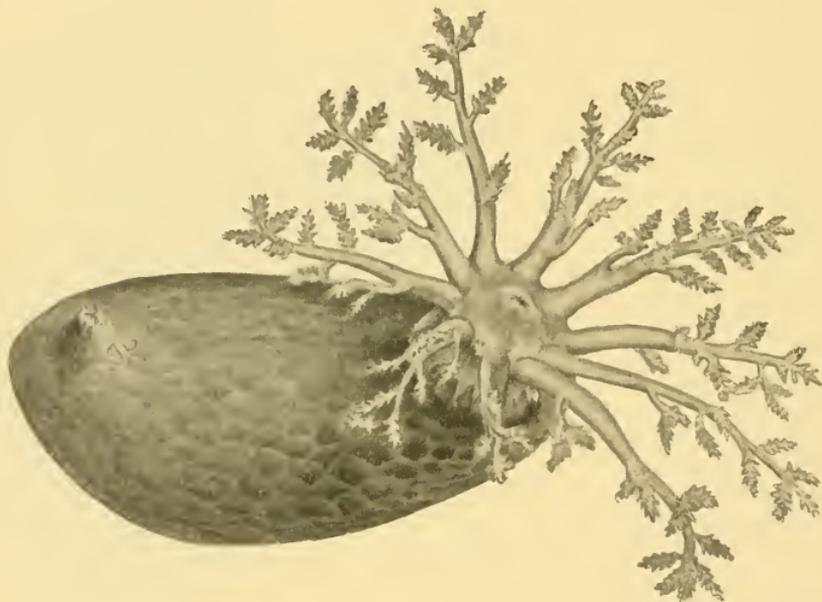


FIG. 346.
Pisidium squamatus, Koren.

rare on the Skagerrack coast, while the mussel, *Lima hians*, has not been met with on the Bohuslän coast of Sweden, though in certain localities of the Norwegian west coast it is one of the most characteristic forms of the littoral fauna. On the other hand, the Skagerrack coast is the home of certain littoral forms which occur but rarely on the coast of the North Sea. Thus on the west coast of Norway *Echinocardium cordatum* is seldom found, and then only in a few special localities, whereas in Bohuslän it seems to be one of the

¹ Théel, "Om utvecklingen af Sveriges zoologiska hafstation Kristineberg och om djurlifvet i angränsande haf och fjordar," *Arkiv. f. Zoologie*, Bd. iv., 1907.

commonest forms. *Ophiura ciliaris*, too, is far more plentiful in the Skagerrack, and the gasteropod, *Nassa reticulata*, occurs in quantities in the littoral zone of the Skagerrack, but is comparatively rare on the North Sea coast.

I have noticed also a difference between the fauna which patronises *Laminaria hyperborea* and the fauna associated with the two other species of *Laminaria*. It is only the first named with its stiff thick stalks which is densely crowded with attached forms, whereas the comparatively thin pliant stalks of the other two are either entirely neglected or only made use of to an inconsiderable extent, with the result that there are nearly always far more individuals in the *L. hyperborea* belt than in either of the other two laminaria communities.

I have already stated that the natural conditions prevailing on the different coasts affect the character of the fauna much more in the littoral zone than at greater depths. Where, for instance, there is nothing in the way of foundation for attached forms, we must expect to find a fauna more suited to another kind of environment. Thus on many North Sea coasts, where the long shallow shores consist merely of sand, like the "vader" of Schleswig and Holland, upon which the waves do not break with any violence, there are immense stretches where practically the sole inhabitants are the lug-worm (*Arenicola*), a tunnelling amphipod (*Corophium grossipes*), and one or two other forms. In such sandy stretches the fauna differs entirely from that found along rocky coasts, and only occasionally do we get attached forms where piles, stone quays, or other suitable foundations happen to occur. The animal life differs again on the sandy Danish coasts, which are unprotected by a line of outer islands, and are therefore exposed to the full force of the breakers, where the constant disturbance produced by the waves upon the sandy bottom is distinctly unfavourable to plant and animal life; consequently the upper littoral zone on such coasts rarely harbours many forms. On the other hand, at slightly greater depths, and in fjords or similar enclosed areas, we get the conditions requisite for the development of *Zostera* vegetation with its special fauna. We may see how much the topography of the bottom affects the development of animal life by studying the conditions on the Kattegat coast of Denmark; wherever reefs, overgrown by algæ, occur amidst the eelgrass, we may be certain of finding a fauna consisting of chitons, snails, bryozoans, and hydroid polyps.

The littoral fauna in the southern portion of the North Sea

comprises quite a number of shallow-water forms that are otherwise foreign to northern regions—Mediterranean immigrants which make occasional visits or have effected a permanent lodgment in comparatively limited tracts. Some of them I shall refer to later on, when dealing with the shallower portions of the North Sea. Their presence may be ascribed to hydrographical conditions, and in no way depends upon the topography of the bottom. To some extent the English Channel acts as a boundary between two littoral faunal areas, a fairly large number of Mediterranean forms living in the Channel but not venturing into the North Sea; while on the other hand several northern forms do not enter the Channel, these last being especially forms of Arctic origin. Many or probably most of the species are common to both areas, since the majority of the boreal species of the North Sea were originally immigrants from southern waters.

The sublittoral zone.

So far as the coasts of the boreal region are concerned the sublittoral zone does not vary much, though certain species from the continental deep-sea zone, which ascend to the sublittoral zone along the North Sea and Atlantic coasts of Scandinavia, are absent from large portions of the Skagerrack and Kattegat as well as from other coasts of the North Sea. They would seem to be forms whose distribution follows the Gulf Stream, and are therefore found mainly along the eastern coasts of the North Sea and Atlantic. They include the holothurian *Psolus squamatus*, the asterid *Pentagonaster granularis*, the gephyrean *Bonellia viridis*, the brachiopod *Waldheimia cranium*, and some mussels. *Munida rugosa*, which is one of the most characteristic decapods belonging to the sublittoral and deep-sea zones is, according to Théel, seldom met with on the Bohuslän coast of Sweden; the true corals and gorgonids of the deep-sea fauna, which elsewhere patronise the sublittoral zone, are much restricted in their distribution throughout the Skagerrack and wide tracts of the North Sea, and seem to be absent from the fjords of the Bohuslän coast. Certain forms, which along the coasts are chiefly sublittoral in their distribution, occur sometimes quite commonly in one area, whereas in another area they may be scarce or even entirely absent. For instance, on the Swedish and Norwegian coasts of the Skagerrack the spatangid *Brissopsis lyrifera* is generally met with in the sublittoral zone, but on the west or North Sea coast of Norway it is comparatively rare. The converse is the case with the

spatangid *Schizaster fragilis*, which is plentiful in the North Sea, but not found in the Skagerrack.¹

We propose now to discuss the fauna of the continental plateaus within the boreal region, dealing firstly with depths less than 100 metres,² and secondly with depths greater than 100 metres.

1. *Continental Plateaus covered by less than 100 Metres of Water.*—In the portion of the North Sea to the south of the Dogger Bank, where the waters are shallow and the summer temperature is high, there are southern forms unknown farther north, though this exclusively southern element in the fauna is very inconsiderable compared with the remaining boreal forms, some of which are more abundantly developed than in more northerly latitudes. During the cruise of the "Michael Sars" in 1904, I was able to carry out investigations with the dredge at a series of stations from the Danish coast to Scotland, in lat. 56° to 58° N. in depths between 14 and 100 metres, an area not previously systematically examined.

The southern and central areas of the North Sea.

The floor of the North Sea is for the most part covered with soft materials (sand, sandy mud, and clay), with areas of stony bottom in places, though even here the rocks and stones are nearly always mixed with softer materials. In some localities the soft materials contain masses of empty shells, which are invaluable to the animal life, acting as a foundation for the hydroids, bryozoans, and other attached forms. This mixed bottom supports a greater variety of forms than the soft bottom, offering suitable conditions to unattached forms, whether they burrow or not, as well as to attached forms.

The abundance of echinoderms characterises to a great extent the fauna of the North Sea. Among the star-fishes *Asterias rubens* occurs at all depths and upon every kind of bottom, though it seems less partial to soft clay bottom at considerable depths. *Astropecten irregularis* is met with everywhere, and the sea-mice *Echinocardium* and *Spatangus purpureus*³ are equally common. *Ophiura ciliaris* (see Fig. 347) may be described as the brittle-star of the North Sea, for we found well-developed specimens everywhere on mixed bottom down to a depth of about 100 metres, and at temperatures varying from 7° to 12° C., but

¹ The continental deep-sea zone not being represented, or only in very limited tracts, in the coastal areas of the Skagerrack, Kattegat, western and southern North Sea, a good many forms characteristic of that zone are absent here.

² As the type for this area we take the southern and central parts of the North Sea, those parts being the best explored.

³ In a trawling at 96 metres we found 500 specimens of the last named.

not on soft clay bottom ; all the individuals from stations in the open North Sea at considerable depths were very much lighter in colour and much larger than those taken along the Norwegian and British coasts. A good idea of the enormous quantities in which this form sometimes occurs was afforded by a haul with the dredge off Aberdeen, in 25 metres of water (temperature 10.26° C.), where they must have literally covered the bottom, and the same remark applies to the west coast of Jutland. In some localities we met with numbers of *Brissopsis lyrifera*, which prefers as a rule clay bottom in deep water at a tem-

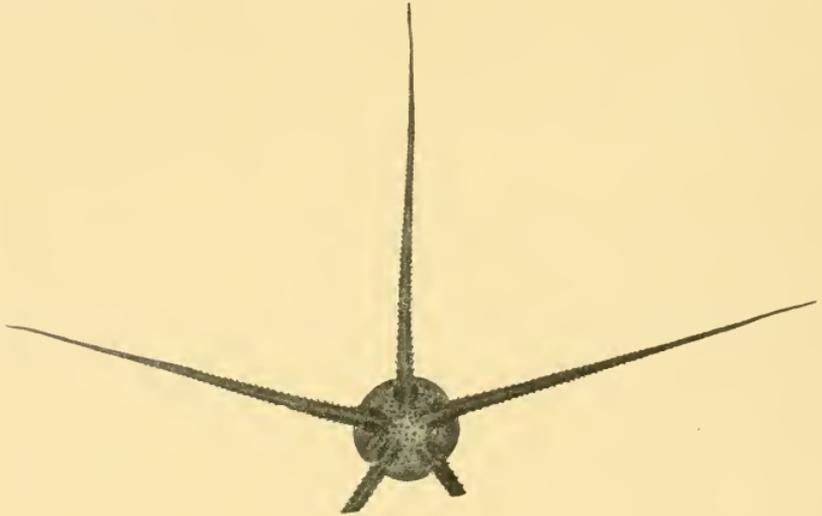


FIG. 347.
Ophiura ciliaris, L. Reduced.

perature of 6° or 8° C., though occasionally specimens may be found on sand. Everywhere, throughout the whole area examined, there were the two brittle-stars *Ophiopholis aculeata* and *Ophiothrix fragilis*, as well as the starfish *Luidia sarsi*, which are numerous here and there, but cannot be called characteristic forms. More local, though plentiful in places, were sea-slugs (*Cucumaria elongata*), which were met with at two stations, together with *Brissopsis*, on muddy bottom in about 50 metres, at a temperature of approximately 8° C.¹

¹ Of other echinoderms found at a few stations, in smaller quantities, I may mention *Ophiura albida* (only at one or two stations in the neighbourhood of the Danish coast and one station off Aberdeen in 25 metres) and *O. sarsi*, *Amphiura filiformis* (*chiajei* ?), *Ophiocten sericeum* (many young-stages in young-fish trawl east of Aberdeen in 62 metres, temperature 8.4° C., and also from the Norwegian depression), *Asterias mulleri*, *Solaster papposus* (only from the edge of the

Special mention must be made of specimens of our common sea-urchin *Echinus esculentus* from two stations in the North Sea: two specimens from 77 metres, temperature 7.1° C., and eight specimens from 96 metres, temperature 6.15° C. The species generally varies very little, and individuals from our littoral zone scarcely differ at all. Normally the shell is high and of a reddish colour, while the spines are violet. The ten specimens from the North Sea, however, all differed from the typical form, having a flattened shape and varying considerably in colour. The shell itself shows variations from the typical red hue to a chocolate brown, and the spines assume every intermediate shade from the most beautiful vermilion (like what we find in *E. elegans*) to pure green. Many specimens have in consequence an outward resemblance to *Strongylocentrotus* or *Echinus miliaris*. Mortensen has described from the North Sea (40 fathoms) two specimens of flattened shape with unusually long bright red spines (like those of *E. elegans*). Norman tells of a variety from deep water near the Shetlands that had very fine spines and an exceptionally high shell, and Sars has described a similar variety from the Great Edge.

These facts appear to justify the conclusion that, whereas in shallow water and along the coasts the species is of a fairly constant type as regards both shape and colour, it has a marked tendency to variation at greater depths, although the normal, or almost normal, form is to be found also in deeper water, as on the Faroe banks. The deeper portions of the North Sea in particular appear to produce very striking variations.

Of shell-bearing snails there are two forms which characterise the area investigated, namely *Neptunea antiqua* and *Sipho gracilis*, both species being met with everywhere from Denmark to the Scottish coast, and sometimes in great numbers.¹ Judging by our investigations *Neptunea* extends into shallower water than *Sipho*, though both species exist plentifully side by side at considerable depths. One biological peculiarity worth recording was that every individual of *Sipho* in the haul referred to had a sea-anemone (*Chondractinia digitata*) on its shell, and at other stations, too, they were found living together in symbiosis. These sea-anemones were likewise found on the

Norwegian depression, from the Danish coast, and east of Aberdeen in 62 metres), *Echinaster sanguinolentus*, *Strongylocentrotus dröbachiensis* (only from the Danish coast, one specimen with *Stylifer turtoni* on its shell), *Echinus esculentus* var., *Echinocyamus pusillus* (only east of Aberdeen in 62 metres), *Cucumaria lactea*.

¹ We secured 130 specimens of *Neptunea* and 375 of *Sipho* at one haul from a depth of 96 metres (temperature 6.15° C.).

shells of *Neptunea*, and on several specimens of this large snail two other large actinians (*Urticina crassicornis* and *Metridium dianthus*) had attached themselves. Our common whelk (*Buccinum undatum*, see Fig. 348) occurred over the whole area down to a depth of 100 metres, as a rule along with the two snails referred to, though never in such great abundance.¹

Nudibranchs yielded, with one or two exceptions, only a very few specimens, and this was particularly the case with *Tritonia*, *Doris*, and *Doto*. At certain stations, however, remarkably enough from muddy bottom where there were no hydroids, the young-fish trawl brought up quantities of

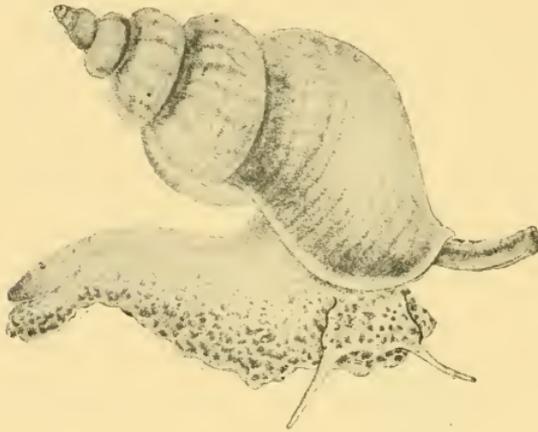


FIG. 348.
Buccinum undatum, L.

Æolis, which had most probably located themselves upon *Virgularia* and *Alcyonium*, although their usual home is among hydroids. *Chato-derma*, a worm-like form belonging to the molluscs, was represented by only a few specimens (depth 47 to 80 metres, temperature 7° to 8° C.); cuttle-fishes by some specimens of *Loligo forbesi* at one station

(depth 38 metres, temperature 10° C.), and a little *Sepiolo* from 94 metres. The almost complete absence of species of *Chiton*,

¹ Of more or less regularly distributed mollusc-forms we may further mention: *Pecten opercularis* (large), *Mytilus modiolus* (from a depth of 96 metres about 70 specimens were taken, averaging 11 or 12 cm. in length and often with *Urticina* attached), *Modiolaria nigra*, *Cardium echinatum*, *Cyprina islandica*, *Venus gallina*, *Mactra elliptica* (very numerous off the coast of Jutland, 14 metres, temperature 12.5° C.), *Solen ensis*, *Cultellus pellucidus*, *Aporrhais pes-pelecani*, *Antalis entalis*. At some stations we came across *Nucula tenuis*, *Leda minuta*, *Kellia suborbicularis*, *Corbula gibba*, *Dosinia lineta*, *Cylichna cylindracea*, all on mud in about 50 metres and at a temperature of 8° C. *Astarte sulcata* was extremely numerous at one station (depth 86 metres, temperature 8.4° C.), but otherwise very scattered. Also *Nicania banksi*, *Pectunculus glycymeris*, *Mactra stultorum*, *Psammobia ferröensis*, *Panopea norvegica* (large specimen, 80 mm. long, 55 mm. high), *Saxicava arctica*, *Pholas crispata* (in pieces of timber on the bottom, depth 32 metres, temperature 10.9° C.), *Abra* sp., *Montacuta* (on *Spatangus*), *Philine* sp., *Velutina levigata*, *Lunatia intermedia* (in enormous quantities at Jammer Bay off the coast of Jutland, 14 metres, together with *Mactra elliptica*, on which latter, judging from the many shells with holes bored in them, it feeds), *Lunatia montagui*, *Natica catena* (strings of eggs were found in large quantities on the north slope of the Dogger Bank, though the animal itself was rarely captured), *Boreofusus bernicciensis*, *Scalaria trevelyana*, *Volutoopsis norvegica* (only at one station, depth 96 metres, temperature 6.15° C., though in fairly large quantities—about 30 specimens).

notwithstanding the apparently suitable bottom of stones and shells, is very remarkable, a few specimens of *Lepidopleurus* (*Chiton*) *cinereus* at one station (57 metres, temperature 7.9° C.) being all that we met with.

The bottom of the North Sea abounds, as already stated, in empty shells, particularly of mussels. The commonest forms are *Cardium echinatum*, *Cyprina islandica*, *Venus gallina*, *Dosinia lincta*, *Mactra*, *Psammobia ferröensis*, *Solen*, etc., all of which were likewise taken alive. *Lucina borealis*, on the other hand, though shells were met with here and there at a depth of 38 to 98 metres, sometimes even in fairly large quantities, was not captured alive out in the North Sea by us, and the "Pomerania" Expedition obtained only empty shells on the Dogger Bank; it is not included by Heincke amongst the molluscs of Heligoland, but we do find it along the coasts of Britain and in the Skagerrack. Empty shells of *Mya truncata* forma *typica* were also found in two localities, one at a depth of 14 metres off the north-west coast of Jutland, and the other midway between Jutland and Scotland at a depth of 68 metres.

The higher crustacean fauna is comparatively poor in species, most of them being restricted in distribution and few in numbers. The hermit crabs *Pagurus bernhardus* and *P. pubescens* are exceptions, as they are pretty generally distributed over the whole area, though only the first named is met with in shallow water, at or below 40 metres; at greater depths both species occur, as in some other areas of the North Sea. Of crabs *Hyas coarctatus* is common in both deep and shallow water, whereas *Portunus depurator* (or *holsatus*?) and *P. pusillus* are more limited in their distribution, and occur mainly in the lesser depths. Other forms are more local, though frequently met with in considerable numbers, like the little *Porcellana longicornis*; as a contribution to its biology I may mention that we found large numbers at two stations (depth 32 metres and 42 metres, temperature 10.9° C. and 8.7° C.), where in one case it had crept into the holes made by the borer-mussel (*Pholas crispata*) in sunken pieces of timber and in the other it occupied cavities in the large clotted lumps of sand constituting the colonies of the tube-worm *Sabellaria alveolata*. At greater depths it was absent, *Porcellana* being to a great extent a littoral form.¹

¹ We also found two other crabs in shallow water west of Jutland (32 metres): the ordinary edible crab (*Cancer pagurus*) and *Hyas araneus*. Single specimens of two species of *Ebalea*

The stone crab (*Lithodes maja*, see Fig. 349) was met with only in the deeper parts where the temperature was lower (77 metres and 96 metres, temperature 7.1° C. and 6.15° C.), as in the deep parts of the Norwegian fjords. The whole central portion of the North Sea proved remarkably poor in shrimps (caridids) though the few species present were frequently in considerable numbers.¹

The ordinary wide-meshed appliances (trawls and dredges) undoubtedly give a good idea of the larger bottom-forms composing the fauna, but are less satisfactory when the fauna consists mainly of small crustaceans, for which we found the young-fish trawl extremely useful, as by its means we secured

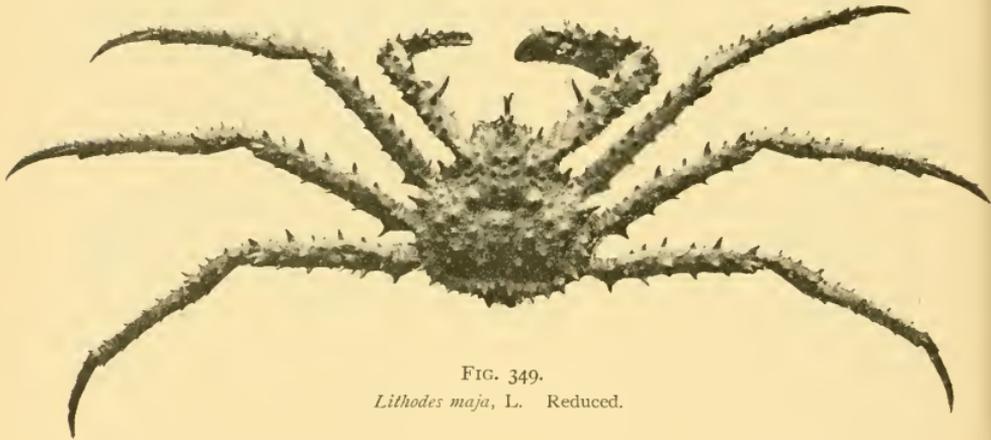


FIG. 349.

Lithodes maja, L. Reduced.

the large numbers of young crangonids already referred to, besides quantities of lower forms of crustaceans, especially amphipods, cumaceans, etc., and larvæ of higher crustaceans, particularly hermit crabs. Even these, however, occur locally,

(*E. cranchi* and *E. tuberosa*) were obtained at depths from 47 metres to 86 metres, with temperatures of 8° to 8.4° C. We also obtained specimens of the crabs *Inachus dorsettensis* and *Stenorhynchus rostratus*, and a single specimen of *Atelecyclus septemdentatus* was taken in the neighbourhood of the Scottish coast in 62 metres at a temperature of 8.4° C. At one station on the coast of Jutland (32 metres, temperature 10.9° C.) the crab *Corystes cassivelanus* was common, but it was quite absent in the central portions. *Galathea dispersa* and *G. intermedia* were got at some stations.

¹ We found, for instance, numerous specimens of a little crangonid (*Cheraphilus nanus*) at a depth of 78 metres, temperature 7° C., a number of individuals belonging to a form related to the common shrimp, *Crangon allmanni*, and *Pandalus annulicornis*. At a station near the Scottish coast, that is to say in the western portion of the North Sea, at a depth of 86 metres, temperature 8.4° C., we found in addition to small specimens of the two last-mentioned forms, of which *Crangon* was in myriads, several specimens of another shrimp (*Hippolyte securifrons*), which is also met with on the eastern side, but not at corresponding depths in the central portion.

being extremely numerous in certain localities and absent in others; no doubt the currents at the bottom are responsible for this, seeing that the depth and temperature are in themselves entirely favourable. These enormous quantities of small crustaceans must have an appreciable influence upon the shoals of fishes, and in particular upon the young fishes, and this I have been able to confirm by direct observation. On the northern slope of the Dogger Bank we captured a number of young whittings and flounders with the trawl at a depth of 38 metres (temperature 10° C.), and their stomachs at first sight seemed to contain only sand, but closer investigation revealed small amphipods (sand-hoppers) which thus formed their principal nourishment, the sand being swallowed simultaneously with them; the stomachs of the larger fishes generally contained hermit crabs and swimming crabs (*Portunus*). The caprellids seemed to be especially associated with a bottom overgrown with hydroids, and were found only exceptionally where hydroids were absent.¹

The central portion of the North Sea is poorly supplied with pycnogonids (sea-spiders), there being only one widely distributed form (*Pycnogonum littorale*), and it was only found in deep water (80 to 100 metres) at low temperatures (6° - 7° C.), where I sometimes found it, as described by Sars, clinging to large sea-anemones (*Urticina crassicornis* and *Metridium dianthus*), into the skin of which it bores its proboscis for sucking; a solitary specimen of *Nymphon strömi* was the only other pycnogonid found in deep water.

The ascidians (sea-squirts) are also poorly represented; the monascidians (simple sea-squirts) were not very conspicuous anywhere in the area examined, but we got large and well-developed specimens of *Ciona intestinalis* in about 80 metres (tempera-

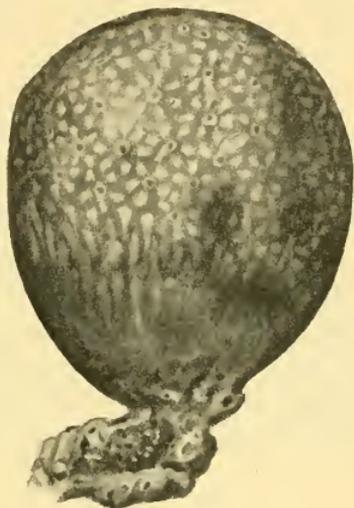


FIG. 350.

Macroclinum pomum, M. Sars.

¹ The commonest is *Caprella linearis* (it seems difficult to discover any invariable difference between this species and *C. septentrionalis*), but stray specimens occur of *Proto pedata*, mainly found along the edge of the Norwegian depression, at a depth of about 100 metres, and one individual of *Protella phasma* was captured at 77 metres, temperature 7.33° C.

ture about 7° C.), whereas along the Norwegian coasts it is chiefly found in quite shallow water, where it attains its fullest development. *Asciidiella virginea* and *Styela loveni* were fairly widely distributed. A large globular compound ascidian (*Macroclinum pomum*, see Fig. 350), although very local, was at times very plentiful.

The attached fauna, which, properly speaking, includes the sea-squirts, is mainly represented by three groups: sponges, hydroids, and bryozoans, the two last forming occasionally regular little forests. On the northern slope of the Dogger Bank (depth 38 metres, temperature 10° C.) there were considerable quantities of large bush-like colonies of two species of bryozoans (*Flustra securifrons*, see Fig. 351, and *Alcyonidium*

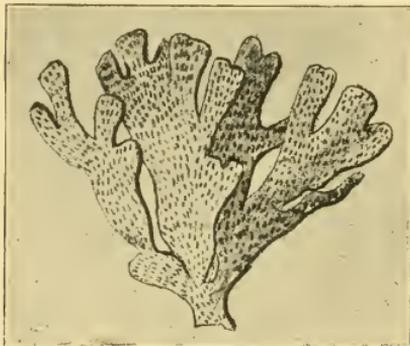


FIG. 351.
Flustra securifrons, Pallas.

gelatinosum), which, with *Flustra foliacea*, are the most characteristic of the North Sea bryozoans; they vary in relative abundance, but on the Great Fisher Bank *Flustra foliacea* appears to be the predominant form. Small bryozoans, sometimes occurring in large quantities, are found growing on the bigger species or on other substances.

Hydroids are distributed over the whole area examined wherever the bottom is suitable, especially where it is covered with empty shells or stones. They sometimes form "communities," but are as a rule scattered about here and there. *Tubularia larynx* is occasionally met with in enormous quantities, and there are sometimes "communities" of *Thujaria thuja* (see Fig. 352), *Hydrallmannia falcata*, *Campanularia longissima*, and *C. verticillata*. The species of *Dicoryne* and *Hydractinia* are very often found on shells inhabited by hermit crabs.¹ The hydroids in the central portion of the North Sea differ to a certain extent from those found in the northern portion or on the other plateaus. *Thujaria* and *Hydrallmannia* are, however, common to both areas.

Among cœlenterates there are really only two forms, if we

¹ *Dicoryne conferta*, *Hydractinia echinata*; other species commonly found in the North Sea are *Campanularia johnstoni*, *Plumularia pinnata*, *Lafœa dumosa*.

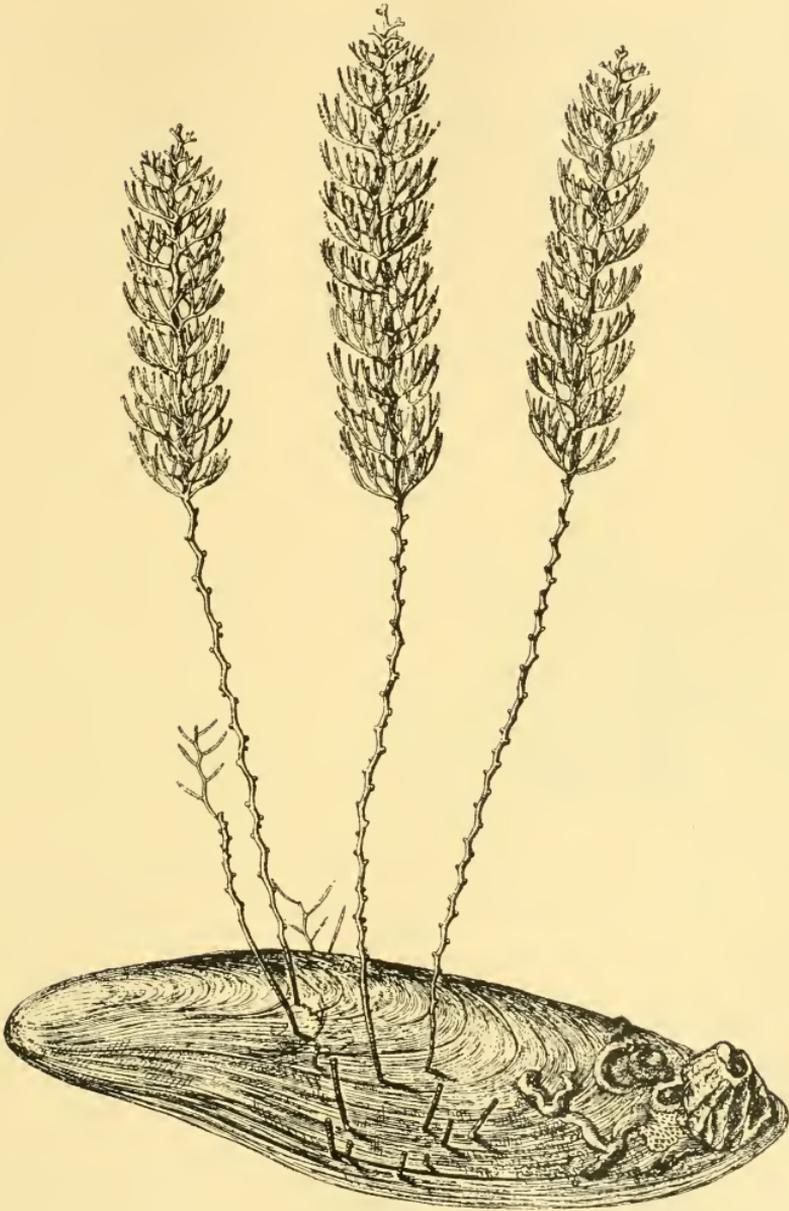


FIG. 352.

Thujaria thuja, L. (After Hincks.)

except the sea-anemones already referred to,¹ which are universally distributed over the central portion of the North Sea, namely dead-men's fingers (*Alcyonium digitatum*) and the sea-pen *Virgularia mirabilis*. The former generally consists of irregularly shaped ramifying masses attached by the base to other substances, but in the area examined by the "Michael Sars" during 1904, in depths between 38 and 96 metres, temperature 10° to 6.15° C., there was an interesting variation in its relation to its foundation. An annelid (*Sabella pavonia*), commonly met with here, inhabits an upright muddy tube attached at the lower end. The whole length of this tube was covered by the dead-men's fingers, which in some instances grew out from the lower end of the tube into the usual irregularly ramifying masses. This symbiosis was no fortuitous occurrence, but was invariable throughout the whole of the central portion of the North Sea where these two forms are everywhere to be found.² On the coasts of Scotland and Jutland, on the other hand, *Alcyonium* occurred in its ordinary form. The common *Virgularia mirabilis*, found at depths of 50 to 100 metres, with a temperature of 7°-8° C., was the only sea-pen met with in the area examined, but we obtained a fairly large number of individuals.

Sponges constitute a group of attached forms abounding in individuals, though remarkably poor in species; they cannot be said to be regularly distributed, but are more or less local. On the north side of the Great Fisher Bank in particular we got enormous quantities of a ramifying whitish form (*Halichondria panicea* var. *bibula*).³ The different variations of *Ficulina* (*Suberites*) *ficus* are, however, the most prevalent. The commonest of these variations, where the sponge grows round shells and gives shelter to the hermit crab *Pagurus pubescens*, are comparatively scarce in the central portion of the North Sea, and we came across them at only one or two stations, but in the more northern parts of the North Sea plateau they were plentiful. Another variety, attached to empty shells of the sea-tooth (*Antalis entalis*) which as a rule shelter the gephyrean *Phascolosoma strombi*, was abundant at

¹ *Urticina crassicornis*, *Metridium dianthus*, chiefly found on large shells of *Mytilus modiolus* and *Neptunea*, *Bolocera tuediæ* and *Chondractinia digitata* on shells of *Neptunea* and *Sipho*; at one or two stations (depth about 100 metres, temperature slightly over 6° C.) we got *Zoanthus*.

² Several of these overgrown tubes were empty, which looks as if the worm benefited least by the symbiosis.

³ Thanks to information kindly sent me by Professor Plate, Berlin, I can add *H. panicea* forma *typica* as being common on the Great Fisher Bank; this form was also abundant on the northern slope of the Dogger Bank.

several stations, for instance on the northern slope of the Dogger Bank (38 metres) and north-west of the Great Fisher Bank (77 metres).

The little tube-worm *Filigrana implexa*, whose slender white irregular tubes are associated in trellis-work colonies, was met with over a large portion of the area examined, but only in the deeper parts. Another common form is *Thelepus circinnatus*, whose sinuous, parchment-like tube, covered with fragments of shells, grains of sand, etc., is attached to foreign substances such as empty mussel-shells, *Flustra*, etc. The annelid *Aphrodite aculeata* is characteristic of the North Sea, but is as a rule limited to the deeper parts with soft or "mixed" bottom, though nowhere found in any great quantity. I have already stated that *Sabella pavonia* is common,¹ and, speaking generally, we may say that as far as worms are concerned the central portion of the North Sea does not differ typically from the boreal portion of the Norwegian Sea.

One peculiarity of the deeper parts of the central North Sea is that on soft bottom there is an absence of the foraminifera so plentiful in the Norwegian fjords; this I can assert after examining very minutely the contents of the fine sieves through which the bottom-material was passed.

It has been mentioned that in the southernmost portion of the North Sea, off the coasts of Belgium, Holland, and south-eastern England, there are many forms of southern origin, which are absent in more northerly latitudes; some of them, however, find their way farther north than the others, though all keep to shallow waters with high temperatures. This is, for

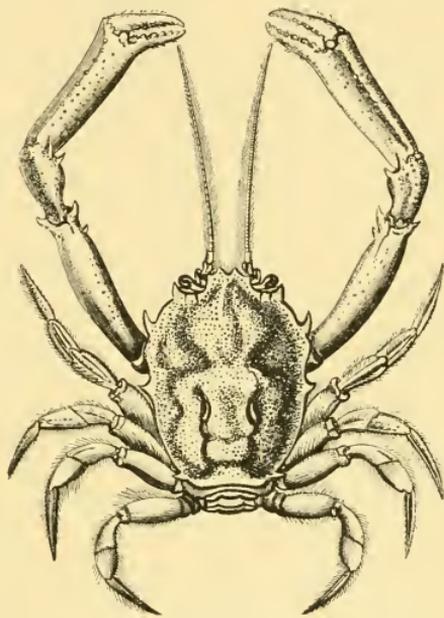


FIG. 353.

Corystes cassivelanus, Mont. ♂ Reduced. (After Bell.)

¹ On deep soft bottom we found representatives of the Maldanidæ, as well as *Eumenia crassa*, *Trophonia glauca*, *Lumbrineris*, and *Nephtys*, which we also find on the coasts.

instance, the case with the crab *Corystes cassivelanus* (see Fig. 353), the mussel *Macra stultorum*, the shelled snail *Natica catena*, and the tube-worm *Sabellaria alveolata*, all of which were found west of Jutland to the north of lat. 56° N. The last mentioned was met with at only one station (depth 41 metres, temperature 8.7° C.), but in large quantities and big colonies; while the other three were taken in shallow water (less than 40 metres) with the highest temperatures observed during the cruise (10° to 12° C.). The characteristic ribbon-like egg-clusters of *Natica* were found as far out as the northern slopes of the Dogger Bank, where the animal itself had been previously captured. According to Professor Plate both *Natica catena* and *Macra stultorum* occur on the Great Fisher Bank, which shows that these forms do sometimes leave the coast region. On the other hand, *Corystes* seems exclusively to follow the coasts of Britain and Denmark, since we did not capture it with our trawl on the Dogger Bank, though depths and temperatures appeared to be favourable, and it has not been recorded at any great distance from the coast. These forms are found along the shores of Britain, and penetrate into the northern part of the Kattegat, but, if we except *Macra stultorum*, they do not reach the coast of southern Norway.

Our knowledge regarding the faunal character of the North Sea may be briefly recapitulated as follows: In the southernmost portion, at depths down to 40 or 50 metres, where the water-layers in summer attain a temperature of 13° - 15° C., but in winter are cooled down to 4° or 5° C., the fauna consists partly of northern elements capable of adapting themselves to variations of temperature, and partly of a special southern contingent that has wandered in through the English Channel and requires high temperatures for at any rate part of the year. Most of these latter forms are limited to the southernmost portion, though a few follow the coasts towards the north, penetrating on the east side even to the Skagerrack, and on the west side to the coasts of Northumberland or perhaps still farther, but avoiding the deeper parts of the central area. The northernmost portion of the plateau, where the depths exceed 100 metres, but where, notwithstanding, the waters are warmer than in the central parts, is characterised in similar fashion, as we shall presently show, partly by special southern deep-water forms that have wandered in past Shetland and only very rarely get as far as the coast of Norway or the Skagerrack, and partly by forms which may either have arrived originally from the

south, or else are true natives, nowadays at any rate widely distributed throughout the northern seas. Most of the forms met with in the central portion are also to be found along the coasts, but numbers of forms frequenting the coasts, especially shallow-water forms, do not inhabit the plateaus.

We have not at present sufficient information to describe in detail other plateaus in depths less than 100 metres. The "Michael Sars" occupied two stations in 50 to 100 metres, off south-eastern and south-western Norway, where the fauna did not appear to differ from that in the outer part of the fjords and in the island belt. Certain forms (for instance *Balanoglossus*, taken off Risør on the south-east coast) have, however, not been taken in the western fjords nor in the central North Sea, but they have been recorded from the west coast of Sweden (Bohuslän). At the localities mentioned we were able to observe the remarkable fact that certain forms (for instance *Echinus esculentus*, *Asterias rubens*, *Ophiothrix fragilis*) occur in comparatively deep water, while in the fjords and island belts they generally occur in the littoral zone only.

The investigations of C. G. J. Petersen in the Skagerrack show, as far as we can judge from his short statements, a marked similarity to the conditions prevailing in the North Sea. At present it is impossible to enter into a detailed account, and we can only state that along with the similarity there are certain discrepancies: thus, for instance, the pennatulid *Pennatula phosphorea* has not been captured by the "Michael Sars" in the central North Sea, but it is frequent on the Norwegian North Sea plateau and in the Kattegat.

2. *Continental Plateaus covered by more than 100 Metres of Water.*—The different lands bounding the Norwegian Sea and North Sea form the emerged portions of larger or smaller submarine plateaus. The bottom on these plateaus varies considerably, though, generally speaking, it may be described as a mixture of stones and rock together with fine or coarse sand; only exceptionally, and in the deeper portions, is it composed of mud. The character of the bottom renders investigations extremely difficult, and the fauna is therefore not so well known as that of the fjords. Where the bottom is covered with softer material the fauna resembles that of the fjords. This is particularly the case in the Norwegian depression or gut, running parallel to the Norwegian coast from the latitude of Stat to the Skagerrack. The depth in the middle averages

approximately 300 or 400 metres, till we come to the inner portion of the Skagerrack where it increases to about 700 metres. The bottom consists of soft mud throughout, except for a long narrow strip of stones and rock that penetrates its north-eastern portion. On the one side the depression is bounded by the Norwegian coast-plateau, which is here only a few miles wide, and on the other side by the plateaus of the North Sea and Skagerrack.

During the cruise of the "Michael Sars" in 1902 investigations were made with the trawl and dredge in its northern portion, the principal forms found being as follows:—

Echinoderms: *Stichopus tremulus* (in quantities), *Bathyplores tizardi*,¹ *Cucumaria hispida*, *Myriotrochus vitreus*, *Amphiura norvegica*, *Ophiocolex glacialis*, *Ophiura sarsi*, *Asteronyx loveni* (on *Funiculina*), *Schizaster fragilis*, *Brissopsis lyrifera*, *Spatangus raschi*, *Psilaster andromeda*, *Pontaster tenuispinus*.

Crustaceans: *Pontophilus norvegicus*, *Pandalus bonnieri*.

Ascidians: *Ascidia obliqua*.

Molluscs: *Abra longicallis*, *Malletia obtusa*, *Portlandia lucida*, *Axinus flexuosus*, *Pecten septemradiatus*, *Sipho islandicus*, *Scaphander punctostriatus*, *Antalis agilis*, *Siphonentalis tetragona*, *Cadulus subfusiformis*.²

Worms: *Lumbrineris fragilis*, *Letmonice filicornis*, *Aricia* sp., *Terebellides strömi*.

Gephyreans: *Sipunculus priapuloides*.

Cœlenterates: *Bolocera tuediæ*, *Actinostola callosa*, *Kophobelemnion stelliferum*, *Funiculina quadrangularis*, *Ulocyathus arcticus*.

Sponges: *Thenea muricata*.

Also the foraminifera *Astrorhiza* and *Rhabdammina*, though these are not numerous.

These animal forms make it tolerably certain that the fauna in the Norwegian depression is practically identical with the Atlantic fauna in the boreal region of the Scandinavian peninsula, and closely resembles the fauna of the western fjords of Norway. Petersen's researches have revealed similar conditions in the deepest portion of the Skagerrack. But along with the fjord forms, which exceed the others in numbers, there is a fauna in the Norwegian depression composed of forms seldom or never occurring among the skerries and in the fjords, but having their home on the plateaus of the open sea.³

¹ On the other hand, *Mesothuria intestinalis* has not been found by the "Michael Sars" nor by other Norwegian and Danish Expeditions.

² This species was found by the Norwegian North Atlantic Expedition.

³ To this fauna I assign the following forms:—Echinoderms: *Spatangus raschi*, *Pontaster tenuispinus*; Molluscs: *Sipho islandicus*, *Antalis agilis*; Crustaceans: *Pandalus bonnieri*; Cœlenterates: *Ulocyathus (Flabellum) arcticus*.

In the depression these are all common enough to be regarded as an essential part of the fauna. *Spatangus raschi*, for instance, appears never to approach the coasts or to enter the fjords, but keeps to the deeper parts of the plateaus where it takes the place of *Spatangus purpureus*; it has also been found by the "Michael Sars" on the continental slopes south of the Faroe Islands. *Pontaster tenuispinus* only exceptionally enters the fjords of West Norway to the south of Stat, though it is found now and then in the Trondhjem fjord, and during the cruise of the "Michael Sars" in 1902 it was found at the mouth of the Sulenfjord near Aalesund.¹ *Antalis agilis* and *Pandalus bonnierii* are only met with occasionally in the fjords,² and *Ulocyathus arcticus* belongs to the forms which do not enter our more southerly enclosed fjords, but may be met with in the more open northern fjords as far as the North Cape; it has also been found, according to Norman, on the Shetland plateau.

All or most of the forms enumerated as belonging to both the fjords and the plateaus, as well as those which chiefly or exclusively belong to the plateaus, may be met with as far north as Lofoten, and probably extend to the North Cape. The Norwegian North Atlantic Expedition came across many of the forms that inhabit the Norwegian depression and fjords in deep muddy hollows on the plateau north of Stat, and some of the forms occur on muddy bottom upon the outer slopes of the continental edge wherever the temperature is above 0° C.

One peculiarity of the Norwegian depression still remains to be mentioned, namely that a deep trench extends along the north-eastern side to about the latitude of the Sogne fjord, approximately 400 metres deep, where experiments with lines revealed a true hard-bottom fauna of corals (*Paragorgia*, *Primnoa*) and sponges; the "Michael Sars" found this to be the case in several places in the trench.³ It is strange that this deeper portion is not full of mud like the adjoining shallower parts, since usually we find a reversed state of things, hard bottom rising up out of the

¹ *Pontaster tenuispinus* is found in two variations of colour, namely a rather pale form of weak structure, which belongs exclusively to the warm area, and a deep-red form much more stoutly built, which as a rule seems to belong to cold areas, though reddish individuals of weak structure occur also in warmer waters.

² A good many individuals of *Pandalus bonnierii*, which used to be regarded as rare, have lately been found in the Norwegian depression and in the fjords north of Stat. It is of interest to state that the Danish research vessel "Thor" has found large quantities off South Iceland. It has also been discovered in the fjords near Bergen during certain years in varying quantities.

³ Large well-developed colonies of *Lophohelia prolifera* were found on the plateau near Stat, together with other forms that are characteristic of such localities.

surrounding mud, and we can only conclude that the bottom here must be scoured by the action of currents.

Some very interesting discoveries were made by the "Michael Sars" in 1904 in a southern part of the depression between lat. 58° and 59° N., at a depth of 292 metres, the temperature being 5.83° C., where the young-fish trawl brought up a quantity of amphipods, cumacea, *Euchæta norvegica*, etc. Among these forms there were two that were particularly noticeable, namely *Epimeria loricata*, of which there were many specimens, full-grown as well as young, and *Acanthozone cuspidata*, of which there was one young specimen. Both these species were hitherto only known to exist in more northern latitudes, the former not having been met with to the south of the Malangen fjord, and the latter not south of the Trondhjem fjord, where several other arctic forms have their southern limit.¹

The faunal conditions on hard bottom and on sand at the upper part of the Norwegian depression, from about 100 metres down to considerable depths, are very like those in the Norwegian fjords, but differ in many respects from those of the central parts of the North Sea. The sponges resemble those taken on hard bottom in the deep parts of the fjords. Among the hydroids there was *Sertularella gayi*, a form that is absent from the central portion of the North Sea, but is one of the commonest deep-water hydroids of the fjords. *Crangon allmanni* and *Pandalus annulicornis* again were represented only by young individuals in the central portion, whereas at the edge of the depression our appliances brought up numbers of full-grown specimens. Other forms that we failed to find in the central area, but which occurred on the edge of the Norwegian depression, were: *Hippasterias plana*, *Solaster endeca* and *S. papposus*, *Antedon* sp., *Psolus squamatus*, *Nymphon strömi* (of which we secured only one solitary specimen in the central portion, in spite of repeated trawlings and dredgings, though quite common on the edge of the depression), *Crania anomala* (common), *Porella* (characteristic of hard bottom in the fjords), as well as one or two other bryozoans, *Scaphander punctostriatus*,

¹ The following are a few of the other forms taken at the same time, showing that the boreal fjord and plateau forms occurred together; several of them are met with in the arctic region, and may perhaps be of arctic origin:—Amphipods: *Epimeria cornigera*, *Pardalica abyssii* (in quantities), *Lilljeborgia fissicornis*, *Rhachotropis* (two or three species). Cumacea: *Eudorella emarginata*, *Camphylaspis verrucosa* and *C. horrida*, *Hemilamprops cristata*. Isopods: *Apsceudes spinosus*, *Munnopsis typica*, *Rocinela dammoniensis*. Decapod crustaceans: *Pontophilus norvegicus*, *Pandalus bonnierii*, *Hippolyte polaris*, *Bythocaris simplicirostris*, *Caridion gordonii*. Molluscs: *Rossia* sp., *Torrellia vestita*, *Portlandia tenuis*, *Pecten hoskynsi*, *Cardium minimum*. Echinoderms: *Ophioscolex glacialis*, *Antedon tenella*. Worms: *Filigrana inflexa* (in quantities).

etc. It must, however, be clearly borne in mind that there were many forms common to both areas,—partly those which belong to the entire boreal region, and partly those which are exclusively or nearly always found on the plateaus.

As already stated, the bottom on the plateaus rarely, and as a rule only in deep hollows, consists of soft mud, being for the most part coarse or fine sand, sandy mud, stones, and rocks. The stony bottom usually predominates near the outer limits of the plateaus, or continental edge. Investigations by Rasch in 1844 and by Sars in 1871 made it clear that large round stones and pebbles are to be met with on the Great Edge to the west of Aalesund at a depth of about 200 metres, and the "Michael Sars" also found round stones and pebbles there, as well as on

Fauna of the
continental
edge.

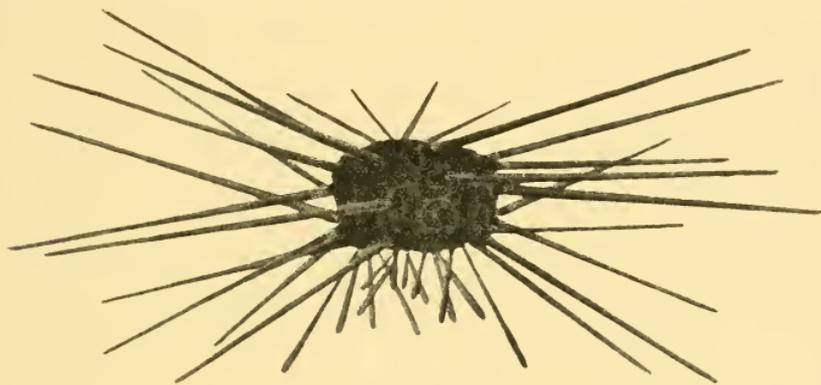


FIG. 354.
Dorocidaris papillata, Leske. Reduced. (After Düben and Koren.)

the rather less sharply defined edge of the Faroe plateau; in the latter locality the dredge brought up from a depth of about 400 metres a mass of loose round stones.

The character of the fauna on the edges of the boreal plateaus, judging from what we have found on the Faroe and the Norwegian plateaus, is fairly uniform. Owing to the nature of the bottom we meet with attached forms, particularly sponges (for instance *Oceanapia robusta*), hydroids, corals, brachiopods, and bryozoans, together with a number of unattached forms, of which the echinoderms are the most characteristic. Among brachiopods we get *Crania anomala*, *Terebratulina caput-serpentis*, *Waldheimia cranium*, and *W. septata*, the last of which inhabits the plateaus of the open sea and never or only exceptionally enters the fjords. The same is the case with several echinoderms: *Dorocidaris papillata* (see Fig. 354),

for instance, easily recognisable owing to its long thick spines, is one of the most characteristic forms of the plateaus and especially of the edges, but hitherto not found within the fjords; a characteristic brittle-star, *Gorgonocephalus lamarcki*, is also a plateau form, represented within the fjords by *Gorgonocephalus linckii*. One species of *Echinus* (*E. acutus* forma *norvegicus*) is often found in quantities, and far exceeds the fjord form in size. There are also the following brittle-stars, some of which are found in large quantities: *Ophiacantha abyssicola* and *O. bidentata*, *Ophiactis abyssicola*, all three of which are pure coast forms that do not go far up the fjords,¹ *Ophiopholis aculeata*, *Ophiura sarsi*, *Ophioscolex glacialis*, and *O. purpurea*, which are commonly found on the edges and are also fjord forms. During a cruise of the "Michael Sars" in 1902, the lines on the Faroe Edge yielded a large number of molluscs (*Sipho glaber*, or a very similar form), which attached themselves to the bait, but they seem to occur in such abundance only in a few localities. The tubeworm *Placostegus tridentatus* is frequently found attached to the stones, and a deep-water barnacle (*Verruca strömi*) also, both of them being characteristic of the rocky bottom in the deep parts of the fjords; and on the spines of *Dorocidaris* there is now and then a *Scalpellum*. There are large quantities of the little mussel *Anomia*, which is also commonly found in the fjords. Corals, too, are found locally on the edges just as much as in the fjords, and the species are the same.²

The spaces between the stones are filled with sandy mud, so that the forms accustomed to soft bottom may be found there. How many of the characteristic species occur on the edges cannot be stated with certainty, but probably many, if not most, of the forms belonging to the soft bottom of the plateaus inhabit the edges also, though not in such great abundance.³

My reason for mentioning the fauna of the plateau-edges separately is, not that the forms constitute a separate faunal

¹ This is true of the Norwegian fjords south of Stat, though these species, like several others, have been found in the Trondhjem fjord.

² The dredge brought up branches of *Primnoa*, *Paragorgia*, *Paraspongodes*, *Lophohelia*, and *Amphihelia*; also *Sertularella gayi*, *Allopora*, sponges, masses of *Ophiacantha bidentata*, *Ophiacantha abyssicola*, *Ophioscolex purpurea*, *Ophiactis abyssicola*, *Gorgonocephalus*. Deep-sea individuals of *Echinus esculentus* were found both by Sars and by the "Michael Sars" in 1906, though as a rule they differed in shape from those found in the middle of the North Sea.

³ Of the forms found by G. O. Sars, by the Norwegian North Atlantic Expedition, and by the "Michael Sars" on the Great Edge and its northerly continuation, as well as by the "Michael Sars" on the Faroe Edge, we may mention *Stichopus tremulus*, *Spatangus raschi*, *Echinocyamus pusillus*, *Schizaster fragilis*, *Astarte sulcata*, *Poromya granulata*, *Limopsis minuta*, *Onuphis*, *Nephtys*, and other annelids, etc.; all these forms belong to soft bottom.

region,—though, probably owing to the influence of currents, forms like *Dorocidaris* and *Waldheimia septata* seem to find their most favourable conditions of existence there, and consequently are extremely abundant,—but because the plateau-edges are the limits of distribution between the fauna inhabiting the plateaus and the totally distinct fauna of the deep central basin of the Norwegian Sea known as the “cold area.” To avoid misunderstanding I may repeat that on the steep slope below the actual edge, and down to a depth of 600 or 800 metres, that is to say, to a depth where the temperature does not fall below 0° C., forms belonging to the boreal fauna may be met with. Still these slopes are as a rule so precipitous in comparison with the wide plateaus that, topographically, one is almost entitled to look upon the edges as a boundary region. The bottom of the slopes below the edge itself seems to consist nearly everywhere of soft mud dotted over with large-sized stones, thus providing a home for both mud-bottom forms and hard-bottom forms.

I have stated that we are still only imperfectly acquainted with the fauna on the bottom of sand and stones upon the plateaus, as only a few systematic investigations have been undertaken here and there. But we know enough to conclude that from a zoo-geographical point of view it is similar to that of the muddy bottom, consisting partly of forms that are common to both the plateaus and the fjords, and partly of forms peculiar to the plateaus which do not enter the fjords. The latter, however, like the corresponding forms of the muddy bottom, are comparatively few. This is confirmed by some dredgings made by the “Michael Sars” in 1906, when researches were carried out on several parts of the Norwegian plateau.

Fauna of the
plateaus.

Without attempting a full description of the lower animal-forms on the plateaus, we may refer to a few of the principal ones. Several hauls by the “Michael Sars” with the trawl in 1902 and 1906 showed an abundance of animal life in the northern portion of the North Sea Plateau, on hard sandy bottom (probably mixed with small stones) at depths of 150 to 200 metres, belonging to both fjord forms as well as plateau forms:—

There were numbers of *Spatangus* (especially *S. raschi* in the greater depths), *Echinus acutus* forma *norvegicus*, and *Dorocidaris papillata*, forms characteristic of the edges, also considerable quantities of *Asterias rubens*, *Porania pulvillus*, *Goniaster borealis* (?), *Echinaster sanguinolentus*, *Pontaster tenuispinus*, *Stichaster roseus*, *Hippasterias phrygiana* (*plana*),

Ophiopholis aculeata, *Ophiothrix fragilis*, *Nephrops norvegicus*, *Pagurus bernhardus* and *P. levis*, *Rossia macrosoma*, *Pecten septemradiatus* and *P. opercularis*, *Oceanapia robusta*, *Ficulina ficus* (with *Pagurus pubescens*) as well as many other sponges. Occasionally we got *Sipho islandicus*, *Natica* sp., *Neptunea antiqua* (with *Chondractinia digitata*), *Bolocera tuediæ*, *Halipterus christi*, *Atelecyclus septemdentatus*, *Inachus dorynchus*, *Portunus tuberculatus*, *Galathea nexa*, *Pagurus meticulosus*, *Onuphis tubicola*, *Nereis* sp., *Stichopus tremulus*, *Brissopsis lyrifera*, *Luidia ciliaris*, *Ophiura ciliaris*, *Ascidia venosa*, etc.

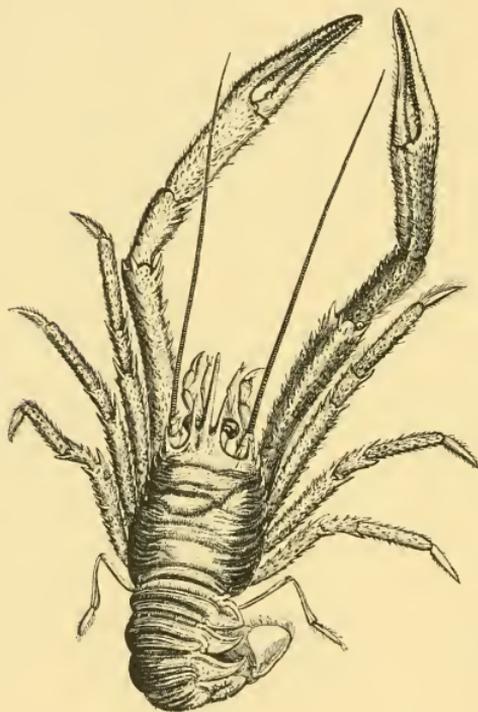


FIG. 355.
Munida rugosa, Fabr. Reduced.

This list shows that several forms found in the Norwegian depression and on the deep muddy bottom occur here also. Two crustaceans (*Hyas coarctatus* and *Munida rugosa*, see Fig. 355) should be noticed in particular, as they inhabit the plateau in large numbers, and seem to furnish an important supply of food to the larger kinds of fish; they were both also taken by the trawl in 200 metres on the Norwegian coast-bank off Stat. In addition we secured a couple of star-fishes (*Pontaster tenuispinus* and *Astropecten irregularis*), while brachiopods, bryozoans,

chitons, etc., were attached to the stones. Among the amphipods we noticed species of the genus *Hoplonyx*, immense numbers of which sometimes collect on dead fish or baited lines.

British investigators have made the plateau round the Shetland islands, to a depth of about 200 metres, one of the most familiar.¹ Most of the Shetland forms are identical with those occurring in the Norwegian boreal region, but we do

¹ For details see *Report of the British Assoc.*, 1868, pp. 232-342.

not find there many of the forms that on the west coast of Norway are chiefly distributed in the great depths of the fjord;¹ there are also certain forms living in deep water at the Shetlands having a southern distribution, Atlantic or Mediterranean forms which find their northern limit there. These differences may to some extent be due to the warm Atlantic water which flows over the Shetland plateau; thus the "Michael Sars" found a temperature of 9.12° C. on the western edge at a depth of 300 metres, and captured with a line a southern shark (*Hexanchus griseus*), frequently taken by British fishermen, which has never been caught farther north in the Norwegian Sea. It is interesting to remark that some of the forms, though no doubt only stray individuals, make their way eastwards along the northern portion of the North Sea plateau as far as the edge of the Norwegian depression, beyond which, however, they never pass, like the crab *Portunus tuberculatus*² and the starfish *Luidia ciliaris*, which were captured on the northern slope of the Viking Bank. Others penetrate even into the Norwegian fjords, like the hermit crab *Pagurus meticulosus (tricarinatus)*, and the crab *Atelecyclus septemdentatus*, small individuals of which were captured on several occasions in the Bergen fjord. Some of the southern forms occurring off the Shetlands wander down along the east coast of Scotland and England, though without spreading farther eastwards, and we find the same faunal agreements and dissimilarities between the east coast of Britain and the west coast of Norway as in the case of the Shetlands.

Certain parts of the plateaus, at a depth of 100 to 150 metres, seem to be favourite abodes of the hydroids, which form regular forests on the bottom, and are plentifully represented by both species and individuals. Just as with the hydroid fauna in the laminaria tracts, so here, too, an assemblage of other animal groups, especially lower crustaceans and naked molluscs, live upon and among these hydroids.³

The hydroids appear to occupy comparatively large tracts of the plateaus, though not regularly distributed over their

¹ For instance, *Stichopus tremulus*, *Bathyplotes tizardi*, *Amphiura norvegica*, *Pandalus propinquus*, *Munida tenuimana*.

² A specimen of this species was also taken on the deeper part of the slope, in 275 metres, with a temperature of 7.94° C.

³ Characteristic and common forms of hydroids were: *Thuyaria thuja*, easily recognisable owing to its verticillate branches, *Hydrallmania falcata*, *Diphasia abietina* and *D. fallax*, *Sertularella tricuspidata*, *Lafœa* sp., *Campanularia volubilis*. Among the lower crustaceans it is especially the caprellids (*Eginella spinosa*) and the arcturids (*Astacilla longicornis* and *Arcturus* sp.) which climb about among the hydroids by means of their specially adapted feet. Eolids too creep about here in great numbers.

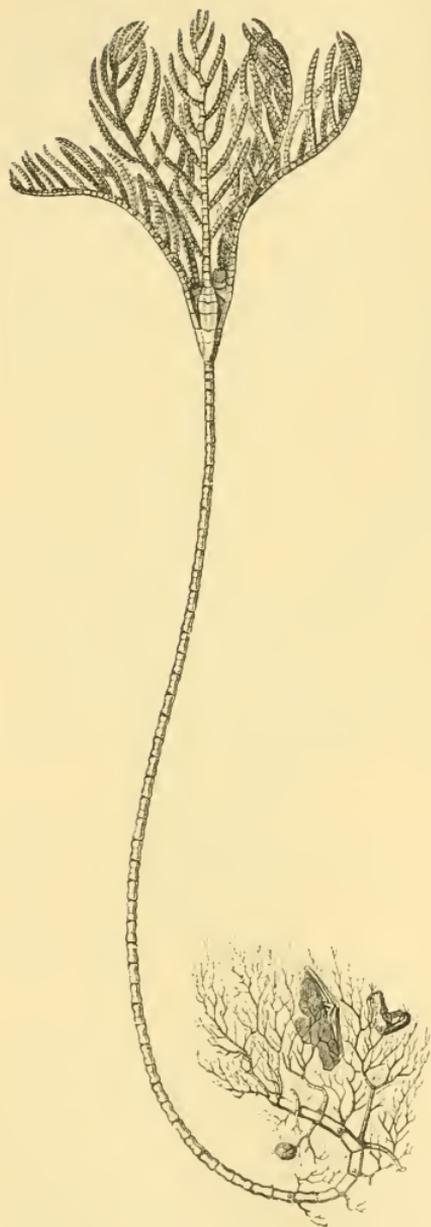


FIG. 356.

Rhizocrinus lofotensis, G. O. Sars. Magnified.
(After Wyville Thomson.)

whole extent. They thrive well apparently on sandy bottom, wherever it is covered with fragments of shells, to which they may attach themselves, and this is even better seen in the central portion of the North Sea. The "Michael Sars" found hydroid-bottom, of the kind described, on the northern portion of the North Sea plateau, on the Faroe plateau east and west of those islands and on the large bank to the south of them, on the Iceland-Faroe ridge, and on the south-eastern Iceland plateau.

A number of species belonging to different groups, which among the skerries and in the western fjords of Norway are littoral forms, or at any rate only occasionally descend below the lower limit of the littoral zone, occur at greater depths out on the plateaus, where they are sometimes very plentiful.

During the cruise of the "Michael Sars" we found on the eastern Faroe plateau, at a depth of 110 metres, on sandy shell-strewn bottom: *Cucumaria frondosa*, *Strongylocentrotus dröbachiensis*, *Pandalus annulicornis*, *Pagurus bernhardus*, *Asterias rubens*, *Mytilus modiolus*, *Buccinum undatum*, *Alcyonium digitatum*, and on the Faroe Bank, south-west of the Faroe Islands, at about 125 metres, *Echinus esculentus* and *Ophiura albida*. On the banks around the Faroes beyond the 100-metres line there

were: *Spatangus purpureus*, *Echinocardium*, *Echinaster sanguinolentus*, *Luidia sarsi*, *Hippasterias plana*, *Ophiopholis aculeata*, *Ophiothrix fragilis*, *Scaphander*, *Hyas coarctatus*, *Pagurus pubescens*, *Inachus dorhynchus*, *Stenorhynchus longirostris*, the annelids *Thelepus circinnatus* and *Leodice norvegica* (both very common), etc. Some of these are mainly littoral forms on our coasts. *Inachus dorhynchus* and *Stenorhynchus longirostris* seem to have a more westerly distribution than the rest, the former being very rarely, and the latter never, found near the Scandinavian coasts, though two other species (*Inachus dorsettensis* and *Stenorhynchus rostratus*) do occur there; these four forms are all met with on the North Sea coasts of Great Britain. From the deep part of the plateaus we may mention the comparatively rare *Rhizocrinus lofotensis* (see Fig. 356), which is fixed in the mud by root-like off-shoots.

One locality examined by the "Michael Sars" in 1902 is entitled to special notice, viz. the extensive Faroe Bank to the south-west of the Faroes, where the bottom at a depth of 100 to 300 metres is peculiar, being quite covered with an enormous quantity of empty shells of different mussels,¹ with a few living specimens among them.² The empty shells were pure white, and it was interesting to see how this white colour affected the other bottom-animals, fishes as well as invertebrates. A couple of species of *Raia*, for instance, had large white spots, and a flounder (*Pleuronectes limanda*) had assumed the light colour of the bottom; *Ophiura albida*, which on our coasts and elsewhere is of a blackish-brown colour, was here perfectly white, and the spines of *Echinus esculentus* were far lighter in colour than usual. *Astacilla longicornis*, which climbed about among the hydroids, had on the other hand assumed their green hue.

Shell-covered
banks.

The geological significance of these shell-covered banks (there are several round the Faroe islands, and fossil shells are also found on the Norwegian coast-banks) has been discussed at considerable length by Professor Brögger.³ They are generally believed, like the Norwegian coast-banks and the plateaus round the Shetlands, etc., to have stood at a higher level during the glacial and inter-glacial periods, forming part of the littoral region of the sea-floor, and to have since subsided. The fossil remains of animals that along our coasts nowadays appear to be able to live, or at any rate to thrive, only in shallower waters are taken as proof of subsidence, it being assumed that with the subsidence of the bottom this shallow-water fauna became extinct.

¹ *Pectunculus glycymeris*, *Venus casina*, *Tellina crassa*, *Arca tetragona*, *Tapes edulis*.

² *Pectunculus glycymeris*, *Venus casina*, *Tellina crassa*, *Maetra elliptica*, *Psammobia tellinella*, and *Dosinia*.

³ "Om de sen-glaciale og post-glaciale nivaåforandringer i Kristianiafeltet (Molluskfaunaen)," *Norges geol. Undersøgelse*, No. 31, pp. 106, etc., Kristiania, 1900-1901.

That there must have been considerable alterations in the physical conditions of the sea on these banks appears evident from the large decayed shells of an arctic form, *Pecten islandicus*, and the remains of other arctic molluscs. The enormous quantities of empty shells of more southern forms may indicate that special forces have been at work, resulting in the destruction of these animals in vast numbers. But, on the other hand, I consider it too hasty an assumption from a biological point of view to maintain that, because these forms are in other localities solely or mainly littoral forms, their extinction must have been due to subsidence of the ocean-floor. As already mentioned, the "Michael Sars" dredged from the bank large living specimens of several of the species represented by empty shells in such abundance, showing that there is still a possibility of finding the necessary conditions of existence there. And there were also some characteristic littoral forms, like *Echinus esculentus*, *Ophiura albida* and *Alcyonium digitatum*, of which the first named was in too great abundance to have been merely the result of chance.

The occurrence of these forms may perhaps be explained by the high temperature ($9.33^{\circ}\text{C}.$) at these depths in the middle of August 1902—a temperature differing very slightly from that prevailing at the same season along the Norwegian coast in the shallower depths principally inhabited by these forms—for temperature and salinity more than depth regulate distribution. An extinct fauna of forms like these at a spot somewhere out on the plateaus does not necessarily imply subsidence of the bottom, but more likely physical changes in the sea-water. Oysters and many other forms are examples of this. A further instance may be cited from the North Sea cruise of the "Michael Sars" in 1904. At Jammer Bay, on the north-west coast of Jutland, at a depth of 14 metres, the dredge brought up great quantities of *Macra elliptica*, *Lunatia intermedia*, *Ophiura ciliaris*, *Echinocardium*, etc., along with a very large number of empty shells belonging to the mussel *Venus gallina*, of which only two living specimens were found. It would be absurd to assert in this case that mortality was due to changes of level, as this form is found elsewhere in quantities at such depths, but the numbers of empty shells point to an encroachment of unfavourable conditions. Another factor must be kept in view, namely bottom-currents, that may possibly, under certain circumstances, accumulate bottom-material such as piles of empty shells at particular localities, which would not

necessarily indicate mortality from extraordinary circumstances, but merely an accumulation, from a considerable area, of individuals whose deaths were due to natural causes. Although certain indications along the coasts of our own and other lands would appear to justify us in regarding currents as a means of conveyance, we know far too little about the matter to be able to discuss it with any profit.¹

In my remarks regarding the edge of the Norwegian depression I endeavoured to show that the fauna of this part of the North Sea differs from that in its more central parts (see p. 506); for this difference, however, the depth, nature of the

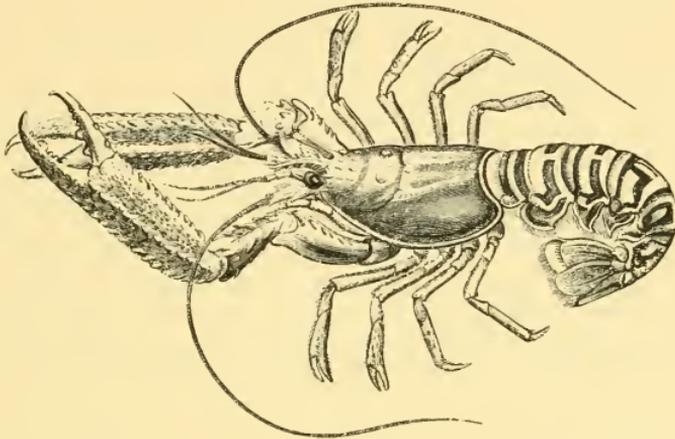


FIG. 357.
Nephrops norvegicus, L. Reduced. (After Bell.)

bottom, and temperature cannot be held solely responsible. This difference holds good also for the continental plateau beyond the 100 metres curve. The "Michael Sars" captured in 110 to 150 metres: the crustaceans *Nephrops norvegicus* (see Fig. 357), *Geryon tridens*, *Sabinea sarsi*, *Pontophilus spinosus*, *Pandalus brevirostris*, *Hippolyte pusiola*, *Caridion gordonii*; the pycnogonids *Nymphon strömi* and *N. mixtum*; the echinoderms *Hippasterias plana* (according to Plate rarely found on the Great Fisher Bank), *Solaster endeca*, *Pteraster militaris* (two small specimens), *Ophiocten sericeum* (quantities of young specimens); the snail *Scaphander punctostriatus*, etc. None of these forms (except one individual of *Nymphon strömi*) were met with in the central portion of the North Sea. Three of them in particular

¹ Compare Heincke, "Die Mollusken Helgolands," *Wissensch. Meeresuntersuch. Komm. f. Untersuchung Deutsch. Meere*, Neue Folge, Bd. 1, pp. 140 et seq.

(*Nephrops norvegicus*, *Nymphon strömi*, and *Hippasterias plana*) furnish unmistakable evidence of the dissimilarity of these areas, for they are widely distributed over the North Sea, occurring even on the coasts of Great Britain in depths both greater and less than 100 metres, and if they existed in the central portion of the North Sea, where we frequently towed our big trawls, they could hardly have avoided capture. Then why should a considerable part of the central area of the North Sea be closed to a number of forms more or less widely distributed elsewhere? We must, I think, conclude that in this central area there are special hydrographical conditions which exclude these forms and their larvæ. As a matter of fact, Helland-Hansen has shown that in the deeper layers there is a circular current of Atlantic water in the North Sea, a branch of the Gulf Stream following the east coast of Scotland, turning north-east just before reaching the Dogger Bank, and afterwards sweeping northwards on reaching the edge of the Norwegian depression. As a result, the periphery of the central portion of the North Sea is bathed by water of much the same composition as the warmer water of the Atlantic, enclosing an area covered by more stagnant and on the whole colder water, having a fauna of its own.¹ Repeated investigations will be necessary to ascertain whether this faunal dissimilarity observed in the summer of 1904 is permanent or not.

ARCTIC AND BOREO-ARCTIC REGIONS OF THE NORWEGIAN SEA

When we speak of an arctic and a boreal fauna it must be clearly understood that there is not always a distinct line of demarcation between the two, either in regard to topographical boundaries or to forms. There are undoubted intermediate areas, where boreal and arctic forms meet, and many forms are as much boreal as arctic, being impartially distributed over either region, and able to thrive amidst very different natural conditions. It is interesting to note, however, that the same species sometimes occurs in two distinct varieties, usually connected by transition forms, and that the varieties conform to the region in which they occur, a fact indicative in all probability of the influence of physical conditions upon organisms.

A circumstance that has especially attracted the attention of arctic investigators is that some animal forms are apt to

¹ I must add that the entire northern part of the North Sea plateau is also covered by Atlantic water.

flourish in some localities in such immense quantities as to displace all others, a phenomenon that may certainly be seen also now and then in the boreal region, though not to such a marked extent. Even when several species occur together the specimens appear to be more numerous than is the case in the boreal region. On one occasion in the Barents Sea the "Michael Sars" brought up in a single trawling over a ton of big sponges (*Geodea*), and near Jan Mayen at another time more than a barrellful of *Pecten grönlandicus*. The prawns again are sometimes in myriads, and Sars relates that during the Norwegian North Atlantic Expedition the trawl came up positively full of the feather star, *Antedon eschrichti*. One reason for such enormous quantities of individuals is that many of the arctic animals produce their young fully developed, without any free pelagic stage, so that in all probability a large proportion continue to live where they were born.¹ Currents, the nature of the bottom, and conditions of nourishment must also be taken into account.²

Direct
development.

Nowhere perhaps do we find such a marked contrast between the boreal and arctic faunas as when we pass from one of the boreal coast plateaus out into the cold area of the Norwegian Sea. If we trawl on the plateaus, where the temperature does not sink below 6° or 7° C., we find a boreal fauna consisting to a great extent of forms which have migrated into the Norwegian Sea from southern latitudes. As soon, however, as we come to the slope of the deep basin (the cold area), at a depth of say 600 to 800 metres,³ where the temperature falls below 0° C., the exclusively arctic element begins to predominate, and we meet with species that are almost entirely foreign to the banks and coasts of the boreal region.

There is the remarkable *Umbellula encrinus* (see Fig. 358), a form belonging to the pennatulids, that may grow several metres high, with large rosette-like polyps at the upper end of the stalk. Of star-fishes we have the beautiful purple *Pontaster*

Arctic fauna
in the upper
part of the
cold area of
the Nor-
wegian Sea.

¹ Römer and Schaudinn, *Fauna arctica*, Einleitung, p. 48; see also Murray, *Trans. Roy. Soc. Edin.*, vol. xxxviii. p. 492, 1896.

² At one locality in the North Sea we captured large numbers of snails (*Sipho gracilis* and *Neptunea antiqua*) and of a sea-mouse (*Spatangus purpureus*). The first named deposits its eggs in capsules, from which the young emerge fully developed, a circumstance sufficient to explain their plentifulness, but *Spatangus* has floating larvæ, so that other factors must have come into operation. There may be an aggregation of individuals in a limited area without direct development, provided the larvæ are not carried away by currents; thus our common ascidian (*Ciona intestinalis*) often forms large congregated masses owing, as far as I could make out, to the fact that the eggs sink in large quantities by the mother's side, and develop in a comparatively short space of time.

³ The depth at which the temperature falls below 0° C. is liable to variation; north of Tampen the "Michael Sars" found such temperatures in 1902 at about 550 metres.

tenuispinus, also found on the plateaus and in the Norwegian depression, the whitish-yellow *Bathybiaster vexillifer* (see Fig. 359, which in the cold area takes the place of *Psilaster andromeda*,

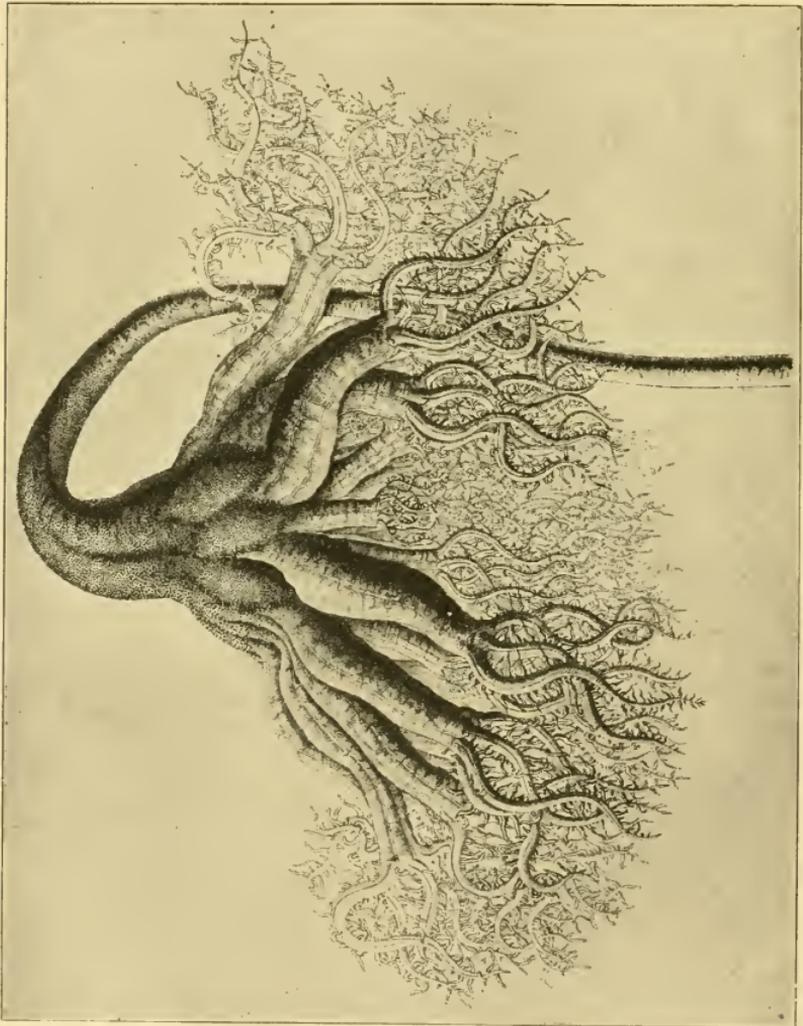


FIG. 358.
Umbellula encrinurus, Cuv. Upper part. (After Daniëlsen and Koren.)

its relative of the plateaus and coasts), and in smaller quantities the semi-transparent *Hymenaster pellucidus* (see Fig. 360). Among brittle-stars the big light-coloured *Ophiopleura borealis* and the smaller gray *Ophiecten sericeum* (also found along the coasts, though in a slightly different variety) are in greatest

abundance. The sea-slugs *Stichopus tremulus* and *Mesothuria intestinalis* so characteristic of the deep parts of our fjords, are entirely absent, but instead of these forms with foot-suckers we have a footless genus *Trochostoma* (see Fig. 361). The sea-mice are represented by *Pourtalesia* (see Fig. 362), a very remarkable genus that in some respects resembles forms long extinct, but *Spatangus*, *Echinocardium* and *Brissopsis* (characteristic of our fjords and coast-banks), and the ordinary sea-urchins are no longer to be

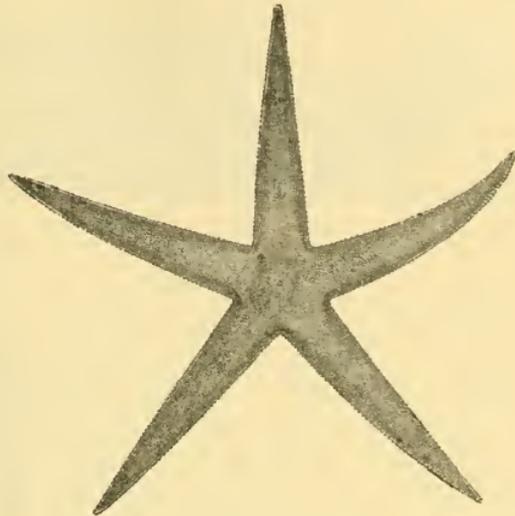


FIG. 359.
Bathybiaster vexillifer, Wy. Thoms. Reduced. (After Bell.)

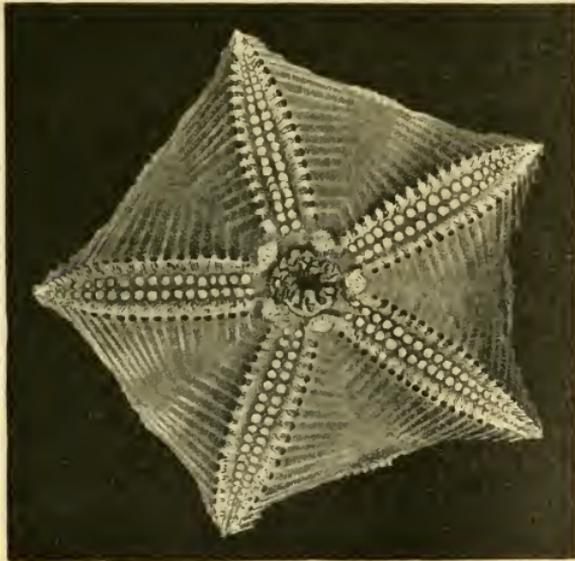


FIG. 360.
Hymenaster pellucidus, Wy. Thoms. "Michael Sars," 1900.

found. Huge sea-lilies or feather-stars (*Antedon eschrichti*, see Fig. 363, and *A. proluxa*), and quantities of the medusa's head (*Gorgonocephalus eucnemis*), are attached most likely either to *Umbellula* or to the numerous sponges, *Cladorhiza* sp., whose hard central axis and tree-like ramifying shape make it so conspicuous, some of which sometimes form regular thickets along the bottom. There are gigantic representatives of the

pycnogonids or sea-spiders, *Colossendeis proboscidea* in particular



FIG. 361.
Trochostoma boreale, M. Sars. Reduced. (After Danielssen and Koren.)

being immense, though *Nymphon robustum* (see Fig. 364) is the most numerous and characteristic species of the cold area, and is easily recognisable by its semi-circular prehensile organs, resembling fingers which incline towards one another. The higher crustaceans consist entirely of shrimp-like forms, such as *Sclerocrangon*

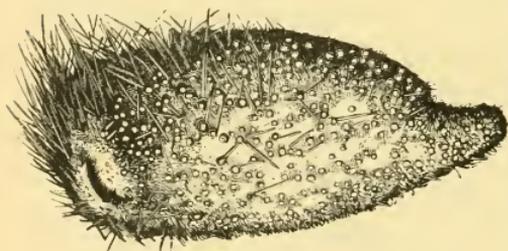


FIG. 362.
Pourtalesia jeffreysi, Wy. Thoms.
(After Wyville Thomson.)

ferox (see Fig. 365), *Bythocaris*, and *Hymenodora glacialis* (the last of which is also found pelagic in the deeper water-layers), whereas crabs are very poorly represented in the arctic areas. On the other hand, the lower crustaceans, especially isopods and amphipods, occupy a very prominent position among the fauna of the Norwegian Sea deep basin, as there are numbers of species, and several attain to considerable size. One of the

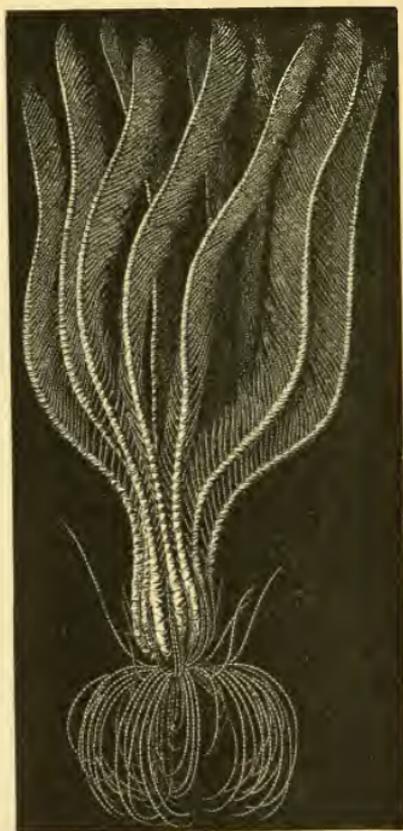


FIG. 363.
Antedon eschrichtii, J. Müller. Reduced.
(After Stuxberg.)

most characteristic of the amphipods is *Amathillopsis spinigera* (see Fig. 366), which has an extremely spinose body.¹ The cold area, moreover, like the plateaus and coasts, has its caprellids climbing about among the sponges and hydroids, the most numerous and common being *Caprella spinosissima*, whose body is covered with dense strong spines. Among isopods we get the remarkable *Eurycope gigantea* belonging to a group with very long legs that easily drop off; it has a relation not nearly

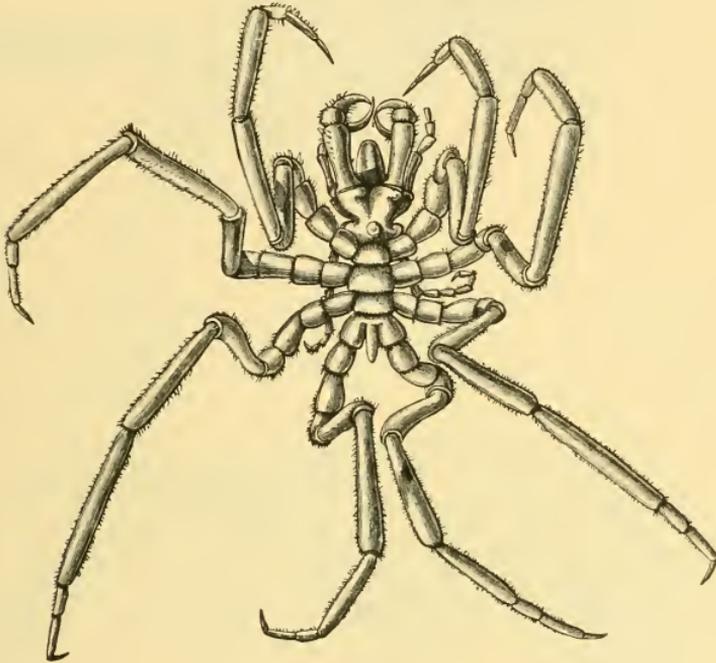


FIG. 364.

Nymphon robustum, Bell. (After Wyville*Thomson.)

so big (*Munnopsis typica*) in the greater depths of the boreal region and widely distributed throughout the arctic seas. The isopod fauna is further represented, often in considerable quantities, by the genera *Arcturus* (*A. baffini*, see Fig. 367) and *Astacilla* (*A. granulata*).

A sea-anemone, *Allantactis parasitica*, is another of the most characteristic forms, attaching itself to the shells of snails belonging to the species of *Sipho* and *Neptunea*.

¹ Other amphipods conspicuous owing to their size are *Stegocephalus inflatus*, the extremely thick forepart of whose body makes it easily recognisable, *Cleippides quadricuspis*, with long spines along the dorsal portion of its posterior segments, *Anonyx* sp., etc.

Hydroids are little in evidence; the vast thickets of these animals found on the plateaus are absent.¹ Alcyonaria are chiefly represented by the genus *Paraspongodes*, with its cauliflower-like colonies, numbers of which also flourish in

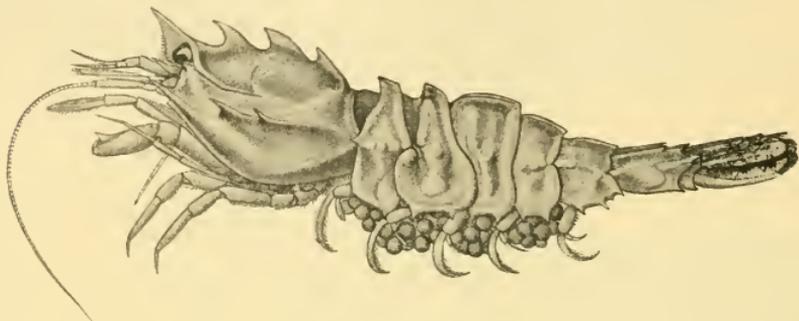


FIG. 365.
Sclerocrangon ferox, G. O. Sars. (After G. O. Sars.)

warmer waters; apparently the same species occur in both areas, the most widely distributed being *P. fruticosa*.

The commonest molluscs are shelled snails of the genera

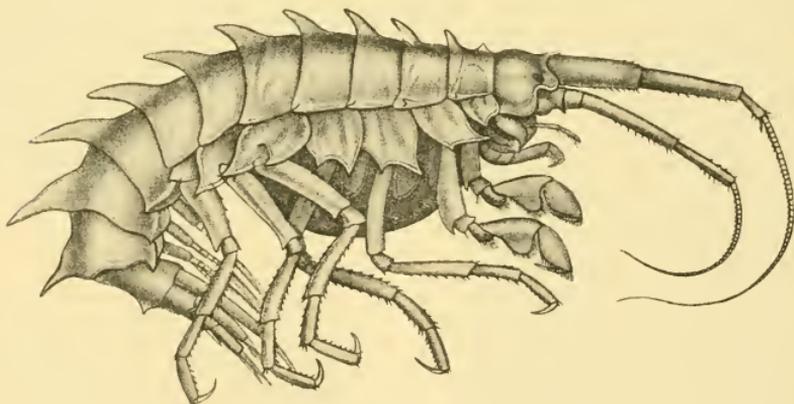


FIG. 366.
Amathillopsis spinigera, Heller. Slightly magnified. (After G. O. Sars.)

Neptunea and *Sipho*. There are cuttlefishes of the genus *Octopus*, though never in any great quantity, and another very remarkable form is the rare *Cirroteuthis mülleri*, one of the eight-armed group, whose members differ from the other in

¹ The most characteristic representatives of this group, belonging to the family Myriothelidae (genus *Lampra*), are rare.

having fins; its arms are united to each other throughout their whole length by a skin attachment. The sea-tooth (scaphopod), *Siphonodentalium vitreum*, is also a very widely distributed form.

In the Norwegian Sea deep basin beyond 2000 metres the conditions seem as a rule to be less favourable for the development of an animal-life abounding in species, as already alluded to by Sars in his report on the first cruise of the Norwegian North Atlantic Expedition. The bottom at these great depths

Fauna of the
abyssal area
of the
Norwegian
Sea.

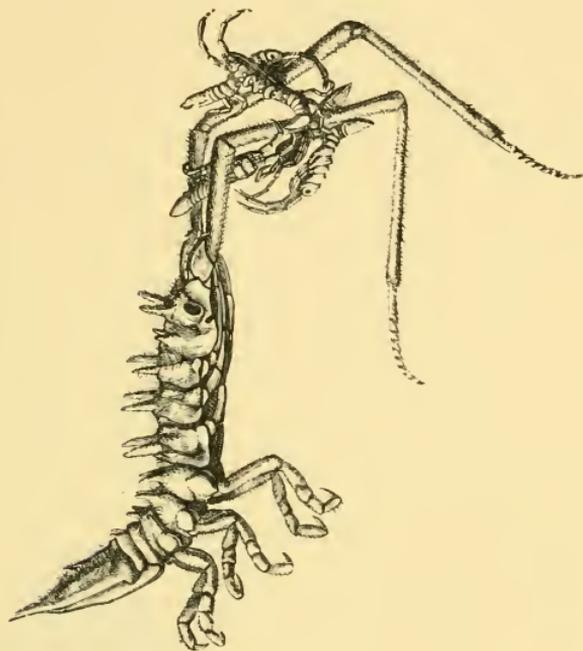


FIG. 367.
Arcturus baffini, Sab. With young.
(After Wyville Thomson.)

consists of Globigerina (or Biloculina) ooze, offering no foundation for attached forms. Only a few species are limited to these profound depths, as the majority occur also in the shallower areas of the Arctic region, or are met with on the slopes of the Norwegian Sea deep basin.

One of the most characteristic deep-sea forms is a sea-lily, *Bathocrinus carpenteri*, that attaches itself to the soft bottom

by means of the root-like ramifications issuing from its stalk (this form has a near relation, *Rhizocrinus lofotensis*, which occurs in the deeper parts of the boreal region). Another characteristic echinoderm is a sea-slug, *Kolga hyalina*, which is never found in depths less than 2000 metres. *Elpidia glacialis* (see Fig. 368), too, must be considered a characteristic sea-slug of the Norwegian Sea deep basin, though it may from time to time be met with in the north at lesser depths. These two holothurians belong to a remarkable group, with few though very large feet arranged in rows on either side; they

occur occasionally in immense quantities. Crustaceans are represented by a characteristic deep-sea form, namely the isopod *Glyptonotus megalurus*, nearly related to a form that occurs in the arctic region in shallower waters; pycnogonids by

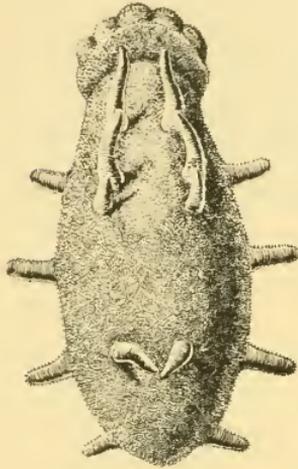


FIG. 368.
Elpidia glacialis, Théel. Magnified.
(After Stuxberg.)

Ascorhynchus abyssi; and molluscs by *Pecten frigidus* (see Fig. 369), *Neptunea mohni*, *Natica bathybi*, etc. There are also some deep-sea sponges, prominent amongst which are the Hexactinellids; although not regularly distributed over the Norwegian Sea, they are found in great quantities to the north of Spitsbergen at a depth of 1000 metres, where they and another group (Tetraxonia) constitute the most characteristic portion of the fauna. Outgrowths on their under sides enable them to hold fast to the soft bottom, which is littered with silicious spicules from dead sponges.¹ Römer and Schaudinn have doubted whether the deep-sea fauna of those northern latitudes is to be considered zoo-geographically as a part

of the fauna of the Norwegian Sea deep basin, or whether it belongs to a separate faunal area, the deep polar basin; deep-sea sponges have, however, been subsequently found in quantities farther south (lat. 72° 23' N., long. 13° 50' W.) at a depth of 2000 metres.²

The forms limited exclusively to the abyssal region, or at any rate only very exceptionally occurring in shallower waters, are not the only ones which characterise the Norwegian Sea deep basin, for we find regularly also a number of other forms met with on the slopes in the cold area.³

Just as the Norwegian Sea deep basin has its own (even though rather few) characteristic forms, which do not ascend to the arctic plateaus but constitute a typical deep-sea fauna, so, too, the plateaus have a



FIG. 369.
Pecten frigidus,
Jensen. "Michael
Sars," 1900.

¹ Römer and Schaudinn, *op. cit.* p. 49.

² Kolthoff, *Till Spetsbergen och nordöstra Grönland*, 1900, pp. 212-213.

³ The "Michael Sars" found at about 2000 metres the echinoderms: *Bathybiaster vexillifer*, *Ophiocten sericeum*, and *Pourtalesia*; the mollusc: *Siphonodentalium vitreum*; the crustaceans: *Bythocaris leucopis* and *Hymenodora glacialis*; the pycnogonid: *Nymphon robustum*; the worm: *Lumbrineris*, etc. The tube-worm, *Myriochele*, with its fine sand-tube, belongs to the forms which occur in quantities in the depths of the Norwegian Sea.

series of species that do not descend to the profound depths. These latter may be designated arctic shallow-water forms, or, to use a different zoo-geographical description, arctic continental forms, though it is as well to remember that the depth on the plateaus averages about 400 metres. As in the case of the boreal plateaus, so here, too, we can distinguish between forms that keep entirely to less depths and those which chiefly inhabit the deeper portions. The bottom conditions of the plateaus are quite different from those that prevail in the abyssal region, since hard bottom is to be found as well as soft, whereas the floor of the deep basin consists almost entirely of soft materials; consequently the plateaus have a far greater abundance of attached animal forms.

Arctic
shallow-water
forms.

Currents, owing to the increased abundance of nourishment they bring with them, are likewise responsible for the greater profusion of attached forms on the arctic plateaus. To what extent they affect the distribution of animal-life may be seen by comparing the fauna of the west and east coasts of Spitsbergen. Römer and Schaudinn, who made careful researches in 1898, found that on the western side non-attached forms, especially echinoderms, were most in evidence, while on the eastern side, where strong currents flow through the sounds, attached forms predominated. Of this latter area Römer and Schaudinn write as follows: "Most of the rocks and large stones are covered with barnacles, while monascidians and synascidians form populous colonies on the bottom. Sponges, which are scarce on the western side, are represented by numerous species, and alcyonids inhabit the deeper channels. The shallower rocky localities accommodate large congregations of actiniæ. The animals, however, which, so to speak, hall-mark the fauna, and are developed in almost fabulous fashion, are hydroids and bryozoa. So dense are the thickets formed in some places by these organisms that the heavy dredge failed to reach the bottom, and merely brought up animals instead of bottom-material." Amongst these attached forms, moreover, there is, just as in the boreal region, a rich fauna of non-attached forms like worms, crustaceans, and molluscs. Römer and Schaudinn drew attention to the fact that the worms, crustaceans, and molluscs, in particular, did not show such a striking difference in their distribution around Spitsbergen as other groups, but were, on the contrary, fairly equally distributed between east and west. Nor are echinoderms absent on the eastern side, where in fact there are actually more species than

on the west, but in regard to individuals they are very much exceeded by the attached forms.

A great difference between the arctic region in high latitudes, where the Gulf Stream has lost its warming influence, and the boreal region, is to be found in the littoral, or more correctly in the strand, zones. The luxurious growth of fucus and laminaria which covers the rocks along the coasts in the boreal region, both above and below low-water mark, is wanting in depths less than about 6 metres. This is due to the ice blocking up the shore for a great part of the year and preventing the development of animal and plant life. The strand zones in high arctic latitudes accordingly exhibit nothing but naked rock, in contradistinction to the rocks of the boreal region, where we find numbers of attached animal-forms right up to high-water mark. As soon, however, as we descend below the limit of the baneful effects of the ice, we meet with a profusion of both plants and animals, sometimes even in greater abundance than in the boreal region.

Arctic littoral forms.

Though we are thus unable to speak of an actual strand-fauna in high arctic latitudes, we can distinguish, to a certain extent, between the littoral, or rather sub-littoral, and the deeper non-littoral forms. The former, however, appear to be comparatively few in number, taking 40 metres as the lower limit as we did in the boreal region, while on the other hand most of the non-littoral forms reach nearly up to or actually pass the littoral limit. Generally speaking, the limits between a littoral and non-littoral zone seem to be less clearly defined in the arctic than in the boreal region.¹ The reason for this is obvious enough, if we remember that temperature largely controls distribution. In high arctic latitudes the difference in temperature between deep and shallow waters is inconsiderable compared with that at corresponding depths in boreal areas. As a result the forms find favourable conditions of existence, so far as temperature is concerned, at very different depths, and the vertical distribution of most of the arctic forms is far more extensive than that of boreal forms. A few instances may be cited: *Hymenaster pellucidus* in the Norwegian Sea deep basin is found even below 2000 metres, while on the east side of Spitsbergen it occurs at 27 metres; *Antedon eschrichti* may be met with in the cold area of the Norwegian Sea at very considerable depths, whereas at Spitsbergen it flourishes in

¹ Cf. Stuxberg, "Evertbratfaunan i Sibiriens ishaf," *Vega-exped. vetenskap. iakttagelser*, Bd. i. pp. 730, etc.

18 metres of water, and the same is the case with *Ophiocten sericeum*; *Nymphon robustum*, which even at depths of 2000 metres is the most characteristic pycnogonid of the Norwegian Sea deep basin, can actually thrive at a depth of 6 metres in the arctic littoral zone; *Gorgonocephalus eucnemis* occurs in the Norwegian Sea deep basin and yet finds itself at home in the arctic littoral zone. Many similar examples could be adduced, but special works on the different groups, indicating the depths at which the various forms have been found, furnish the clearest evidence. The character of the water in different arctic areas must also be taken into consideration. Species which almost invariably live in water at a temperature below 0° C. will not be met with in shallow depths except where truly polar water predominates; thus on the west coast of Spitsbergen there are echinoderms found only in deep water, which on the east side occur very much nearer the surface, owing to the fact that on the west side the Gulf Stream makes its influence felt to a considerable depth, while on the east coast the water is everywhere polar. I shall return to the influence of warm currents upon animal life in arctic tracts.

It must not be supposed, however, that the vertical distribution in arctic tracts is entirely devoid of system. No doubt there are a great many forms with a far more extensive distribution than would be possible in the boreal region, still the arctic plateaus shelter numerous forms that do not descend into the Norwegian Sea deep basin, and apparently therefore are unable to thrive in such deep water. In their case it is evidently not temperature but other factors that regulate distribution, and besides it is actually possible to point to a purely littoral arctic fauna, although its representatives are far from numerous.

Hard bottom as well as soft are to be found in the deeper parts of the arctic plateaus; where the bottom is of mud it differs from the brownish Globigerina (or Biloculina) ooze of the Norwegian Sea deep basin, being of a grayish colour like what we find in the Norwegian fjords and on the boreal coast banks; in the Barents Sea, however, we get greenish-gray mud. The arctic mud, like the boreal, contains many foraminifera, though the species differ to a certain extent.¹

We may divide the species composing the arctic fauna into

¹ The species named by Kier (*Norwegian North Atlantic Expedition*, Thalamophora, p. 12) as characteristic of the gray mud in northern arctic areas are: *Astrorhiza crassatina*, *Lagena apiculata*, *Pulvinulina karsteni*, *Globigerina pachyderma*, *Biloculina levis*, *Globigerina bulloides* and *G. pachyderma*, *Haplophragmium latidorsatum*, *Truncatulina wüllerstorffi*, *Rotalina orbicularis*, and *Lagena apiculata* are common in the Globigerina (or Biloculina) ooze of the Norwegian Sea deep basin; some of them belong also to boreal areas.

three categories. The first category may be termed purely arctic, occurring in water having a low temperature all the year round.¹ Allowing for slight variations it is safe to assert that the majority of them require a temperature considerably below what prevails in the deeper parts of the boreal region (6° to 7° C.), though a few coast and shallow-water forms are able to exist at higher temperatures for a short portion of the year; this is particularly the case with those arctic forms that come as far south as the Lofoten, Murman, and Finmark coasts. Still even within the purely arctic areas we find faunal differences that are due to temperature. Some forms are never, or very rarely, found in water having a temperature above 0° C., others appear to thrive impartially throughout the whole arctic region in whatever temperatures prevail, while others again avoid the coldest water and keep as much as possible to temperatures slightly above 0° C.

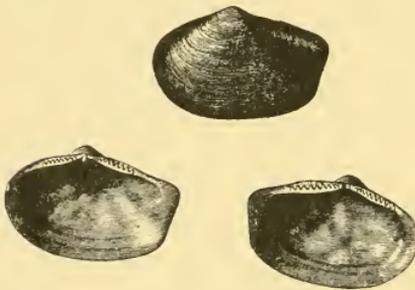


FIG. 370.
Yoldia arctica, Gray. (After Stuxberg.)

As regards horizontal distribution within the arctic region we may assume that most of the species are widespread, even if they have not yet been met with everywhere, for we are still only imperfectly acquainted with the fauna over a large portion of the arctic plateaus, especially that off East Greenland. Some species, however, will undoubtedly prove to be more or less local, judging from what we have found in the boreal region.

A few of the larger forms that characterise the arctic coasts and plateaus are given in the following list:²—

Molluscs: *Margarita cinerea*, *Onchidiopsis glacialis*, *Natica clausa*, *Amauropsis islandica* (rarely found on the Norwegian west coast), *Neptunea despecta*, *Sipho curtus*, *S. turgidulus*, *S. krøyeri*, *S. glaber*, *Buccinum glaciale*, *B. hydrophanum*, *B. grönlandicum*, and a few other species of *Buccinum*, species of *Bela*, *Siphonodentalium vitreum*, *Nucula tenuis* var. *expansa*, *Yoldia hyperborea*, *Y. (Portlandia) arctica* (see Fig. 370) and *Y. limatula*, *Arca glacialis*, *Pecten grönlandicus*, *P. islandicus*, *Astarte (Nicania) banksi* var., *A. borealis*, and *A. crebricostata*, *Axinopsis orbiculata*, *Axinus gouldi*, *Tellina calcarea* (rarely found alive on the Norwegian west coast, though extremely abundant in the arctic region),

¹ There are a few exceptions, for instance, *Pecten islandicus*, *Ctenodiscus crispatus*, *Onchidiopsis glacialis*, which are more boreo-arctic than arctic (see p. 534).

² In this list I deal only with the molluscs, echinoderms, crustaceans, and ascidians.

and a few other species of *Tellina*, *Venus fluctuosa*, *Cardium ciliatum*, *C. grönlandicum*, *Thracia truncata* (rarely found in the boreal region), *Pandora glacialis*. Brachiopods: *Rhynchonella psittacea* (see Fig. 371), *Terebratulina spitsbergensis*. Echinoderms: *Asterias lincki*, *A. panopla*, *A. grönlandica*, *A. hyperborea*, *Stichaster albulus*, *Ctenodiscus crispatus*, *Ophiopleura borealis*, *Ophiura nodosa*, *Amphiura sundevalli*, *Ophiopus arcticus*, *Gorgonocephalus eucnemis* and *G. agassizi*, *Antedon eschrichti*, *A. proluxa*, *Cucumaria minuta*, *C. glacialis*, *Eupyrus scaber*, *Trochostoma boreale*, *Ankyroderma jeffreysi*, *Chirodota lævis*, *Myriotrochus rinki*.

Decapod crustaceans: *Sclerocrangon ferox*, *S. boreas*, *Sabinea septemcarinata*, *Hippolyte turgida* and *H. spinus*, *Bythocaris payeri*, *Idotea entomon*. Two species of pycnogonids, *Nymphon robustum* and *N. hirtipes*, are very abundant in the arctic region; the former is largely a deep-sea form, which descends far down into the cold area of the Norwegian Sea deep basin, whereas *N. hirtipes* belongs more to the banks and plateaus. Both species were trawled by the "Michael Sars" on the Jan Mayen plateau, showing that they may be abundant in shallow waters also. The largest pycnogonid of the Norwegian Sea is *Colossendeis proboscidea*, found both on the slopes of the deep basin and on the banks. There are also several other species of *Nymphon*, such as *N. elegans*,



FIG. 371.

Rhynchonella psittacea, Chemn.
(After G. O. Sars.)



FIG. 372.

Dendrodoa aggregata, Rathke.
Nat. size.

N. macronyx, and *N. gracilipes*, which are common arctic forms. The hydroids have comparatively few purely arctic species, though the magnificent large *Tubularia regalis* is one that deserves special notice; in congenial localities like the Bear Island shoal and the banks of Jan Mayen it forms regular thickets on the bottom. Among ascidians *Dendrodoa (Styela) aggregata* (see Fig. 372) is a very characteristic arctic form, and is often found in little colonies composed of a number of cohering individuals. Another characteristic though rarer species is *Chelyosoma macleyanum*, easily recognisable owing to its extremely flattened shape and the squares into which its surface is divided. *Ciona intestinalis*, one of our commonest boreal forms, occurs in the arctic tracts as a distinct variety (*longissima*). The compound ascidians are represented by several species, amongst which the tuberous *Synicum incrustatum*, whose surface is encrusted all over with grains of sand, may be easily recognised. Other forms are *Molgula retortiformis*, *Amaroucium nutabile* (tuberous and of a reddish-violet colour), and *Sarcobotrylloides aureum*.

The second category of forms in the arctic region is made up of those which are at the same time extensively distributed

Arctic-boreal forms.

over the boreal parts of the Norwegian Sea, and are thus just as much boreal as purely arctic; I append a short list:—

Molluscs: *Lepeta cæca*, *Margarita grönlandica* and *M. helicina*, *Lunatia grönlandica*, *Littorina rudis*, *Cylichna alba*, *Leda pernula*, *Modiolaria lævigata* and *M. nigra*, *Astarte* (*Nicania*) *banksi* with varieties, *Astarte compressa*, *L.* (= *elliptica*, Br.), *Mya truncata* (chiefly arctic, whereas *M. arenaria* is the typical boreal form), *Saxicava arctica*, *Pecten hoskynsi*, *Portlandia frigida*. Echinoderms: *Strongylocentrotus dröbachiensis*, *Pontaster tenuispinus*, *Echinaster* (*Cribrella*) *sanguinolentus*, *Solaster papposus* (occurs as a rule in the arctic region as a distinct variety, *S. affinis*), *Pteraster militaris*, *Ophiura sarsi* and *O. robusta*, *Ophiocten sericeum*, *Ophiopholis aculeata*, *Ophiacantha bidentata*, *Ophioscolex glacialis*, *Cucumaria frondosa*, *Psolus phantapus*. Decapod crustaceans: *Pandalus borealis*, *Hippolyte gaimardi*, and *H. polaris*, *Pagurus pubescens*, *Hyas araneus* and *H. coarctatus*. Isopods: *Munnopsis typica*. Pycnogonids: *Nymphon grossipes* (and a few other species of *Nymphon*). Ascidians: *Peloniaia corrugata*, *Styela rustica* and *S. loveni*, *Styelopsis grossularia*, and *Ascidia prunum*. Worms: a number of species of *Harmothoë*, *Lumbrinereis fragilis*, *Onuphis conchylega*, *Nereis pelagica*, *Arenicola piscatorum* (*marina*), *Owenia assimilis*, *Nicolea zostericola*, *Thelepus circinnatus*, and *Terebellides strömi*.

These forms are very interesting biologically, as they show to how great an extent the same species is able to adapt itself to different natural conditions. Many of them¹ are quite common in the littoral zone of the boreal region, where during a large portion of the year the temperatures are comparatively high, and yet they are also to be found in arctic tracts, where temperatures are all the year round below 0° C., or at any rate not more than a few degrees above 0° C. during a very short period. Others, again, are more consistent, as they inhabit only the greater depths of the boreal region, where throughout the whole year the temperature is fairly uniform and comparatively low (though never sinking below 6° or 7° C.), whereas in the arctic region they exist in shallow water; thus on the Norwegian west coast we find the mussel *Portlandia frigida*, the brittle-star *Ophiacantha bidentata*, and the prawn *Hippolyte polaris* (see Fig. 373) only as a rule beyond 100 metres, whereas in high arctic latitudes they may be met with at a depth of about 10 metres. The species included in this second category do not all by any means show the same distribution throughout the arctic region; some forms occur every-

¹ *Margarita grönlandica* and *M. helicina*, which both occur in the boreal laminaria belt, *Saxicava arctica*, *Strongylocentrotus dröbachiensis*, *Echinaster sanguinolentus*, *Ophiopholis aculeata*, *Cucumaria frondosa*, *Hippolyte gaimardi*, *Pagurus pubescens*, *Hyas*, *Styela rustica*, *Nereis pelagica*, *Arenicola*, *Nicolea*, etc.

where in both the arctic and the boreal regions, while others are generally limited within the arctic region to water having temperatures just about or above 0° C. These last are intermediate forms between this and the following category, and include, for instance, the prawn *Pandalus borealis*.

A third category of species composing the arctic fauna consists of boreal forms that are able to enter the arctic region owing to the warmth introduced by various branches of the Gulf Stream, which counteracts the chilling effects of the icy coastal and polar currents. On the coasts of East Finmark and on the Murman coast these are particularly in evidence. These boreo-arctic intermediate areas occupy that portion of the Norwegian Sea where the waters of the Gulf Stream and polar currents intermingle, or where the shallow coast waters

Boreal forms
with boreo-
arctic
distribution.



FIG. 373.
Hippolyte polaris, Sab. Reduced. (After Parry.)

acquire a high summer temperature in consequence of the comparatively milder climate produced by the proximity of the Gulf Stream.

This boreo-arctic area contains certain forms of truly arctic origin, less sensitive in regard to temperatures above 0° C., and attaining here the extreme limits of their advance in a boreal direction. It also contains genuine boreal species, which may range as far south as the Mediterranean, and have their northern limit within this area.

Along the north-west coast of Norway from Lofoten to the North Cape (West Finmark) the character of the fauna is very complicated, owing to the diversified hydrographical conditions, especially in the deeper places of the coastal area compared with those in the inner basins of the fjords. Many of these north-western fjords are open to the ocean for part of their length, so that their seaward portions may fairly be regarded

Boreo-arctic
areas.

as inlets, while their landward portions are cut off by submarine barriers which are often comparatively shallow. As a consequence the warm water of the Gulf Stream flows along the bottom of the fjords till it reaches the barriers, but is unable to penetrate into the inner basins, which are therefore greatly affected by climate, their water-masses at comparatively shallow depths being stagnant and at a low temperature. We find accordingly an arctic fauna predominating in the inner basins, while the boreal forms met with on the coast and in the seaward portions of the fjords in corresponding depths are for the most part absent.¹ Still there are arctic forms in these latitudes along the coast in the shallow waters of the littoral (and sublittoral) zones, where climatic conditions occasion low temperatures for at any rate part of the year. The fauna at greater depths along the coast, on the other hand, is purely boreal owing to the influence of the Gulf Stream. We are accordingly justified in regarding Lofoten as the southern limit of the boreo-arctic area, so far as the coast tracts are concerned, even though the boreal element preponderates there, and similarly we are entitled to call the inner basins of the fjords boreo-arctic, although in their case it is the arctic element that predominates.²

The coastal areas and fjords east of the North Cape (East Finmark) are altogether boreo-arctic. The fjords here are open arms of the sea, in which there is no distinction between the fauna of the outer and of the inner portions, and, owing to the intermingling of Gulf Stream and polar waters, the purely boreal character of the fauna predominating in West Finmark is absent even in the deeper parts. Moreover, the farther east we go and away from the influence of the Gulf Stream the more do these conditions assert themselves, the fauna becoming gradually more and more purely arctic. A comparison between this area and large parts of one of the best-known areas in high arctic latitudes, namely Spitsbergen, shows how perfectly justified we are in calling it boreo-arctic, for we find a fauna on the Murman coast which, in addition to purely arctic species, includes littoral³

¹ G. O. Sars, "Some Remarks on the Character of the Marine Fauna along the Northern Coasts of Norway," *Tromsø Museums Aarshefter II*, 1879, p. 60; Nordgaard, *Hydrographical and Biological Investigations in Norwegian Fjords*, Bergen, 1905.

² It must be distinctly stated, however, that this fauna is made up mainly of forms which, although undoubtedly of arctic origin, are distributed over both the boreal and arctic regions; whereas the purely arctic forms are comparatively few. These fjord areas are entitled to be characterised as boreo-arctic owing to the presence of a small number of purely boreal forms with boreo-arctic distribution otherwise.

³ *Purpura lapillus*, *Littorina littorea*, *Nacella pellucida*, *Mytilus edulis*, *Tellina baltica*, *Asterias rubens*, *Balanus balanoides*, *Crangon vulgaris*, *Dynamena pumila*.

and deeper-living¹ boreal forms that are never met with at Spitsbergen.

Another boreo-arctic area lies in the south-western portion of the Norwegian Sea on the ridge connecting Iceland and the Faroes. The crest of the Wyville Thomson Ridge between the Faroes and Shetland has not been examined by the "Michael Sars," but undoubtedly it may be included. On the broad ridge between the Faroes and Iceland we took up several stations in 1902, at a depth of 450 to 480 metres, the temperature varying between 3.12° C. and 3.98° C.; the greatest depth on the top of this ridge is about 500 metres. Here we came across the same mixed fauna already described as characteristic of the north-eastern boreo-arctic area, the "Michael Sars" securing distinct arctic forms,² together with boreal forms³ which penetrate into the boreo-arctic portion of the Barents Sea. If we remember that the polar and Atlantic currents meet about the middle of the Iceland-Faroe ridge, it will be easy to understand the boreo-arctic character of the bottom fauna. It is remarkable that such distinctly cold-water forms as *Hymenaster* and *Nymphon robustum* were found in water with a temperature of 3° or 4° C.; no doubt the individuals were few (only one specimen of *Nymphon robustum*, for instance, being taken), still their occurrence seems to show that the bottom-water on the ridge has not always the high temperatures we recorded—the temperatures must often be considerably lower, perhaps even below 0° C. at times.⁴ Boreal deep-water forms are furthered in their advance occasionally by warm currents, and yet they can endure low and varying temperatures; the converse probably holds good with various purely arctic forms, which owe their distribution to the cold arctic water, but can endure the higher temperatures when that is displaced by Gulf Stream water. In spite of this *Hymenaster* and *Nymphon robustum* are just as much arctic forms as *Hippasterias*, *Pentagonaster*, and *Pontophilus* are boreal forms.

¹ *Antalis entalis*, *Schizaster fragilis*, *Hippasterias plana*, *Pentagonaster granularis*, *Verruca strömi*, *Hippolyte securifrons*, *Crangon allmanni*, *Nephrops norvegicus* (?), *Pontophilus norvegicus*, *Munida rugosa*, and several others. The hydroids, on the other hand, are very widely distributed, as most of the species met with in these tracts are commonly distributed throughout the boreal region; some species of hydroids seem able to adapt themselves to all temperatures (eurythermal forms).

² *Hymenaster pellucidus*, *Solaster squamatus*, *Antedon eschrichti*, *Rhachotropis aculeata*, *Epimeria loricatea*, *Nymphon robustum*, *Lampra purpurea*.

³ *Hippasterias plana*, *Pentagonaster granularis*, *Schizaster fragilis*, *Antedon tenella*, *Gorgonocephalus lincki* and *G. lamarcki*, *Pontophilus norvegicus*, *Sabinea sarsi*, and amongst hydroids *Thuyaria thuya* and *Hydrallmania falcata*, although not in any great quantities.

⁴ The Danish "Ingolf" Expedition recorded a temperature of $+0.5^{\circ}$ C. at about 510 metres.

I have already stated that the north and east coasts of Iceland are boreo-arctic areas. Even as far south as lat. $64^{\circ} 17' N.$ and long. $14^{\circ} 44' W.$, that is to say, quite close in to the coast, the "Michael Sars" found purely arctic forms at a depth of 75 metres, namely, the prawn *Sclerocrangon boreas* and the ascidian *Molgula retortiformis*, together with forms that are either widely distributed throughout both regions, or are boreal with a boreo-arctic distribution.¹ Here again, therefore, the character of the fauna was evidence of the meeting of the

two great currents, the East Iceland Polar Stream and the Atlantic Stream.

Before leaving the arctic fauna I have still to mention a few characteristic forms, which penetrate for a short distance into the boreal region along the coast of Norway. The starfish *Ctenodiscus crispatus* is found as far south as Christiansund, where it occurs in enormous quantities; and another starfish, *Leptoptychaster arcticus*,² has its south-

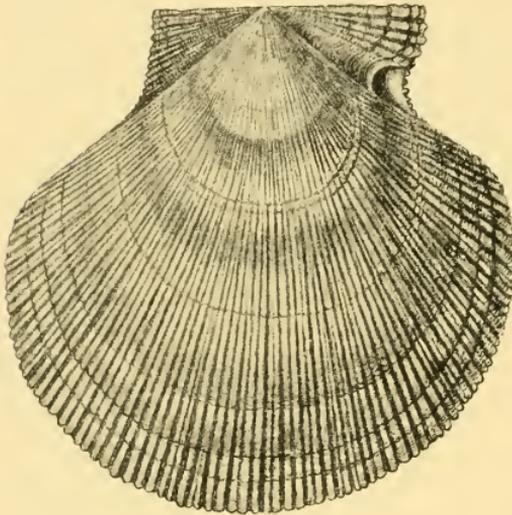


FIG. 374.
Pecten islandicus, L. Reduced. (After G. O. Sars.)

ern limit in the Trondhjem fjord. A very characteristic arctic species of mussel, *Pecten islandicus* (see Fig. 374), is very numerous and of large size in the Trondhjem fjord, and may be met with even farther south, while the same fjord is the southern limit for the molluscs *Onchidiopsis glacialis*, *Dendronotus velifer*, and a few others. We have thus another instance of the difficulty in fixing definite boundaries for the different regions. The Trondhjem fjord shelters too many forms which

¹ I append the names of a few forms:—Ascidians: *Ascidia obliqua*, *Peloniaia corrugata*, *Macroclinium pomum* (numerous), *Distoma crystallinum*. Crustaceans: *Hyas coarctatus*, *Pagurus*, *Pandalus annulicornis*, *Hippolyte polaris*, *Crangon allmanni*, *Arcturus* sp. Echinoderms: *Asterias rubens*, *Echinaster sanguinolentus*. Pycnogonids: *Pycnogonum littorale*, *Nymphon mixtum*, *N. hirtipes*. Coelenterates: *Metridium dianthus*, *Corymorpha glacialis*, *Tubularia indivisa* (common), *Hydrallmania falcata*, and a few other hydroids. Also some sponges and worms.

² The peculiarity about this form is that it lives mainly in boreo-arctic areas, and is thus neither purely arctic nor purely boreal.

do not enter the boreo-arctic area to be designated an intermediate area. Possibly both *Ctenodiscus crispatus* and *Leptotychaster arcticus* live chiefly in isolated basins, where the temperature for part of the year sinks lower than in the other parts of the fjord, though I do not know that this has actually been confirmed.

Occasionally too we find in far more southern areas a few forms that must be considered purely arctic, although they are quite acclimatised and plentiful. They are survivals (relicts), and date from the glacial age when the northern seas were inhabited by an arctic fauna. The milder climate which succeeded the glacial period brought about the elimination of all those species that are now purely arctic, and such forms are at present practically limited to arctic tracts. Only a few were able to adapt themselves to the altered conditions,¹ and are to be found to this day

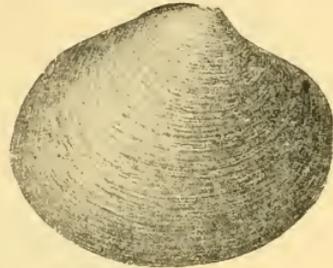


FIG. 375.

Tridonta borealis, Chemn.
(After G. O. Sars.)

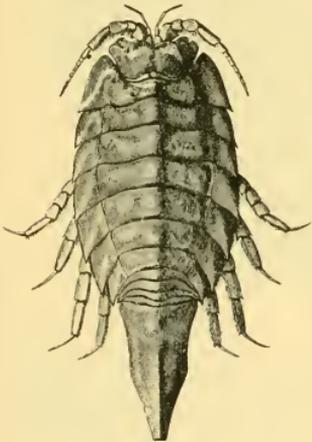


FIG. 376.

Idotea entomon, L. (After Stuxberg.)

in isolated areas, located outside the range of this chapter, though owing to the interest attached to them, they may be briefly alluded to.

There is, for instance, the mussel *Astarte (Tridonta) borealis* (see Fig. 375), large quantities of which are found in the arctic tracts from Lofoten northwards. In the south we do not find it till we come to Öresund, The Belts, and the Western Baltic, where it is very plentiful. In the intervening waters it is merely a stray guest, having been found once or twice in the neighbourhood of Bergen. The survival forms include also a few crustaceans, for instance, the isopod *Idotea entomon* (see Fig. 376), some worms, and a sea scorpion (*Cottus quadricornis*), which are mostly to be found in the Baltic, and in a few lakes of North Europe that were connected with the sea in the glacial age.

¹ On the other hand there are, as already stated, a number of forms from the glacial age which became thoroughly acclimatised, and, in contradistinction to the relict-forms, are widely distributed throughout both regions.

DEEP-WATER FAUNA OF THE NORTH ATLANTIC

It is easy to see how much the configuration of the bottom, and the hydrographical conditions associated with it, affect the distribution of animal-forms, if we compare the fauna of the Norwegian Sea north of the submarine Iceland - Faroe - Shetland and Iceland-Greenland ridges, with the fauna of the Atlantic Ocean to the south of these ridges. Thanks to the painstaking researches of the Danish "Ingolf" Expedition, and the subsequent investigations of the "Michael Sars" in

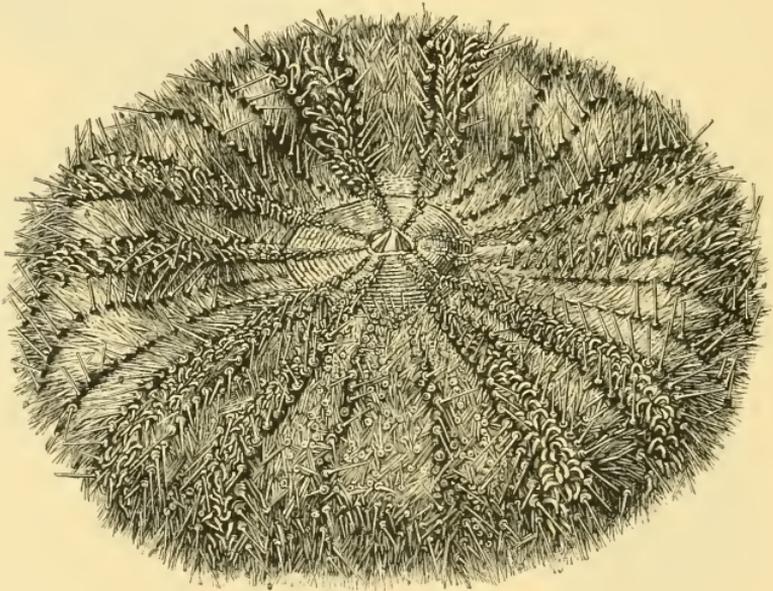


FIG. 377.

Calveria hystrix, Wy. Thoms. Reduced. (After Wyville Thomson.)

1902, we are now acquainted with the principal characteristics of both. The chief hydrographical differences in these two marine areas are due to the intervening ridges, covered on an average by 550 to 600 metres of water, which prevent the icy bottom water of the Norwegian sea from entering the Atlantic, and conversely the warm Atlantic water from flowing over the floor of the Norwegian Sea.¹ Two temperature-readings are sufficient to make this clear: in 1902 the "Michael Sars" found a temperature of -0.41° C. in the Faroe-Shetland channel at

¹ On the other hand, the Atlantic and Polar currents meet, as already stated, over the Iceland-Faroe ridge.

a depth of 1100 metres, while at a similar depth hardly a

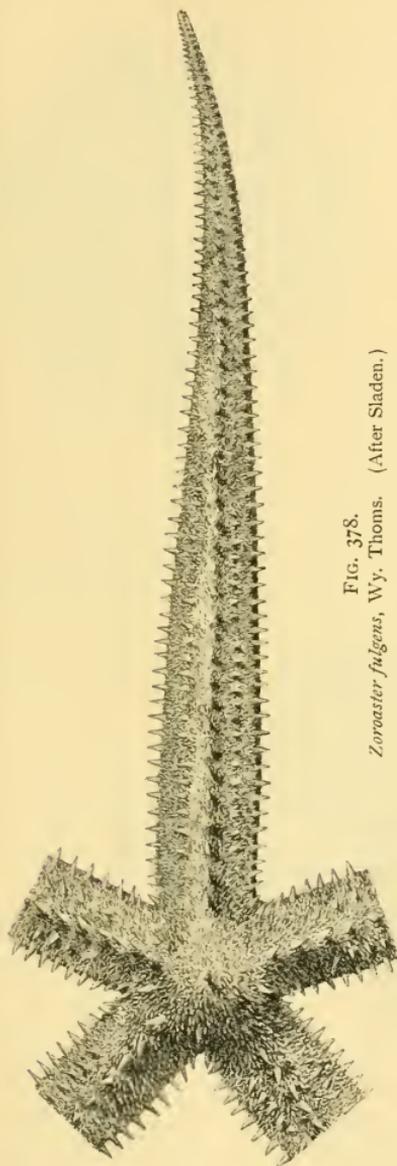


FIG. 378.
Zoroaster fulgens, W. y. Thoms. (After Sladen.)

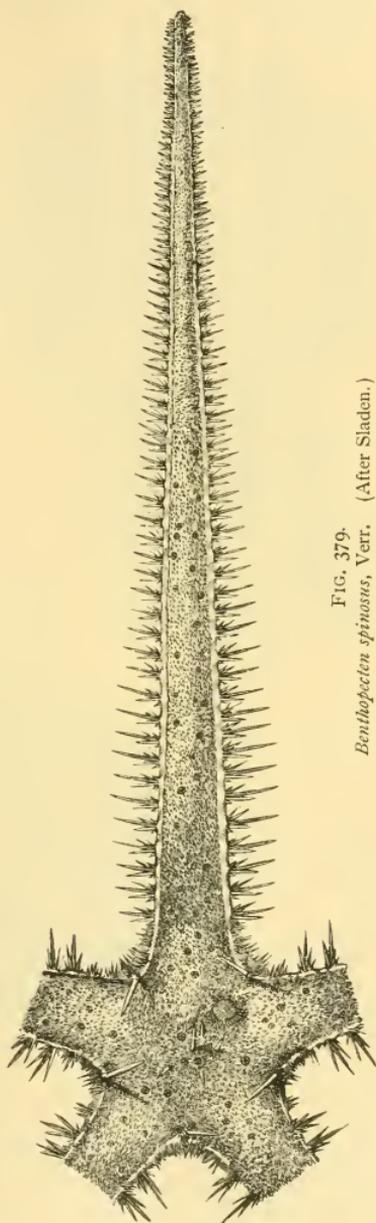


FIG. 379.
Benthopecten spinosus, Verr. (After Sladen.)

degree farther south the temperature was as high as $+8.07^{\circ}$ C.

Such great temperature differences produce a corresponding dissimilarity in the fauna (see pp. 13 and 661). We have trawled in the cold Norwegian Sea deep basin and captured more or less familiar arctic forms, and then only a few hours steam farther south we have trawled again on the southern slope of the Wyville Thomson Ridge, and taken forms, fishes as well as invertebrates, which one would expect to find in quite southern areas.

Among the deep-water forms of the Atlantic that are present in large quantities on the southern slopes of the ridges and plateaus we have first some species of sea-urchins belonging to the remarkable family of the Echinothuridæ (see Fig. 377).¹ They differ from all other sea-urchins in the structure of their shells, for, instead of having continuous plates of lime, their plates are connected by non-calcareous attachments of skin, so that their shells are flexible and more or less like leather. One species of holothurian, *Lætmogone violacea*, is very abundant. It belongs to the same division as the forms *Elpidia* and *Kolga*, which are so plentiful in the Norwegian Sea. The "Michael Sars" also found large numbers of the starfish *Zoroaster fulgens* (see Fig. 378).

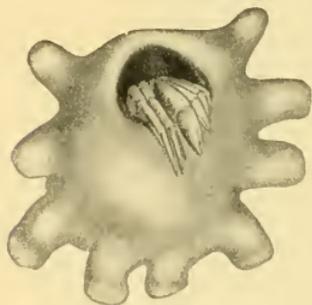


FIG. 380.

Epizoanthus paguriphilus, in symbiosis with *Parapagurus pilosimanus*. Reduced. "Michael Sars," 1902, 750 metres.

The following are a few other forms met with on the southern slopes of the ridges :—

Regular sea-urchins: *Echinus alexandri* and *E. affinis*, *Porocidaris purpurata*. Irregular sea-urchins: *Urechinus naresianus*, *Pourtalesia wandeli*, *Echinisigra phiale*, *Hemiaster expergitus*. Starfishes: *Bathybiaster robustus* (a species which outwardly resembles *B. vexillifer* of the Norwegian Sea, though the structure of its skeleton is different),² *Plutonaster bifrons*, *Benthopecten spinosus* (see Fig. 379), *Pentagonaster perrieri*, *Solaster abyssicola*. Ophiurids: *Ophiopleura aurantiaca*, *Ophiomusium lymani*, *Amphiura denticulata*. Cœlenterates: *Epizoanthus paguriphilus* (in symbiosis with *Parapagurus pilosimanus*, see Fig. 380), the pennatulids *Anthoptilum murrayi* and *Umbellula lindahli*, the true corals *Stephanotrochus diadema* (see Fig. 381) and *Flabellum* sp. (see Fig. 382), the horn-corals *Acanthogorgia armata* and *Strophogorgia challengerii*. Decapod crustaceans: *Lispognathus thomsoni*, *Scyramathia carpenteri*, *Geryon affinis*, *Cymononius normani*, *Neolithodes grimaldi*, *Parapagurus pilosimanus*, *Munida microphthalma*, *Munidopsis curvirostra*, *Uroptychus rubro-vittatus*, *Polycheles sculptus* and

¹ The species occurring here include *Phormosoma placenta*, *Calveria* (*Asthenosoma*) *hystrix*, and *Sperosoma grimaldii*.

² According to J. A. Grieg, Conservator of the Bergen Museum.

P. nanus, *Nephropsis atlantica*. Molluscs: *Dentalium caudani* and others.
Sponges: *Pheronema carpenteri* (see Fig. 383).

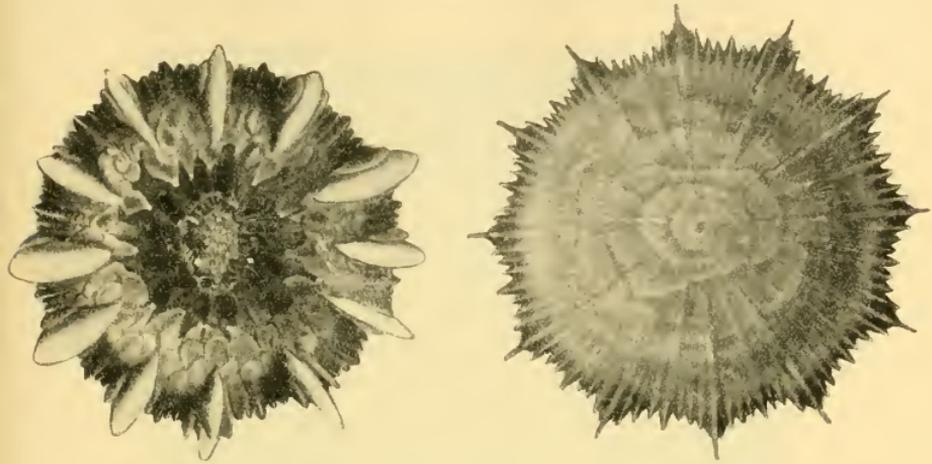


FIG. 381.

Stephanotrochus diadema, Moseley. "Michael Sars," 1902, 750 metres.

This list is very far from complete, but it shows what a number of forms there are which do not belong to the Norwegian Sea.

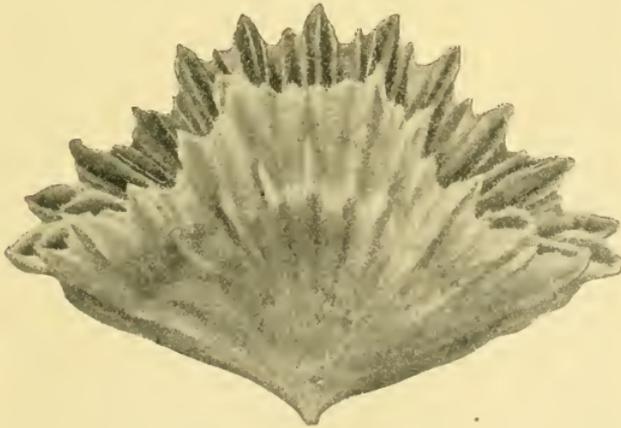


FIG. 382.

Flabellum sp. "Michael Sars," 1910, Station 101, 1853 metres.

Besides these specifically Atlantic forms, the fauna on the southern slope of the ridges and plateaus comprises others familiar to us from the boreal region of the Norwegian Sea, and from the North Sea, where they occur either on the plateaus or in the deeper parts of the fjords, including:—

Sea-slugs: *Stichopus tremulus*, *Bathyplores tizardi*, and *Cucumaria hispida*. Starfishes: *Psilaster andromeda*, *Astrogonium pareli*, *Pteraster multipes*, *Peltaster nidarosiensis*, *Brisinga coronata* and *B. endecacnemos*.

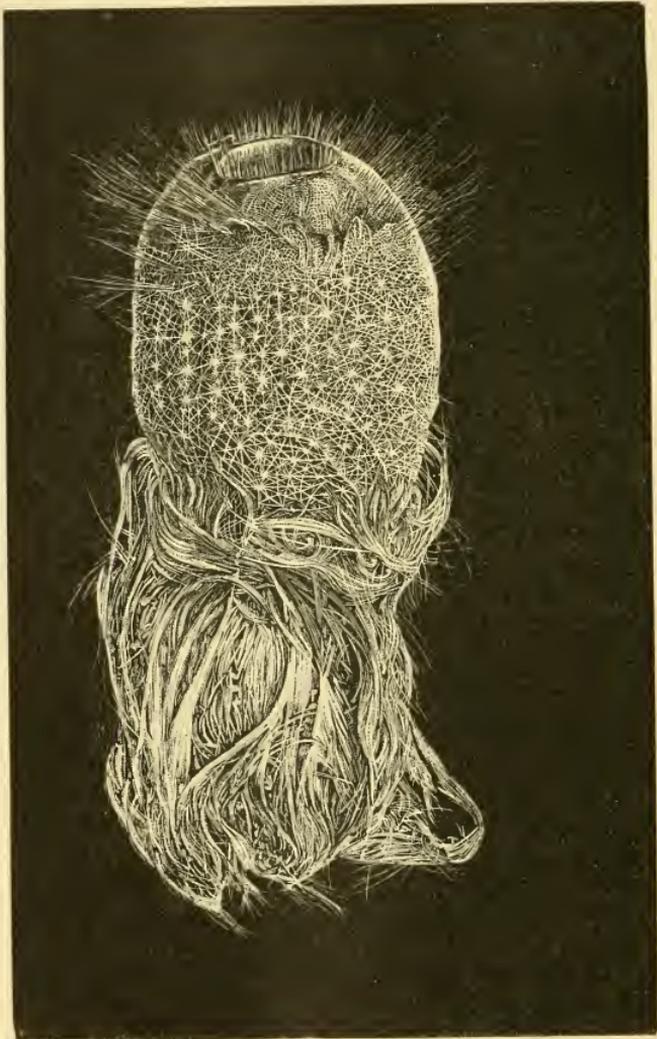


FIG. 383.

Pheronema carpenteri, Wy. Thoms. Reduced. (After Wyville Thomson.)

Brittle-stars: *Ophiacantha abyssicola*, *Ophiactis abyssicola*, *Ophiocten sericeum*, *Asteronyx loveni* (on *Funiculina quadrangularis*), *Gorgonocephalus lincki*. Sea-mice: *Spatangus raschi*, *Schizaster fragilis*. Sea-lily: *Rhizocrinus lofotensis*. Crustaceans: *Munida tenuimana*, *Pasiphæa*

tarda, *Pontophilus norvegicus*, *Pagurus pubescens*, *Calocaris macandreae*, *Geryon tridens*. Worms: *Aphrodite aculeata*, *Lætmonice filicornis*, *Lumbrineris fragilis*. Brachiopod: *Waldheimia septata* (in large quantities).

This list also might easily be extended. We see, therefore, that the fauna in the continental (archibenthal) deep-sea area of the Northern Atlantic consists partly of species peculiar to it, and partly of others that regularly belong to the continental deep-sea fauna of the Norwegian Sea. Two questions arise: How is the Atlantic archibenthal (and abyssal) fauna distributed outside the Norwegian Sea? Is there any real resemblance between this fauna

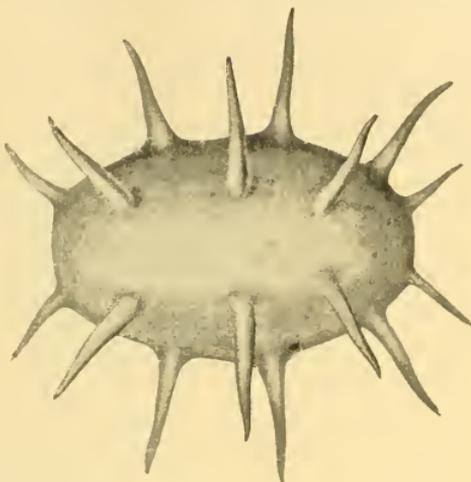


FIG. 384.

Deima fastosum, Théel. "Michael Sars," 1910, Station 48.

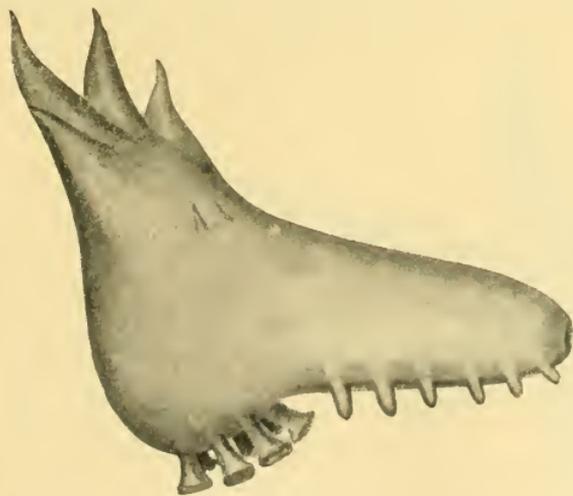


FIG. 385.

Peniagone wyvillii, Théel. "Michael Sars," 1910, Station 53, 2615 to 2865 metres.

and its counterpart in the cold area of the Norwegian Sea?

There seem to be some reasons for fixing the lower limit of the archibenthal fauna at about 2000 metres, and the upper limit at about 800 or 1000 metres. The charts of the area south of the ridges published by the Danish "Ingolf" Expedition show that beyond 2000

Limits of the archibenthal fauna.

metres the slope of the bottom becomes less steep downwards to the vast abyssal plain whose upper limit may be put some-

where between 2000 and 3000 metres; the temperature at the same time falls to about $2\frac{1}{2}^{\circ}$ C., which prevails everywhere in

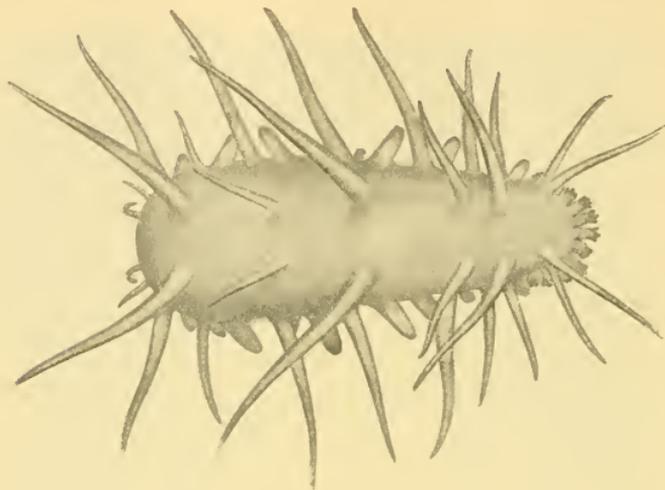


FIG. 386.

Oneirophanta sp. "Michael Sars," 1910, Station 10, 4700 metres.

the abyssal tracts of the Atlantic and other non-arctic waters. The upper limit certainly presents greater difficulties, but I

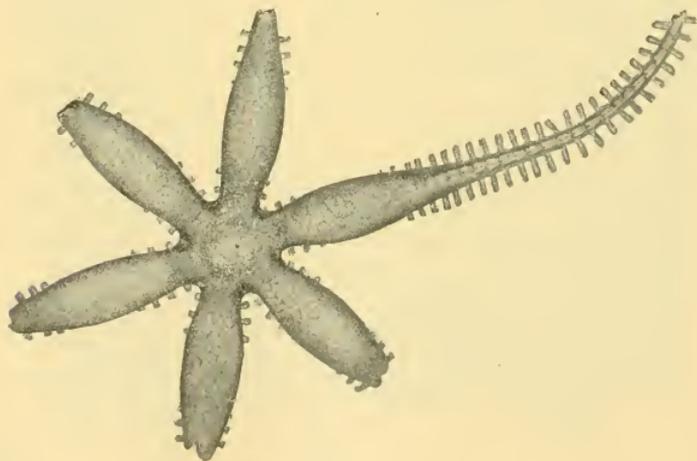


FIG. 387.

Freyella sexradiata, Perrier. "Michael Sars," 1910, Station 10, 4700 metres.

believe that a great many of the forms which characterise the archibenthal belt do not as a rule extend into depths less than

800 metres, though it is quite possible that certain forms may be met with at 600 metres. We have not yet acquired sufficient knowledge of the factors regulating vertical distribution to be able to divide the different parts of the Atlantic into vertical zones, and a division of this kind will, I fancy, always be more or less a matter of personal opinion. Besides, it is undeniable that forms which properly belong to the abyssal fauna may find their way to the lower parts of the archibenthal zone, and that

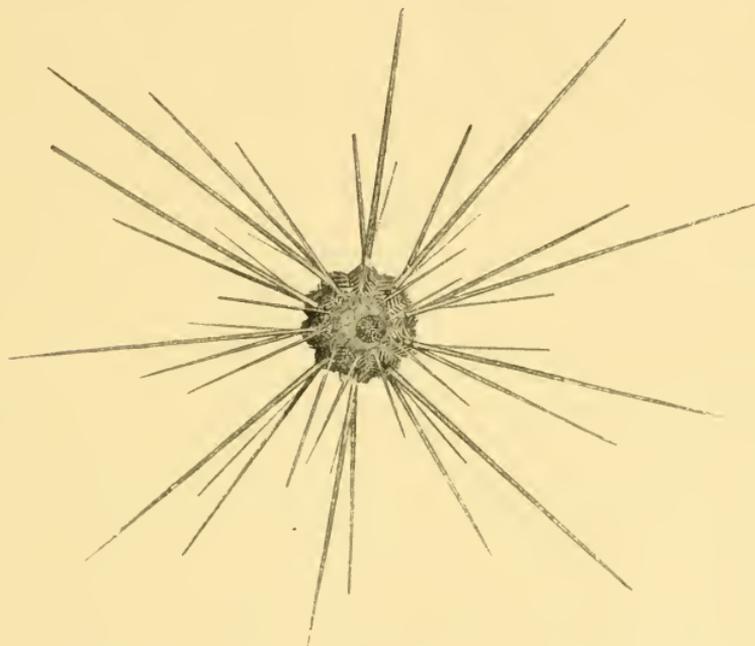


FIG. 388.

Salenia hastigera, Agassiz. Reduced. "Michael Sars," 1910, Station 88, 3120 metres.

archibenthal forms may go down into the abyssal region, while, given favourable conditions, certain littoral and sub-littoral forms may descend below the upper limits of the archibenthal belt. In any case there is no clearly defined boundary between archibenthal and abyssal areas.

Real abyssal forms are, for instance, the following: *Deima* Abyssal forms, *fastosum* (see Fig. 384), *Peniagone wyvillii* (see Fig. 385), *Oneirophanta* sp. (see Fig. 386), *Freyella sexradiata* (see Fig. 387), and *Salenia hastigera* (see Fig. 388), the last mentioned being found, however, also in the archibenthal zone.

I have already stated, with regard to the horizontal dis-

Archibenthal-
abyssal fauna
of the North
Atlantic.

tribution of the Atlantic deep-sea¹ fauna, that some of the forms occur likewise in the deeper parts of the boreal areas of the Norwegian Sea. This, however, refers only to a small proportion, since the majority consist of specifically Atlantic forms which do not cross the boundaries of the Norwegian Sea. As to the distribution of this specifically Atlantic fauna opinions differ. One very prevalent view is that, throughout the North Atlantic at any rate, temperatures, salinities, and other external physical conditions are extremely uniform, and that consequently the various forms have a correspondingly extensive distribution. Certain facts seem to me to contradict this, for instance, in such well-known groups as the echinoderms and decapod crustaceans, of which there are numbers of species. Mortensen's work on the North Atlantic echinids, and Koehler's description of the material collected by the Prince of Monaco, show that the West African coastal seas shelter 28 species of echinids, and that immediately to the south of the ridges 21 species of the same group have been trawled by the "Ingolf" and "Michael Sars." In all these two areas yielded 39² species, but not more than 10 of them are common to both.

We find much the same position of affairs when we compare the deep-sea fauna of the European or African Atlantic side with its counterpart on the West Atlantic (American) side.³ Merely taking the echinids, which may be regarded as specifically belonging to the archibenthal-abyssal fauna on both sides, there are altogether 74 species, but only 24 of them are common to both areas. The other groups of echinoderms have not yet been so carefully studied, but we know enough to show that in their case, too, a similar difference exists between these archibenthal-abyssal areas of the Northern Atlantic.

If we take decapod crustaceans the result is still the same. The northernmost portion of the European Atlantic area immediately south of the ridges has been examined by Danish and Norwegian expeditions at many stations, and 15 archibenthal-abyssal species of *Brachyura* and *Anomura* have been discovered at depths of 1000 to 2000 metres, while the researches of the Prince of Monaco, and the "Travailleur" and "Talisman" Expeditions, have resulted in 40 species being found at the same depths in West African Atlantic waters;

¹ I wish to make it clear that in what follows no distinction will be made between the archibenthal and abyssal faunas, unless expressly stated, but would merely remark that the bulk of the species belong to the archibenthal zone.

² I have omitted one or two species that have a very extensive bathymetrical distribution, inasmuch as they occur also in the littoral and sub-littoral zones of the coastal areas.

³ No account has here been taken of pelagic deep-water forms.

there are altogether 45 species in the two areas, 10 of which are common to both. A comparison between the West Atlantic (American) and the East Atlantic (European-African) deep-sea crustaceans shows an equally small number of common forms.

These instances show that, in spite of temperatures and salinities appearing identical in widely separated localities, it is possible to distinguish between the faunal communities of the deeper tracts of the ocean, and we perceive accordingly that temperature and salinity are not the only factors which regulate the distribution of species. Unquestionably there are other physical conditions which are of considerable importance, and it must further be remembered that biological factors, such as competition between species, exert a decided influence.¹

Murray showed in 1895 that the results of the "Challenger" Expedition afforded no confirmation of the opinion that a universal deep-sea fauna was spread all over the floor of the ocean; he compares the catches at six deep-water stations scattered over the Atlantic, Pacific, and Southern Oceans, the total number of species recorded being 290, but not a single species was common to the six stations.² At the same time we must remember that whole groups of forms, showing common characteristics in bodily structure, and belonging to types quite distinct from the littoral ones, belong either entirely or principally to the deep sea. These types are as a rule very extensively distributed, even if their species and genera may be limited to more circumscribed areas. Among fishes, for instance, we have the Macrurus-type, which is to be found in all the greater depths of the oceans of the world, although particular species have a comparatively limited distribution. The big group of holothurians known as Elaspoda is a particular type, separated in all essentials from the littoral and sub-littoral forms of holothurians. They belong almost entirely to the archibenthal and abyssal tracts of the different oceans, and are often abundant enough to give a distinct character to the deep-sea fauna. The same is true also of the Echinothuridæ, though in their case there are littoral and sub-littoral species; some species, however, have a comparatively limited distribution. Among crinoids we find survivals from remote ages of the earth, namely, the stalked genera (*Rhizocrinus*, *Bathycrinus*, *Pentacrinus*, etc.), as typical inhabitants of widely

¹ I must, however, point out that in all probability some faunal groups show a greater uniformity in widely separated localities than others.

² See Summary of Results Chall. Exp., p. 1438.

separated areas of the deep sea. And so, too, we could mention deep-water types of particular structure in the case of most of the invertebrate classes.

Now as these types are distributed over a large portion of the great oceans, and occur there sufficiently generally to give the deep-sea fauna its character, it is fair to assert that this fauna is more uniform than the fauna of the littoral and sub-littoral zones. As is well known, we get great differences in the physical conditions of the different areas of both littoral and sub-littoral zones, consequently we find there greater variations of the fauna than in the deep sea, where physical conditions are uniform, or, in other words, there are more coastal faunal areas than there are deep-sea faunal areas.

We may briefly characterise the deep-sea fauna as follows: It is largely composed of groups of forms, which morphologically differ in many essentials from the types of the littoral fauna. These groups are distributed over very extensive tracts of the deep sea, but the different species (genera, families) within the groups may be limited to more circumscribed areas. It is evident, therefore, that we can distinguish between the various faunal areas of the deep sea, though we may not yet be able to fix their boundaries.¹

The second question is how far the deep-sea fauna of the Atlantic resembles that of the Norwegian Sea, or in other words whether the Atlantic area with its higher bottom-temperatures shares many species with the "cold area" of the Norwegian Sea. As indicated on p. 13, Murray in 1886 summarised the results obtained in the Faroe Channel by the "Lightning," "Porcupine," "Knight Errant," and "Triton" Expeditions, and showed that of 385 species recorded from the "warm" and "cold" areas, only 48 species (or 12½ per cent) were common to both areas.²

The Lycods are especially characteristic of the cold area of the Norwegian Sea, whereas the Macrurids are typical of the deeper parts of the Atlantic, and Jungersen has drawn attention to the abundant horn-corals and joint-corals (Gorgonids and Isids) as well as the "star-corals" (*Oculina*, *Amphihelia*) and other corals of the Atlantic deep water, none of which occur in the Norwegian Sea deep basin.

The finding of such differences in the general character of

¹ In regard to the boundaries, however, the cold area of the Norwegian Sea forms an exception, and the same may possibly be true of the Antarctic deep sea (Chun, *Aus der Tiefe des Weltmeeres*; Mortensen, *Echinoidea of the "Ingolf" Expedition*).

² See also Murray and Tizard, *Proc. Roy. Soc. Edin.*, vol. xi. p. 638, 1882.

the two faunas led to a closer examination of certain forms which had formerly been looked upon as common to both areas, and as a result the Danish zoologist Jensen came to the conclusion that not a single species of *Lycodes* belonging to the cold area occurs in either the Atlantic or the boreal parts of the Norwegian Sea. He further succeeded in showing that one of the most characteristic mussels of the cold area, formerly designated *Pecten fragilis* and included as such among the fauna of the Northern Atlantic, is in reality a form peculiar to the cold area of the Norwegian Sea, and he has accordingly named it *Pecten frigidus*. Other naturalists have made similar discoveries in the case of a number of other forms. Thus, the irregular sea-urchin of the Norwegian Sea, *Pourtalesia jeffreysi*, is quite distinct from the Atlantic forms of the same genus. The characteristic starfish of the Norwegian Sea, *Bathybiaster vexillifer*, was formerly said to be distributed throughout the Atlantic, but it is now known to be different from the Atlantic form, which is *Bathybiaster robustus*. Another starfish, *Pontaster tenuispinus*, is represented by different varieties in the two areas, and the same is true of the ophiurid *Ophiocten sericeum*. The one characteristic pennatulid of the Norwegian Sea, *Umbellula encrinus*, is not found outside that sea, though there is a species closely related to it in the Atlantic, namely, *Umbellula lindahli*. Further evidence of the difference in the two areas is supplied by a pycnogonid belonging to the genus *Colossendeis*. A form in the Norwegian Sea deep basin, *Colossendeis angusta*, is said to occur also in the Northern Atlantic, but if we compare Atlantic and Norwegian Sea specimens we immediately recognise considerable differences in their structure, the latter being much more robust and furnished with shorter legs and claws. Any one seeing the two forms side by side would be able to tell the respective areas from which they came, though it may be difficult to find sufficient dissimilarities to designate them separate species.

These are merely a few instances. It must be admitted that nothing like a complete comparison of the species has yet been made, but we know enough to justify us in looking upon the cold area of the Norwegian Sea as a distinct deep-sea faunal region, which with Mortensen and Jungersen we may term the arctic abyssal.¹ No doubt, this arctic-abyssal region owes its

Cold area
of the
Norwegian
Sea an arctic-
abyssal area.

¹ In my description of the fauna in the cold area on pp. 517-524, I have made a distinction between the continental slopes and the abyssal region below 2000 metres, but no such distinction has been made here, for in instituting a comparison between the fauna of the cold area and the fauna of the Atlantic, I have included everything below 800 metres.

distinctive character chiefly to the low temperature of its bottom water, and to its isolated position due to the submarine ridges, which are responsible for the low temperature.

Formerly homogeneous fauna in the deep water of the Norwegian Sea and North Atlantic.

Though the cold area of the Norwegian Sea must be regarded on these grounds as a separate faunal region, it undoubtedly had formerly more direct connection with the deep water of the Atlantic. The many closely allied species in both areas point to a common origin. Most probably the fauna was at one time homogeneous in both areas, and the bottom water of the Norwegian Sea had then the same temperature as we find in the Atlantic nowadays. When physical conditions changed in the Norwegian Sea, either owing to the formation of the submarine ridges or from other causes, the fauna responded in two ways. Some of the warm water forms, including a number of present Atlantic forms, died out, while others were able to adapt themselves to the altered physical conditions and survived. Their adaptation, however, led to morphological alterations in the species, and in some cases these alterations were considerable enough to produce distinct species differing from the primitive Atlantic forms. Naturally, the isolation brought about by the submarine ridges had much to do with the development and establishment of their characteristics. In fact, it seems like an experiment carried out by nature herself on a large scale, and shows that external conditions can probably alter the bodily structure of a species, and consequently give rise to the formation of new species and varieties.

To understand properly the composition of the fauna in the Norwegian Sea at the present time we must go back to the Glacial Age, when uniform arctic conditions prevailed, and the fauna was everywhere arctic. This is confirmed by the marine deposits of the Glacial Age, containing exclusively arctic animal forms, met with in what are now boreal areas. When subsequently the ice melted, and the climate became milder, southern forms were able to immigrate, gradually distributing themselves throughout the boreal (and boreo-arctic) waters.

Origin of the present-day fauna of the Norwegian Sea.

The question as to what happened to the arctic fauna of the Glacial Age admits of a thoroughly satisfactory answer. In areas which at the present day are arctic, we still find arctic species, but in boreal areas the changes have been great. Some of the arctic forms which formerly inhabited what are now boreal areas have gradually died out from failure to adapt themselves to the new conditions; their remains may

be seen in glacial deposits, though they no longer live in the neighbourhood. Considerable numbers of the arctic species have succeeded in adapting themselves to the altered conditions, and constitute at the present day a regular portion of the boreal fauna, being at the same time distributed throughout the arctic region; these are the arctic-boreal forms.

The present-day fauna of the Norwegian Sea thus consists of two elements of different origin: (1) an *endemic* arctic element, and (2) a *southern* element derived from the littoral, sub-littoral, and the deeper parts of the Atlantic and Mediterranean. Thus we may divide the present-day fauna into groups, as follows:—

(1) One group consists of two categories of endemic arctic forms, viz. the purely arctic species, and the arctic-boreal species widely distributed throughout both arctic and boreal waters. Both categories existed everywhere in the Norwegian Sea throughout the Glacial Age, but only species of the last-named category have since been able to adapt themselves to the boreal areas. These species, therefore, in contradistinction to the remaining boreal forms, are of genuine arctic descent; that is to say, when a species occurs normally in both arctic and boreal areas, it is as a rule arctic in its origin.

The purely arctic species are not generally limited to the arctic region of the Norwegian Sea, but are usually widely distributed over the other arctic seas as well. Very frequently they inhabit all the areas round the pole (European, Asiatic, and American), and are in that case designated *circumpolar* species. The arctic-boreal species have precisely the same arctic distribution, but within the boreal region their southern boundaries have strict limitations; the bulk of them on the European side never leave the Norwegian Sea, being absent from the coast banks south of the British Islands and deeper parts of the Atlantic,¹ owing to the physical differences of the sea-water. A great many of the arctic-boreal forms, in boreal areas at any rate, inhabit the littoral or sub-littoral zone along the coasts and in the North Sea, and it is precisely in these zones to the south of the English Channel that the hydrographical conditions (and especially the temperature) differ

¹ There are, however, a few exceptions to this rule in the case of archibenthal and abyssal forms, some arctic-boreal deep-water species being distributed throughout the northern Atlantic as far as the Azores, including among others the echinoderms *Cribrella sanguinolenta*, *Pontaster tenuispinus* var., and *Ophiacantha bidentata*. An explanation may perhaps be found in the fact that the temperatures in the deeper boreal areas of the Norwegian Sea and Atlantic are fairly alike and uniform.

most from those of the Norwegian Sea. It seems, then, that the arctic-boreal species have not been able to adapt themselves to such conditions, or in other words that their power of adaptation is limited.

Outside the Norwegian Sea the species of this group have another area of distribution on the western side of the Atlantic, north of Cape Cod. The cold polar current sweeps down over the shallow parts of the American coast, and produces conditions that vary from arctic to boreo-arctic. As a result we find there arctic species, such as normally occur in the boreo-arctic areas of the Norwegian Sea and similar waters, and also the majority of the arctic-boreal species of the Norwegian Sea, a few of the latter being found as well a little to the south of Cape Cod, where conditions are more boreal.

(2) The second group consists of the boreal species, that is to say, those species which are limited to boreal areas within the Norwegian Sea, and those which are able to penetrate as well into boreo-arctic areas, though not into arctic tracts. Most of them are widely distributed over the northern Atlantic, either in its littoral and sub-littoral or in its deeper zones. We find their southern limit accordingly in the Mediterranean or at the Azores and the Canary Islands, while the deep-sea forms also go a long way south on the American side. Very few of the shallow-water forms, however, which extend southwards along the coasts of Europe are to be met with on the American side of the Atlantic, either because they cannot pass across the profound depths separating the two continents, or because they are debarred from advancing over the shallow northern parts of the Atlantic by the arctic conditions prevailing there. No satisfactory explanation can, therefore, be given for the presence of the very few boreal shallow-water forms which are common to both sides.

I have already stated that most of the species of this group have migrated into the Norwegian Sea in post-glacial times, and their present distribution is evidence of this; but there are some species nowadays confined on the eastern side to the boreal and boreo-arctic areas of the Norwegian Sea, and on the western side occurring to the north, and in some cases also a little to the south, of Cape Cod. As to their origin it is difficult to form an opinion, but most probably a number of them have been developed from arctic species after the ice-period came to an end, and have adapted themselves to their boreal

environment without any considerable changes in their bodily structure, as for example the decapod crustaceans *Hippolyte securifrons* (boreal)—*Hippolyte spinus* (arctic), *Sabinea sarsi* (boreal)—*Sabinea septemcarinata* (arctic). These forms are so alike that I cannot help thinking they must have had some phylogenetic connection in a geologically not very remote past. Other forms of the same category have no near relations in the arctic region, and cannot, therefore, be of arctic origin. That these species lived in the Norwegian Sea in late glacial times, when more boreo-arctic conditions prevailed, seems evident from their normal distribution nowadays in boreo-arctic areas, but it is impossible to decide whether they migrated into the Norwegian Sea from the American or the European side, or are derived possibly from southern species which have become morphologically so altered in their new home that the specific differences are unmistakable.

There are other species in the Norwegian Sea which, so far as is known, are strictly confined to the boreal and boreo-arctic areas, extending neither southwards nor to the coasts of North America in the west. They are, however, not very numerous. Like the forms just mentioned they could not have lived in the Norwegian Sea during the Glacial Age, and have probably originated there in post-glacial times, through development from southern immigrants that have been morphologically altered by adaptation to their environment. Several of them are closely allied to species known outside the Norwegian Sea. In some cases there would seem to have been a variation from the immigrated species, and we find inhabiting the Norwegian Sea both the primitive form and its descendant, like the crustaceans *Pagurus chiroacanthus* (a purely boreal endemic species)—*Pagurus levis* (immigrated primitive form), *Cheraphilus* (purely boreal endemic)—*Craignon* or *Pontophilus* (immigrated primitive form), *Virbius fasciger* (purely boreal endemic)—*Virbius varians* (immigrated primitive form). We may take it for granted, in view of what we know nowadays regarding the larger invertebrate forms, that the majority of these species have not a widespread distribution either southwards or westwards, and this might give grounds for believing that they had immigrated in their present form.

I have already mentioned that the littoral and sub-littoral faunas differ greatly in different areas of the Atlantic, and we find similar differences when we compare the Atlantic and

Distributional
areas.

Norwegian Sea. Certainly, many species are common to both, but there are far more peculiar species, the difference becoming more pronounced the farther south we go. The British Isles and the English Channel, the shallow-water fauna of which has been thoroughly studied, may be taken as the boundary where the northern and southern forms meet, both categories having reached their respective southern and northern limits of distribution. Along the British coasts and the Channel we get, accordingly, a kind of coalition territory, which has often been considered a separate faunal "province," and has actually been termed Lusitanian, though in my opinion without sufficient justification. The shallow-water faunas of Iceland and the Faroe Islands are so little known that it is impossible to say whether they are coalition territories or not. We must remember that it is much more difficult for shallow-water forms to find access to insulated areas like these, cut off as they are by profound depths and special conditions of temperature, than to the British coasts.

It is now admitted that faunal resemblances and dissimilarities between different marine areas are chiefly due to the physical conditions of the sea-water, but we must not regard them as the sole factors that regulate distribution. Two marine areas may have similar physical conditions and yet differ greatly faunistically. The Northern Pacific and Northern Atlantic have in many cases similar hydrographical conditions, but their faunas are on the whole quite distinct. There are other factors at work, and *isolation* probably does more than anything else to cause faunal differences. Two areas may be isolated from each other owing to the topographical character of the bottom, or because the physical properties of the water prevent any faunal connection, and consequently their faunas develop in different directions. *Temperature* is another of the chief physical conditions affecting distribution, and this explains why the British coasts, the Mediterranean, the Azores, and the Canary Islands, not to mention tropical coastal areas, shelter many forms which do not occur in the Norwegian Sea, although there do not seem to be any obstacles of a topographical character in the long connected coast of western and northern Europe.

We often see the limit of the arctic fauna in the Norwegian Sea put at about lat. 67° N., it being apparently forgotten that, owing to the hydrographical conditions, a large arctic area (part of the arctic-abyssal) extends as far south as lat. 60° N.,

while a purely boreal area (the deeper parts of the plateaus) extends to lat. 71° N. How little latitude affects faunal marine areas is evident when we compare the conditions on either side of the northern Atlantic, for on the American side the southern limit of the arctic shallow-water area lies about lat. 42° N., whereas on the European side it lies about lat. 67° N.

It has already been mentioned that intervening areas of a different hydrographical character can always prevent connection between two marine areas. The northernmost parts of the Pacific and Atlantic are arctic, and so also is the sea between them lying to the north of America. As a result the arctic faunas of the two areas have an uninterrupted connection and resemble each other. It is otherwise with the temperate parts of these oceans, for their boreal forms are isolated by the arctic tracts which intervene, though they share a few boreal species like *Crangon vulgaris*, as well as some others that are too closely allied for any one to doubt that they have formerly been identical. This probably arises from hydrographical changes in what are now arctic areas, which caused an isolation of specimens belonging to the same species in both areas, for there are indications that higher temperatures prevailed during post-glacial times in the coast-waters of some of these arctic tracts, and we may assume that the boreal species now occurring normally in boreo-arctic areas could exist then in what have since become purely arctic waters, and that by way of the shores of Canada and Alaska they had uninterrupted connection from ocean to ocean. When subsequently arctic conditions set in, the individuals of these boreal boreo-arctic species were compelled to retire southwards either to the Atlantic or to the Pacific, and all connection between them ceased. There is, of course, the possibility that these species lived as long ago as the tertiary age—in which case their present distribution can be easily explained—for tertiary fossils make it perfectly certain that a warm climate existed at that time in these latitudes.

The theory of a warmer post-glacial period is based upon the sub-fossil boreal molluscs found in certain arctic areas, like those from the south-west coast of Greenland described by Adolf Jensen, comprising shells of present-day boreal species no longer found there (*Anomia ephippium*, *Cyprina islandica*, *Zirphæa crispata*). In the Gulf of St. Lawrence, too, where conditions are nowadays arctic or boreo-arctic, we get quantities of empty mussel-shells belonging to undoubtedly southern forms. In the purely arctic waters of Spitsbergen there are sub-fossil

Warm climate
in post-glacial
period.

shells of *Mytilus edulis*, *Littorina littorea*, and *Cyprina islandica*, all boreal forms requiring a higher temperature and not living there now. Again, in northern boreal areas there are sub-fossil deposits of molluscs which require greater warmth than generally prevails in the boreal region (*Tapes decussatus* in Denmark, *Isocardia cor* in Norway, etc.), and it is held in some quarters that they could only have existed there when the temperature of the sea was higher.

Without criticising this theory, I should like to point out that we ought not always to take these finds of sub-fossil shells, belonging to species no longer inhabiting the adjoining seas, as evidence that great hydrographical changes have necessarily taken place in these areas. *Tapes decussatus*, for instance, which is now quite extinct along the coast of Denmark, is still to be found at various places along the west coast of Norway, from Bergen down to the south coast, but only in restricted localities where there are special natural conditions, that is to say, in shallow, well-sheltered, sandy bays, dry at low water, but affording full access to the salt water of the sea. These bays differ greatly from the "pools," which have a layer of fresh water at the surface and a muddy bottom smelling unpleasantly of sulphuretted hydrogen, but one feature they do possess in common, namely, that the sun raises their temperature considerably above the normal, so much so, in fact, that I have sometimes recorded 23° or 24° C. in the shallow water of these "Tapes bays" during the summer. Beyond question this high summer temperature, in combination with favourable bottom-conditions and the salt water, enables *Tapes decussatus* to thrive, and, what is still more important, to reproduce itself. It is not difficult to imagine that these rather limited localities may have been silted up, or cut off from the inflowing of salt water in some way or other, thus giving rise to sub-fossil deposits of *Tapes* shells. Nevertheless, in the case of boreal forms found fossil or sub-fossil in arctic areas, it seems to me that the warmer sea-water theory is the only reasonable one, since there is nothing to indicate that other important factors have been instrumental in their extinction.

It is important to ascertain how changes of temperature affect a species, whether they influence chiefly the development and growth of the young stages or the full-grown animals through other physiological processes. This question has not been deeply studied, though we have acquired sufficient knowledge to enable us to draw one or two conclusions. We know, for

instance, that a high temperature is required for the development of the oyster larvæ, and that along the Scandinavian coast it is only in the so-called pools that reproduction on any large scale takes place. Most probably the same is the case with many other inhabitants of the pools. The eggs and larvæ of the lobster are only developed during the warmest part of the year, though the female often carries spawn in winter, and it has been found by experiment that a fall of a few degrees in temperature is sufficient to retard the development of the larvæ several weeks. We can understand, therefore, why these forms do not live in arctic or boreo-arctic areas. Even though the fertile eggs or larvæ of boreal forms do not demand a higher temperature for their development, additional warmth may nevertheless be absolutely essential for the production and development of the ova within the mother's body. This, again, limits the distribution of many forms. The converse naturally holds good, and the development and other physiological processes of forms living exclusively in arctic waters can only take place at a low temperature.

We have already seen that many species are common to both boreal and purely arctic areas, and we must ascribe their widespread distribution to their power of adapting themselves to very different temperatures. Most likely we are dealing here with physiologically distinct species, even though the differences do not appear in corresponding morphological alterations in bodily structure. Not that differences of this latter kind are by any means excluded, as I have previously shown how a species may vary morphologically in certain directions, according as it occurs in arctic or boreal tracts. Future researches regarding the time when reproduction begins in these widespread forms in the respective areas will possibly show that the temperature at which development takes place varies a good deal less than the temperature prevailing in the different areas seems to indicate. For forms which live in boreal deep water, where the temperature is comparatively low all the year round, the difference is in any case not particularly great, and if it should prove that the widespread shallow-water forms develop during the winter in boreal areas, the difference there again is relatively small. Now we find that two of our typical littoral animals, the sea-slug *Cucumaria frondosa* and the starfish *Echinaster (Cribrella) sanguinolentus*, both of which inhabit arctic tracts, deposit their eggs in boreal waters early in March when the upper water-layers have a low

temperature. Experiments have taught us that the eggs of *Cucumaria*, which float near the surface, are so much affected by the surface-temperature of the coast-water in summer, that they are destroyed before a single larva is hatched, and it follows that the existence of this form in the littoral zone of the boreal region depends upon its period of reproduction being in the coldest months of the year; this is probably true also of *Echinaster*. Again, in the case of another arctic-boreal species, *Hippolyte gaimardi*, which along the west coast of Norway lives only in the littoral zone, the eggs develop during the cold months of the year, and the young are hatched in April. On the other hand, the lobster and the oyster, which are typical boreal forms inhabiting the littoral zone, have their period of reproduction in the months between June and August.¹ It must be admitted, however, that too few researches have been made upon which to base any general conclusions, and that the conditions in arctic tracts are quite unknown.²

Eurythermal forms.

Little is known as yet regarding the power of withstanding variations of temperature in different species, though most of the littoral animals, which are eurythermal and exposed to extreme variations, are astonishingly hardy. The Swedish zoologist Aurivillius has found, from observations made on the coast of Bohuslän in Sweden, that the barnacle (*Balanus balanoides*), the periwinkle (*Littorina littorea*), the sandgaper (*Mya*), the cockle (*Cardium*), and the lugworm (*Arenicola*) are able to endure for a considerable period a temperature below freezing point, and that the barnacle after being quite a long time in the ice had actually got vigorous young.³ Other littoral forms can protect themselves by descending into deeper water or by burrowing downwards into the mud. Still we cannot expect every species to be equally hardy, and wholesale destruction sometimes takes place under specially unfavourable circumstances, as, for instance, when the ice lasts too long or when the bottom freezes to too great a depth. That many of our littoral animals are able to live in boreo-arctic areas at a

¹ The German naturalists Samter and Weltner have published an interesting account of several arctic survival forms in North German lakes, illustrating their mode of life and reproduction. One crustacean, *Mysis relicta*, lives during the summer in the depths of cold lakes, and migrates landwards during autumn and winter, reproduction chiefly taking place at a temperature of 3° C. With another crustacean survival-form, *Pontoporeia affinis*, also, reproduction takes place in winter at temperatures varying between 0° and 7° C.

² It will be interesting to find out whether the boreal forms which penetrate into boreo-arctic areas with high temperatures for a short portion of the year have a short period of reproduction there, seeing that farther south their reproduction is known to extend over several months.

³ Aurivillius, "Littoralfaunans förhållande vid tiden för hafvets isläggning," *Öfvers. Kgl. Vet. Akad. Förhandl.*, 1895.

low temperature depends upon their finding the conditions necessary for reproduction, namely, higher temperatures during a portion of the year.

With regard to vertical distribution, it should be noted that the deeper a species lives the more uniform is the temperature to which it is exposed (stenothermal forms). This is true especially of the boreal areas, whereas in arctic tracts there is, as a rule, less difference between the temperatures in deep and in shallow water. It is not so much the depth as the temperature which regulates the distribution of animals. Another factor affecting distribution is salinity. Many forms, particularly the littoral ones, can stand a considerable variation of salinity (euryhaline species), while others are limited to water varying little in salinity (stenohaline species); the former includes those littoral forms which are as much at home among the skerries as far up the fjords or even in the mouths of the rivers, while the latter are only to be found off the coast or at considerable depths.

Stenothermal forms.

Euryhaline and stenohaline forms.

I have already tried to make it clear that no arrangement of vertical faunal zones applies to the whole of the Norwegian Sea. Forms which near the coast inhabit the littoral zone may be met with, normally apparently, out on the plateaus, in the sub-littoral zone, or perhaps in the deep-sea zone. Thus in the northern portion of the North Sea the trawl brought up from a depth of 180 to 190 metres *Ophiothrix fragilis* and large specimens of *Eupagurus bernhardus*—forms which are distinctly littoral along the Norwegian coast, and on the Faroe plateau we found these and a number of others at 110 metres. When we compare the North Atlantic with the Norwegian Sea we find still more striking differences, some of the species belonging to the Norwegian Sea occurring at far greater depths in the Atlantic. Now if we remember that the physical conditions in the medium in which a species lives are largely responsible for its vertical distribution, we may assume that in the littoral zone of the coastal waters and in the deeper parts of the Norwegian Sea and Atlantic there are at any rate certain identical conditions—temperature is most decidedly not one of them—which permit these species to live impartially in these areas. If it were merely a question of adaptation to quite different conditions, we might expect them to adapt themselves also to the deeper water-layers along the coasts.

Light is unquestionably one of the principal factors affecting vertical distribution. During the Atlantic Expedition of the

Effect of light.

“Michael Sars” in 1910 tests were made at various depths, and it was found that the light was far stronger south of the Azores than in the northernmost portion of the Atlantic at corresponding depths. But whether light is in itself sufficient to explain the different vertical distribution of a species in different marine areas, or whether there are other contributing factors, are matters yet to be decided. So far the question has not been sufficiently studied.

Effect of
currents.

The animals of the ocean-floor owe their distribution mainly to the agency of currents, since these serve to transport their pelagic larvæ, and perhaps also carry along full-grown bottom-forms like the amphipods and most of the prawns, which creep almost as much as they swim. It is through transportation of larvæ that the Norwegian Sea acquired most of its southern forms, and to this day these forms are still being disseminated in similar fashion throughout its component parts. We must bear in mind that most bottom-animals are attached, or, if we except a few crustaceans, very limited in their locomotion, and that consequently distribution by direct migration is all but impossible. The distribution of larvæ is subject to physical laws, and is dependent on the occurrence of the adult animals, and on the hydrographical conditions that prevail. Larvæ of arctic forms which inhabit only polar areas will, as a rule, only be transported by polar currents, so that the bottom they will reach, when their development is completed, will lie within the arctic region. In the same way the species belonging to Gulf Stream areas will be retained in boreal waters.

In addition to the two main currents of the Norwegian Sea there are several others consisting of blended layers, such as mixtures of the Gulf Stream, polar water, coast water, North Sea water, and bank water in various combinations. Probably every one of these plays its own particular part in distributing the larvæ, and consequently the bottom-animals, but we do not yet know to what extent. It seems absolutely certain, in view of what we have learnt regarding pelagic animals, that the larvæ in an area bordering on two currents may be swept away by one or the other, and so conveyed to a strange area. This, I fancy, explains why a coast-form like our common sea-urchin, *Echinus esculentus*, may be exceptionally met with in deep water out in the North Sea and Atlantic, where it succeeds in existing as a somewhat different variety. The occurrence of the arctic amphipods, *Epimeria loricata* and *Acanthozone*

cuspidata, far south in the Norwegian depression, is probably also due to the same cause, as they have most likely been carried there by one of these blended currents and have managed to adapt themselves to more boreal conditions. That larvæ may be transported in quantities to areas where they are unable to develop was proved during the autumn of 1903, when the fjords near Bergen were found to be full of *Actinotrochæ* (larvæ of *Phoronis*, a form related to the bryozoans, which occurs in the south parts of the North Sea and other southern waters), but in the following year repeated dredgings failed to reveal a single full-grown animal either there or anywhere else on the coast of Norway.

Currents also carry nourishment to the bottom-animals and sweep away the finer particles of mud and other soft substances, leaving, in sounds especially, nothing but the bare rock, or perhaps a slight covering of coarse sand and shells. This enables attached forms to thrive, since the current prevents their being buried, and at the same time supplies them with the nourishment they require.

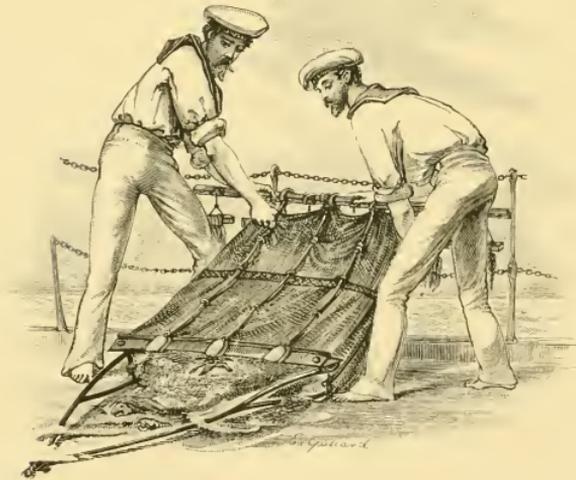
It is strange that a few boreal forms are peculiar to the plateaus and do not enter the fjords, for the fjords and plateaus have most of their forms in common. Whether it is due to the fact that these peculiar forms develop at a time when the Atlantic water, in which they probably live during both their larval and full-grown stages, does not penetrate into the fjords, or whether the physical conditions of the fjords are in some way uncongenial, is unknown. Similarly we are unable to explain why a number of boreal forms, which are widely distributed elsewhere, avoid the North Sea and Skagerrack, or why some plateau-forms enter fjords north of Stat, like the Trondhjem fjord, but are absent from fjords farther south.

Distribution is of course very much affected by the character of the sea-floor, since whole groups of animals are limited by their structure or mode of living to some particular kind of bottom. No doubt there are forms which appear to be equally at home everywhere, but there are others again which are extremely exacting in their requirements. This is especially the case with burrowing forms, like the lancelet and numbers of mussels and worms, and as a result we find, when conditions are favourable, that extensive stretches of the bottom are occupied by one or more of these. Some forms like sponges and corals, belonging to groups most of whose members are attached and therefore confined to rocky bottom, have developed special organs in the

Effect of
bottom-
deposits.

way of root-like outgrowths, by means of which they adhere to soft bottom and can accordingly reside there normally. Plant-growths have much to do with the distribution of bottom-animals, providing foundations for attached forms; some few species appear to be associated solely with one particular kind of plant, whether it be eelgrass or laminaria or some other congenial alga.

A. A.



CHAPTER IX

PELAGIC ANIMAL LIFE

IN the "Challenger" Summary, Sir John Murray writes as follows: "The tow-net experiments carried out on board the "Challenger" during several years in all parts of the world led me to the conviction that these intermediate regions were inhabited, although with a much less abundant fauna than the waters near the bottom or those near the surface of the ocean. Thousands of hauls of the tow-nets were taken in the surface and sub-surface waters, and the contents were daily submitted to microscopic examination; the forms present in these waters became quite familiar to the naturalists. When, however, the tow-nets were sent down to deep water, and dragged in depths as nearly as possible of 500, 1000, and 2000 fathoms, organisms—such as the *Tuscaroridae* among the *Radiolaria*—were nearly always observed in the gatherings in addition to the usual surface organisms. Organisms from these intermediate layers of water appear to have a much wider horizontal distribution than the surface fauna or flora. These oft-repeated experiments produced a strong belief that all the intermediate zones of depth were inhabited. I am not aware that the *Tuscaroridae* have ever been taken in the surface or sub-surface waters. It is probable that the animals in the intermediate zones of depth obtain their food by the capture of the dead organisms continually falling from surface to bottom. It is well known that the deposits at the bottom are in most regions chiefly made up of the dead shells and skeletons of surface organisms."¹

During the cruise of the Italian ship "Vettor Pisani," Captain G. Palumbo constructed a closing-net with which Lieutenant Gaetano Chierchia collected animals from accurately determined depths. At the zoological station at Naples this work was continued by Eugen von Petersen and Professor Carl Chun.

¹ Summary of Results Chall. Exp., p. 1455, 1895.

When Chun in 1898 fitted out the "Valdivia" Expedition, special arrangements were made for the purpose of obtaining an accurate knowledge of the animal life in "mid-water." Hundreds of hauls with closing-nets and with other large nets were taken at various depths, the material procured proving that the main conclusions drawn from the "Challenger" Expedition were quite correct. Even in hauls between 5000 and 4000 metres living crustaceans as well as larvæ of the same animals were captured—a sufficient proof that these organisms not only live but also breed at these depths.

The conception of a "pelagic" mode of life, originally associated with the animal-life of the ocean-surface, thus gradually proved to hold true for life in mid-water also, and to apply to floating or drifting organisms as well as free-swimming animals. The main characteristic of pelagic life is its independence of the bottom. The term "bottom-animals" is applied not only to the animals fixed to or creeping along the bottom, but also to those animals which, like certain crustaceans and bottom-fishes, swim and feed along the bottom. But it is impossible to draw a perfectly sharp limit between these migrating bottom-dwellers and some of the deep-living pelagic animals, which have been called "bathypelagic." In accordance with the varying conditions in deep and shallow water and in different parts of the ocean, the pelagic animals have been subdivided into groups: thus Ernst Haeckel¹ introduced the idea of "Holo-pelagic" (wholly pelagic) to distinguish those forms leading an entirely pelagic life from those forms having a bottom-stage like the Hydromedusæ, which he called "Meropelagic" (partly pelagic); he further distinguished those forms found only in coastal waters by the term "Neritic" from those found only in the open sea, which he called "Oceanic."

As in all geographical comparisons of animals we may divide the pelagic organisms into tropical, subtropical, boreal, arctic, and antarctic forms. It has also been proposed to arrange the pelagic fauna in certain bathymetrical zones, distinguishing between those forms living in profuse light, or in the region of twilight, or in the dark abyssal waters, but such distinctions are arbitrary, because our knowledge of the bathymetrical distribution of animals is limited, because the laws of distribution are imperfectly understood (for instance, the effects of light), and because the bathymetrical

¹ Ernst Haeckel, *Plankton-Studien*, Jena, 1890. Haeckel used the words "holoplanktonic" and "meroplanktonic," but I prefer "holopelagic" and "meropelagic," as the word "plankton" is not so clearly defined, and is used in different ways (see Chapter X).

occurrence of certain species is subject to great variation in different regions. We shall, therefore, dispense with the many Latin and Greek terms employed to define such groups of pelagic organisms, and simply use the term "bathypelagic" to denote those animals that live deep in the intermediate layers. Hensen proposed the term "plankton" to denote every kind of organism floating or drifting in the water, either shallow or deep, "dead or living," and Haeckel applied it so as to include all pelagic animal and plant life as a whole, in contrast to bottom-life as a whole, which he terms "benthos."

In this chapter I propose to consider only the different species or communities of pelagic animals, not the pelagic life as a whole. Pelagic forms occur in all classes of the animal kingdom from the unicellular Protozoa to the fishes; to mention them all would be to write a text-book on zoology. The chief aim of this book is however to give some of the general and special results of the cruises of the "Michael Sars." A discussion of the results relating to pelagic animals (as with the bottom-fish) calls for some information about the principal forms, so I commence with a short review of pelagic animals.¹ In the absence of descriptions of the animals, the illustrations will give the reader an idea of some of the forms referred to. Their geographical distribution, as known from previous expeditions, is briefly indicated, and in a later section I shall deal with the distribution of the most important animals in their communities in the different areas of the North Atlantic and the Norwegian Sea.

I. SHORT REVIEW OF PELAGIC ANIMALS

Among unicellular animals the Foraminifera and the Radiolaria may be given prominence. Being exceedingly rich in species, as well as individuals, they play an enormous part in the economy of the ocean, and their shells constitute an essential portion of the deposits on the ocean-floor.

The pelagic foraminifera have shells of carbonate of lime, usually divided into several chambers communicating with each other, allowing the protoplasm to penetrate the whole shell, which is perforated by innumerable small apertures (foramina), through which the finest threads of the protoplasm (the pseudopodia) may pass. In Chapter IV. p. 172, a list is given of all the species known to be pelagic, and certain important forms are figured. The list embraces eight genera and twenty-six species, fourteen of which belong to the genus *Globigerina*, also represented by an enormous number of individuals. During the

Foraminifera.

¹ A very useful review of the results of modern (especially German) investigations is given in Steuer's *Planktonkunde* (Leipzig and Berlin, 1910), with extensive lists of literature.

cruise of the "Challenger" Sir John Murray captured them from a boat in calm weather floating at the surface of the ocean, where they were just visible to the naked eye. On the ocean-floor in moderate depths in tropical and sub-tropical regions the dead shells occur in such enormous numbers that the deposit is called Globigerina ooze. The species and individuals decrease in number as we go north or south from the tropics, and in the Norwegian Sea only one species, viz. *Globigerina bulloides* (see Fig. 118, p. 150), occurs in any abundance either at the surface or in the bottom deposits.¹

Radiolaria.

The Radiolaria occur in a profusion of species. The cell possesses a central capsule containing the nucleus or nuclei and an outer layer of protoplasm capable of throwing out very thin threads (pseudopodia). The skeleton is developed in various ways and facilitates the discrimination of an enormous number of sharply separated forms (see Figs. 110 to 117 in Chapter IV.). In his report on the "Challenger" Radiolaria, Haeckel described no less than 20 orders, 85 families, 739 genera, and 4318 species, taken partly from the deposits and partly in the townettings; in one single bottom sample from 4475 fathoms in the Pacific 338 species were found. The Radiolaria are wholly pelagic, and occur in all oceans where the salinity is not too low (as it is in the Baltic), over deep water as well as over shallow water, attaining their maximum development in the Pacific.

In order to discuss their distribution we may mention some of the typical groups:—

The Acantharia are mostly spherical; the perforations of the central capsule are regular. The skeleton consists of acanthin, a peculiar elastic organic substance, in the form of twenty needles radiating from the centre of the sphere. The majority of the species occur in tropical waters and in the upper layers of the ocean. They are divided into two groups, Acanthometra and Acanthophracta.

In a vertical haul in the Atlantic Popofsky² found no less than 75 species of Acanthometra alone, and a haul in the Indian Ocean procured a similar number. North and south from the equator the number of species decreases, the majority living between lat. 40° N. and 40° S. The different regions of this warm belt have many species in common. According to Popofsky the total number of known species is 179, of which only 18 have been found in the Atlantic to the north of lat. 50° N., and 10 of these are known only as casual or seasonal visitors. The commonest forms in northern waters are *Acanthochiasma fusiforme*, *Acanthometron pellucidum* (Fig. 389), *Acanthonidium echinoides* (Fig. 390), *Phyllostaurus quadrifolius*, *Acanthostaurus nordgaardi* (Fig. 391).

It is generally supposed that the temperature limits the bathymetrical distribution of the Acantharia, just as it is known to limit their horizontal occurrence. In the Atlantic the German Plankton Expedition found the deepest living species at a temperature of 9.4° C. In the Mediterranean, where high temperatures occur deeper, they have been

¹ See Murray, "On the Distribution of the Pelagic Foraminifera at the Surface and on the Floor of the Ocean," *Natural Science*, vol. xi. p. 17, 1897.

² Popofsky, "Acanthometriden," *Ergeb. Plankton-Expedition*, Bd. iii., 1904; "Die nordischen Acantharien," *Nordisches Plankton*, No. xvi.

taken down to a depth of 1200 metres. In northern waters several species have been taken just at that time of the year when the temperature is highest.

The Aulacanthidæ, the Challengeridæ, the Tuscaroridæ, and the Medusettidæ have silicious skeletons and prefer mainly cold water.

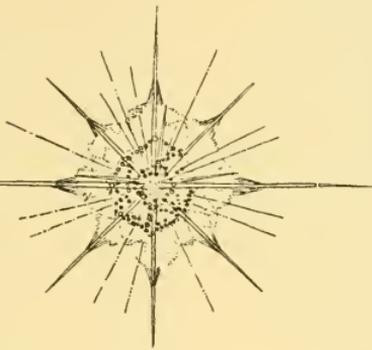


FIG. 389.

Acanthometron pellucidum, J. Müller.
(After Hertwig, from Steuer.)

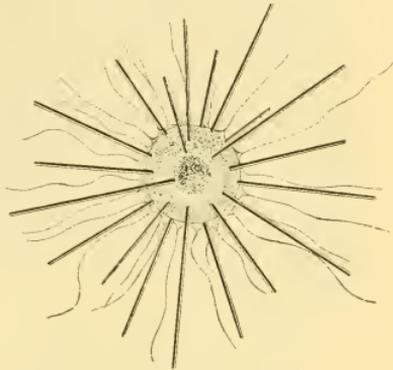


FIG. 390.

Acanthonidium echinoides, Claparède and
Lachmann. (From Popofsky.)

The Aulacanthidæ are spherical, the skeleton consisting of numerous isolated hollow needles, some of which radiate from the centre while other smaller ones are arranged along the surface of the sphere. The great majority of the Aulacanthidæ have been found in the north-western corner of the Atlantic (the Irminger Sea and Davis Straits), and also south of the Cape Verdes, but several species are very widely distributed, for instance *Aulographis pandora* (Fig. 392) taken in the Mediterranean, Indian Ocean, Pacific, and also in the Atlantic north and south of the Equator. This species occurs between 400 and 1000 metres, and is considered specially characteristic of these depths. One of the best-known species, *Aulacantha scolymantha* (see Fig. 393), is found, like several other radiolarians, in two races distinguished by their difference in size. One is a pygmy 0.6 to 1.8 mm. in diameter, the other a giant about 3 millimetres in diameter. At Naples, and during the cruise of the "Valdivia," Haecker¹ studied the bathymetrical

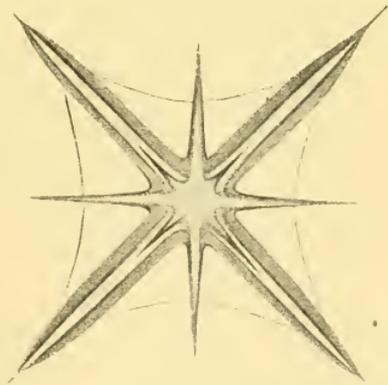


FIG. 391.

Acanthostaurus nordgaardii, Jörgensen (1909).
(From Jörgensen.)

¹ V. Haecker, "Tiefsee-Radiolarien," *Wiss. Ergeb. "Valdivia" Expedition*, Bd. xiv. (Jena, 1908).

distribution of these forms, and found the small one (var. *typica*) occurring in all depths, the large one (var. *bathybia*) in depths between 400 and 1000 metres; the giant form occurs very rarely in Norwegian fjords.

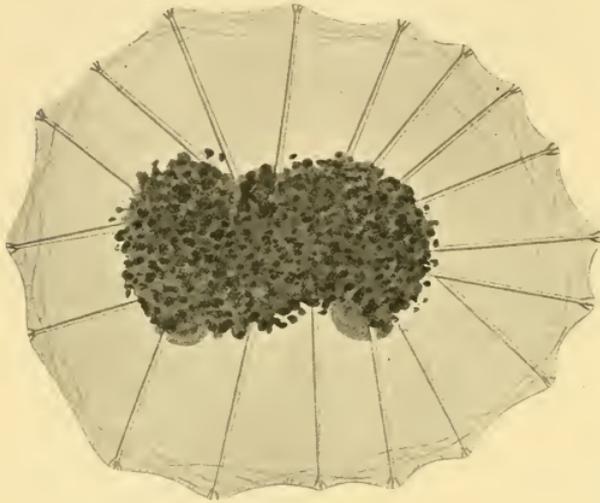


FIG. 392.
Aulographis pandora, Haeckel (about $2\frac{1}{2}$). (From Haecker.)

The Challengeridæ have an egg or lentil-shaped silicious shell of most delicate structure, the aperture being provided with a collar or tube-shaped moulding (see Fig. 394). They occur in all oceans, but sometimes their distribution is very peculiar, for some species live only in abyssal depths under the equator, others at both poles, others only in Antarctic waters; some species live in the surface waters, others between 50 and 400 metres, others between 400 and 1000 metres, others again between 1500 and 5000 metres. From Haecker's report on the Radiolaria of the "Valdivia" Expedition we reproduce some of these species. *Protocystis* (*Challengeria*) *tridens* (Figs. 394, 2 and 3) occurs in the northern and southern cold zones, having been taken as far north as Spitsbergen, in the Norwegian fjords, the Skagerrack, round Greenland, in the Labrador current, and also in Antarctic waters by the "Valdivia"; in Norwegian waters it has been taken in deep water up to 50 metres below the surface. *P. swirei* (Fig. 394, 1) has been taken only in the Antarctic from the surface down to a depth of 4000 and 5000 metres. *P. thomsoni* (Fig. 394, 4) belongs to a group of

The Challengeridæ have an egg or lentil-shaped silicious shell of most delicate structure, the aperture being provided with a collar or tube-shaped moulding (see Fig. 394). They occur in all oceans, but sometimes their distribution is very peculiar, for some species live only in abyssal depths under the equator, others at

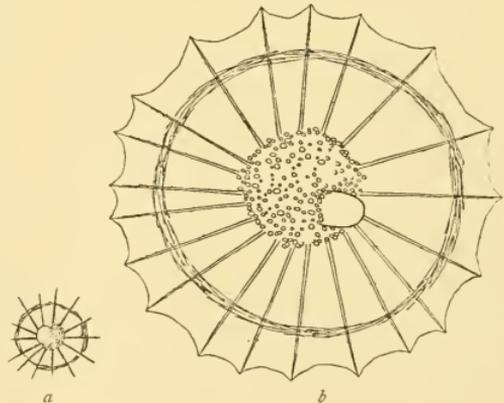


FIG. 393.
Aulacantha scolymantha, Haeckel. *a*, var. *typica*; *b*, var. *bathybia*, deep-sea form. (After Haecker, from Steuer.)

large forms, of which the species *P. naresi* is the largest. These forms have been taken in abundance only at the greatest depths, as is the case with the giant race of *Aulacantha scolymantha*. Among Norwegian Sea forms we may mention *Protocystis bicornis* and *P. harstoni*, *Challengeria xiphodon*, and *Porospathis holostoma*, the three latter being found in the Atlantic as well. *P. holostoma* has been taken at great depths in the Norwegian Sea and in the Sargasso Sea.

The Tuscaroridae are genuine deep-sea forms, having a bottle-shaped shell provided with large strong spikes arranged in rings around the main axis (see Fig. 395). In hauls with closing nets they have never been taken in less than 400 metres of water; some species, for instance *Tuscaretta tubulosa*, occur in all oceans.

Remarkable deep-sea forms, as well as certain small surface forms, belong to the Medusettidae. *Medusetta arcifera* has been taken in the Norwegian fjords.

On the basis of his study of the Radiolarians of the "Valdivia" Expedition, Haecker distinguishes the following bathymetrical regions:—

(1) An upper Acanthometra-layer.

(2) A Challengeria-layer (50 to 400 metres).

(3) A Pandora-layer (from *Aulographis pandora*, 400 to 1000 metres), in which the Tuscaroridae are also found.



FIG. 394.

Challengeridae ($2\frac{1}{2}$). 1, *Protocystis swirei*, John Murray; 2 and 3, *Protocystis tridens*, Haecker; 4, *Protocystis thomsoni*, John Murray. (From Haecker.)

(4) An abyssal layer (1500 to 5000 metres), in which the large Challengeridæ (*Protocystis naresi*, *P. thomsoni*) are found.

The multicellular animals are all represented among the pelagic forms, from the medusæ to the fishes.

Commencing with the Cœlenterates we may mention the Medusæ, the Siphonophores, the Ctenophores, and the larval Actiniæ.

Medusæ.

The Medusæ are generally bell-shaped or globular, with a more or less transparent jelly-like body. On the edge of the bell some forms have a band-shaped fold or moulding ("craspedon"), and accordingly the medusæ are divided into two main groups: Craspedota with a craspedon, and Acraspeda without a craspedon.

The Craspedota comprise four groups: Anthomedusæ, Leptomedusæ,

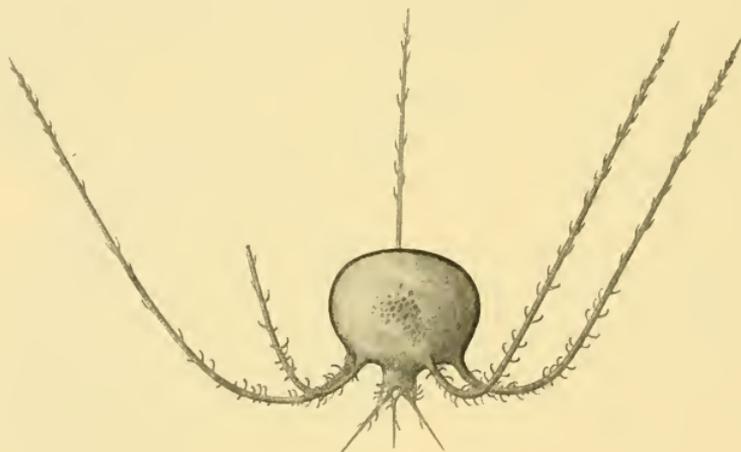


FIG. 395.

Tuscaretta globosa (Borgert), subsp. *chuni*, Haecker (about 2 $\frac{1}{2}$). (From Haecker.)

Trachymedusæ, and Narcomedusæ, of which the first two are meropelagic and the last two holopelagic. The meropelagic forms pass through an "alternation of generations," *i.e.* the eggs produced by the medusæ develop into larvæ which attach themselves to the bottom and grow into hydroid polyps or zoophytes; by "budding" the zoophytes produce small medusæ, which lead a swimming pelagic life and produce eggs. Fig. 396 shows a colony of hydroids with different stages of medusæ developing, and Fig. 397 shows one of the medusæ just after leaving the colony. The Craspedota are therefore termed hydroid medusæ or hydromedusæ, although they include two groups with no alternation of generation and no bottom stages, which are supposed to be descended from neritic forms. The hydromedusæ having an alternation of generations are represented by a vast number of species in the surface waters off all coasts where the temperature is not too low. They do not occur far from land nor in deep water. Their pelagic life

is short and they die unless they reach the bottom within a certain limited time.

Damas and Koefoed¹ mention as the most important forms in Scandinavian waters the following species: *Sarsia tubulosa*, *S. eximia*, *Euphysa aurata*, *Corymorpha nutans*, *Hybocodon prolifer*, *Bougainvillia superciliaris* var., *Dysmorphosa octopunctata*, *Tiara pileata*, *Linneandra norvegica*, *Melicertidium octocostatum*, different species of *Obelia* and

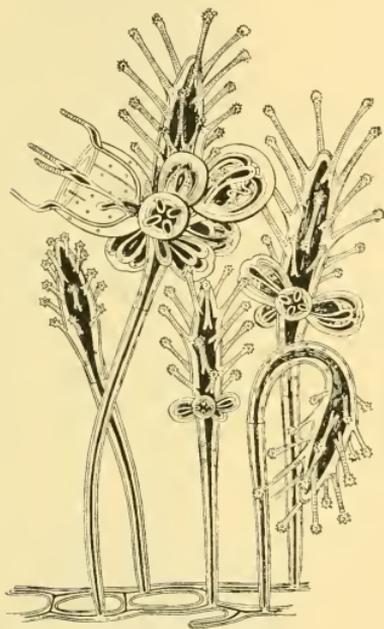


FIG. 396.
Hydroid colony of *Syncoryne pulchella*.
(From Allman.)

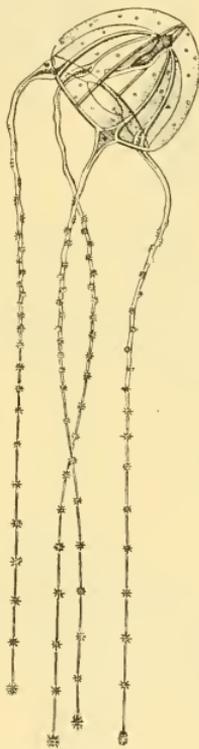


FIG. 397.
Medusa, just after leaving
colony.

Phialidium, *Mitrocomella fulva*, *Tiaropsis multicirrata*, and *Lutonia socialis*. From the Arctic plateau between Spitsbergen and Bear Island they mention *Sarsia flammea*, *Codonium princeps*, *Catablema campanula*, *Hippocrene superciliaris* (see Fig. 398). These forms do not play any part in the fauna of the open ocean.

The Trachymedusæ have a direct development without a hydroid or bottom stage. In northern waters we meet with only one species in such numbers, and so frequently, that it may be considered truly northern

¹ Damas et Koefoed, "Le Plancton de la Mer de Groenland," Duc d'Orleans' *Croisière océanographique* (Bruxelles, 1905).

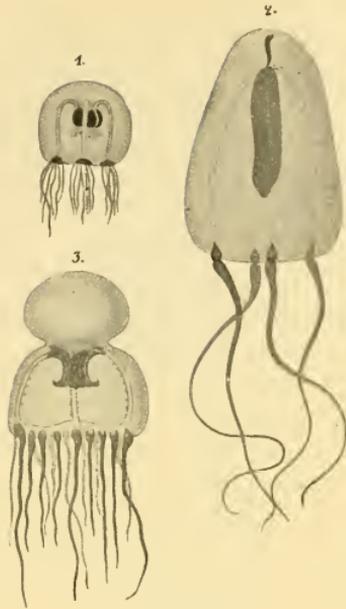


FIG. 398.

Arctic Medusæ: 1, *Hippocrene superciliaris*, Ag.; 2, *Codonium princeps*, Haeckel; 3, *Catablema campanula*, Haeckel. (From Vanhöffen.)

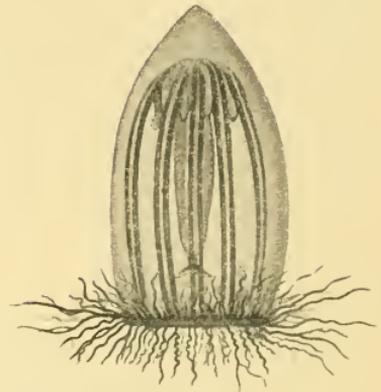


FIG. 399.
Aglantha digitalis, O. Fabr. ($\frac{2}{3}$).
(From Vanhöffen.)



FIG. 400.

Liriope tetraphylla, Chamisso and Eysenhardt (about $\frac{2}{3}$). (From Vanhöffen.)



FIG. 401.

Crossota brunnea, Vanhöffen ($\frac{2}{3}$).
(From Vanhöffen.)

(boreal), viz. *Aglantha digitalis* (see Fig. 399), which sometimes plays an important part in the pelagic life of the Norwegian Sea; in the North Sea Sea ferns fell in with a shoal of these medusæ which he estimated at $23\frac{1}{2}$ billions of individuals. As mentioned by Haeckel, it is characteristic of this form that it suddenly appears in enormous quantities for some days and then suddenly disappears for some months.

As rare visitors in the north may be mentioned, *Pantachogon haeckelii*, *Pectyllis arctica*, and *Crossota norvegica*.¹ Other species are strictly limited to the warm zone of the ocean, which may be said to

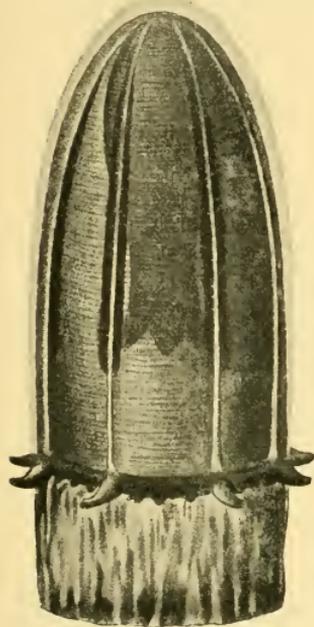


FIG. 402.

Agliscra ignea, Vanhöffen ($\frac{2}{1}$).
(From Vanhöffen.)

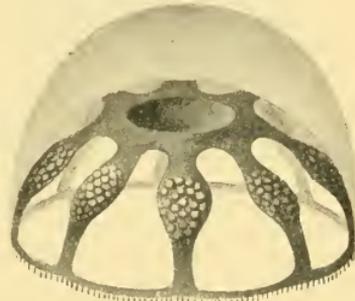


FIG. 403.

Halicreas rotundatum, Vanhöffen ($\frac{2}{1}$).
(From Vanhöffen.)

reach the 40th or 50th degree of latitude, where we find some small forms living entirely in the upper layers of the Atlantic and Indian Oceans, as for instance *Rhopalonema velatum*, *Aglaura hemistoma*, and *Liriope tetraphylla* (Fig. 400); they are devoid of colour or only faintly tinted, some of them being only a few millimetres in diameter. Others are genuine deep-sea forms, found only below 600 or 1000 metres. *Crossota brunnea* (Fig. 401) is dark brownish, *Agliscra ignea* (Fig. 402) is a flaring red, and *Halicreas rotundatum* (Fig. 403) is distinguished by bright red markings.

The Narcomedusæ are oceanic forms, including some small colourless surface forms and strongly tinted (brown) deep-sea forms.

¹ This species was taken by me in a deep haul in the Norwegian Sea, and Vanhöffen placed it very near to the tropical species *Crossota brunnea*, see *Wiss. Ergeb. "Valdivia" Expedition*, Bd. 3, 1902; and "Die Fauna und Flora Grönlands," *Grönland Expedition* (Berlin, 1897).

The Acraspeda include the common jelly-fish, and excepting the genus *Pelagia* they all go through an alternation of generations. The free-swimming medusæ produce eggs, the larvæ fixing themselves to the bottom and developing a zoophyte differing from the hydroid-zoophyte in that it produces only one kind of bud; the division is transverse, the medusæ not being produced, as in the hydroida, by evagination (Fig. 404).

In northern waters, for instance on the coast banks and in the fjords of Scandinavia, the brown stinging jelly-fish *Cyanea capillata* and the transparent jelly-fish *Aurelia aurita* are the most important species; in the southern part of the North Sea we find the blue *Cyanea lamarckiana*, which annually drifts up to the Skagerrack and the west coast of Norway. Distantly related to these is *Rhizostoma octopus*, which is similarly dis-

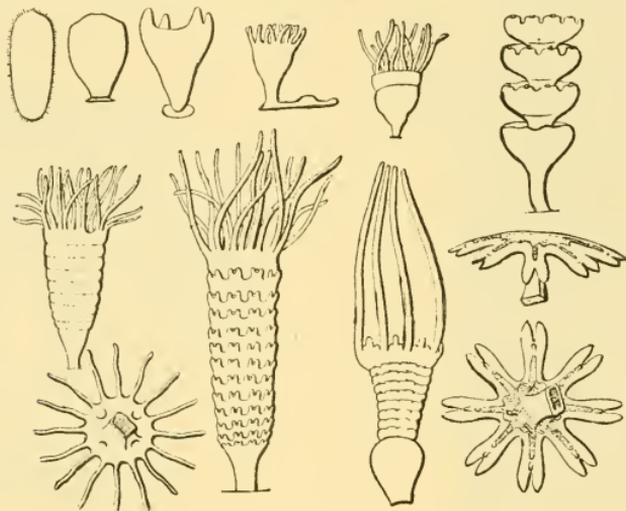


FIG. 404.

Development of *Aurelia aurita* from the ovum. The upper series shows the development of the larva (planula) into Scyphostoma; the lower series shows stages in the formation of small medusæ by division. (After Hatschek, from Hertwig.)

tributed and occurs in Scandinavian waters as a visitor. The oceanic genus *Pelagia*, as already indicated, has a direct development, and is thus holopelagic (see Fig. 405). Of certain smaller groups resembling the Trachymedusæ, I may mention the genera *Atolla*, *Periphylla* (Fig. 406), and *Nausithoë*, which are wholly oceanic forms widely distributed mainly in deep water.

During the cruises of the "Michael Sars" the distribution of medusæ in the Norwegian Sea and in Norwegian coast waters has for years been investigated, and Damas, who is working up the material, has found 64 species, of which 14 are new to science; some are shallow-water forms, and others belong to the deep fauna of the fjords. In 1900 I noted the occurrence of *Cyanea capillata* all over the warm part of the Norwegian Sea, and later on the drift of this form from the coasts has been traced, as also the drift of *Cyanea lamarckiana* from the North Sea to the west coast of Norway (see Chapter X.).

During the Atlantic cruise in 1910 a large collection of medusæ was obtained, of which only the Acraspeda have been determined by Broch, who records the following forms from the stations specified:—

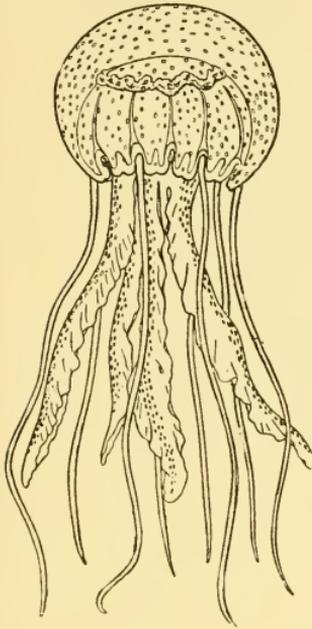


FIG. 405.

Pelagia perla, Slabber.

(After McAndrew and Forbes, from Steuer.)

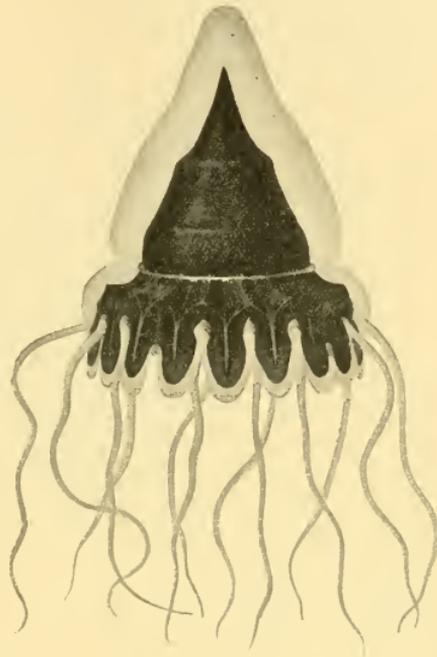


FIG. 406.

Periphylla hyacinthina, Steenstrup.
About nat. size. (From Vanhöffen.)

Periphylla hyacinthina, Steenstrup, Stations 10, 19, 34, 42, 45, 51, 52, 53, 56, 58, 62, 64, 66, 67, 70, 80, 81, 82, 84, 88, 92, 94, 98, 101.

P. regina, Haeckel, Stations 19, 49, 56, 62, 63, 64, 84, 92.

Nausithoë atlantica, n. sp., Stations 56, 90, 92.

„ *globifera*, n. sp., Stations 10, 88, 90, 98, 101.

Atolla wuyvillei, Haeckel, Station 62.

„ *bairdii*, Fewkes, Stations 10, 23, 25, 29, 35, 42, 45, 49, 51, 53, 56, 62, 64, 66, 67, 70, 80, 81, 82, 84, 87, 88, 90, 92, 94, 98, 101.

Pelagia perla, Slabber, Stations 10, 25, 51, 52, 56, 81, 82, 84, 86, 87, 88, 90, 92, 94.

Chrysaora mediterranea, Peron et Lesueur, Algeciras.

Poralia sp. (*rufescens*?), Station 85.

Aurelia solida, Browne, Station 56.



FIG. 407.

Diphyes arctica,
Chun (♀). (From
Vanhöffen.)

This list shows that *Periphylla hyacinthina* and *Atolla bairdii* are so widely distributed in the North Atlantic that they may be said to occur everywhere; they are, as we shall see later, both

deep-living forms. Among surface forms only *Pelagia perla* was taken abundantly, and its distribution was peculiar, the species being most numerous along the line of stations crossing the Azores in a north and south direction, coinciding with the submarine ridge on which these islands are situated (see Map III.).

Siphonophora.

The Siphonophores are an interesting group, sometimes referred to the hydromedusæ, but entirely independent. They are oceanic, and have no bottom-stage, their development being a direct one. This class of animals is exceedingly rich in species, and we can only mention some North Atlantic forms.

Only three species are wholly indigenous to northern waters: *Diphyes arctica* (Fig. 407), peculiar to the Gulf Stream north of lat. 59° or 60° N., extending to Spitsbergen in lat. 81° N., and *Galeolaria biloba* and *Cupuliata cara*, which are less common. In the Atlantic we find a wealth of both deep-sea and pelagic forms, some of the latter being known as visitors in the North Sea and the Norwegian Sea, a few having been found on the west coast of Norway and described by Michael Sars as long ago as the 'thirties, like *Agalmopsis*

elegans and *Physophora hydrostatica* (Fig. 408); in the Sognefjord Hæckel also found *Circalia stephanomma*. These forms have numerous swimming bells and long tentacles, and are interesting as immigrants from the Atlantic into the North Sea and the Norwegian Sea. Among forms peculiar to the warm surface layers we may mention the "Portuguese man-o'-war," *Physalia arctusa* (Fig. 409), and the "By the wind sailor," *Velella spirans* (Fig. 410), which belong to the regions south of the 40th degree, but have occasionally been found as visitors on the shores of the British Islands.

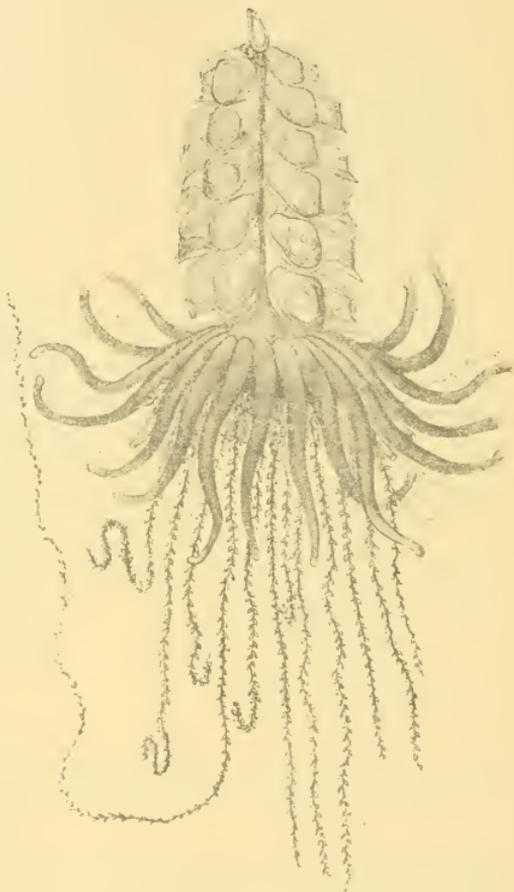


FIG. 408.

Physophora hydrostatica, Forskal. About half nat. size.
(From M. Sars.)

Together with these forms we often find *Cestus veneris*, one of the Ctenophores, a class including many pelagic forms, both surface and deep sea. Four species of Ctenophores have been observed in the arctic region: *Mertensia ovum*, *Pleurobrachia pileus*, *Bolina infundibulum*, and *Beroë cucumis*. After studying the collections of the "Belgica" and the "Michael Sars," Damas and Koefoed state that *Pleurobrachia pileus*



FIG. 409.
Physalia. (From Steuer.)

is a coast form occurring from the channel *infundibulum* and *Beroë cucumis* have a occur in deeper water, for instance, in the fjords; *Mertensia ovum* is an arctic form, norwegian fjords. *

Pelagic larvæ are encountered among animals either holopelagic or meropelagic. Among the higher organised rule seems to be that the mature stages eggs and larvæ are pelagic, whereas stages are generally pelagic. Pelagic, stages are found in the echinoderms etc.), annelida, bryozoa, and in various cirripeds to the lobsters and crabs; snails and mussels also have pelagic young.

In spring especially the coast-waters teem with the larvæ of all these animals, the larval forms very often differ from the adult, and an enormous amount of work has been devoted by zoologists to the description of all these forms. Some of these larvæ seek the bottom after a lapse of only a few days, but many species lead a long pelagic life and during this period go through metamorphoses, among the most

to Spitsbergen; *Bolina* far wider distribution, and deep waters of Norwegian also found in deep Nor-

all the higher groups of Pelagic larvæ pelagic, from the medusæ to forms of the latter the general lead a bottom life while the among the medusæ the mature swimming or floating, young (starfishes, holothurians, crustaceans from the sessile and mussels also have pelagic

remarkable being the larvæ of starfishes, ophiuridæ, and sea-urchins. In the larvæ of the ophiuridæ (see Fig. 411) the skeleton consists of rigid

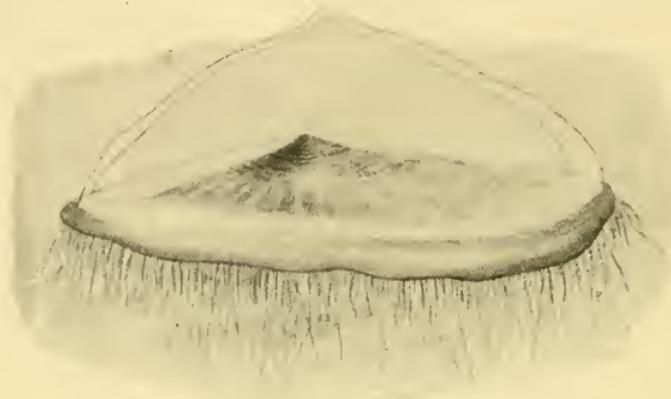


FIG. 410.
Velella spirans, Esch. (From Steuer.)



FIG. 411.
Larva of *Ophiothrix fragilis*, O. F. Müller (about $\frac{500}{100}$). (From Mortensen.)

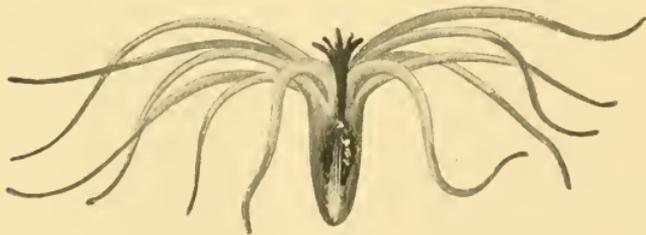


FIG. 412.
Arachnactis albida, M. Sars. Nat. size. (From Sars.)

rays of carbonate of lime, with a belt of cells provided with whip-like hairs, by the aid of which they swim; these larvæ go through wonderful metamorphoses before finally attaining the adult form.

The larval Actiniæ are biologically of great interest, especially *Arachnactis albida*, first described by Michael Sars (Fig. 412). The north-eastern corner of the Atlantic is its main area of distribution, principally between the Hebrides and the Faroe Islands, but at certain seasons it is carried into the North Sea and the Skagerrack, and to the west coast of Norway, where Sars found it (see Fig. 480). Actiniaria.

A description of the larvæ peculiar to the different groups would lead us too far, but in order to prepare the reader for the next chapter some of the forms have been mentioned.

The Worms are comparatively rare among the pelagic forms. Of Vermes. the lowest worms (platyhelminthes) the pelagic Nemertines are of interest. Nearly all Nemertines live along the bottom, but a pelagic genus (*Pelagonemertes*) was described by Moseley in the "Challenger" Reports. Subsequently several species have been described, all represented by isolated specimens. These remarkable forms are red or orange coloured, and their digestive tract is extremely ramified. According to Brinkmann, who is examining our material, most of the previously known species, as well as some new species, have been taken during our Atlantic cruise, and prove that several species hitherto regarded as distinct are really identical: thus *Nectonemertes grimaldi*, *N. lobata*, and *N. pelagica* are all identical with *N. mirabilis*. The genus *Nectonemertes* with *N. mirabilis*, and also the genus *Hyalonemertes* with *H. atlantica*, were established by Verrill. The two forms (see Fig. 413) differ, as shown by later investigations, only in one single character, *N. mirabilis* having two long appendages on the head, which are lacking in *H. atlantica*. The abundant material collected by the "Michael Sars" has enabled Brinkmann to show that all the individuals of *N. mirabilis* are males, while all the individuals of *H. atlantica* are females, and he concludes that both belong to the same species, the difference between them being only a sexual one.

Very interesting were some gigantic specimens belonging to this group secured during the cruise. One form, *Dinonemertes investigatoris* (see Fig. 414), was 20.5 cm. long, and when living was of a bright red tint and nearly transparent, all the ramifications of the digestive tract being plainly visible. As we shall see when reviewing the captures of the "Michael Sars," all these Nemertines are deep-sea forms with a very characteristic vertical distribution. Several of the species are very widely distributed, *Nectonemertes mirabilis*, for instance, being known from Davis Straits, from the Pacific off California, and all through the Atlantic; *Dinonemertes investigatoris* is known from the Atlantic as well as from the Indian Ocean.

The most abundant group of pelagic worms as regards number of



FIG. 413.
Nectonemertes mirabilis,
Verrill. Slightly enlarged.
a, male; b, female.

individuals is the Sagittidæ or Chaetognaths, which, along with copepoda, salpæ, pteropoda, and radiolaria, everywhere constitute the bulk of the small pelagic organisms captured by our fine-meshed tow-nets. They are perfectly transparent, of slender build, and swift of motion. On the head are some bristle-like gripping appliances, and an elastic film-like rim, reminding one of the fin of a fish, runs along the body and the "tail" (see Fig. 415).

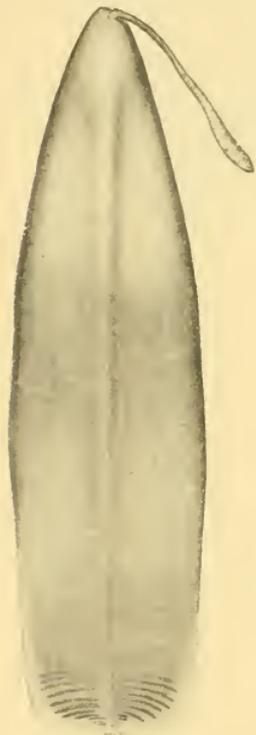


FIG. 414.
Dinonemertes investigatoris,
Laidlaw. Half nat. size.

Among the best known is the genus *Tomopteris*, which has many beautiful surface forms, some of these (like *T. septentrionalis*) being boreal, some belonging to warm waters. In his narrative of the cruise of the "Valdivia," Chun tells us that nearly every haul from deep water in the Antarctic brought up beautiful specimens of *Tomopteris*, as long as the finger, transparent, and with rose-tinted feet (parapodia). Individuals belonging to the genus *Tomopteris* were taken in several of the deep hauls and also in the surface hauls of the "Michael Sars," but the material has not yet been worked up.

The Sagittidæ comprise only a few genera, the most prolific in species being the genus *Sagitta*, which is represented in all oceans; some of the species are very widely distributed, such as *Sagitta hexaptera*, *S. serratodentata*, *S. bipunctata*. In northern waters *Krohnia hamata*, *Sagitta arctica*, and *Sagitta gigantea* are characteristic forms, the last mentioned having been taken by the "Michael Sars" in deep hauls in the Norwegian Sea, while *Sagitta inflata* is a form peculiar to warm waters. All these species are perfectly transparent, but during the Atlantic cruise we found specimens of a bright red colour, precisely like that of the pelagic Nemertines, belonging to *Sagitta macrocephala* and *Eukrohnia fowleri*; they were very abundant, and occurred, like the Nemertines, only in deep hauls.

The very numerous families of higher worms, especially the Annelida, contribute very little to the pelagic fauna of the ocean.

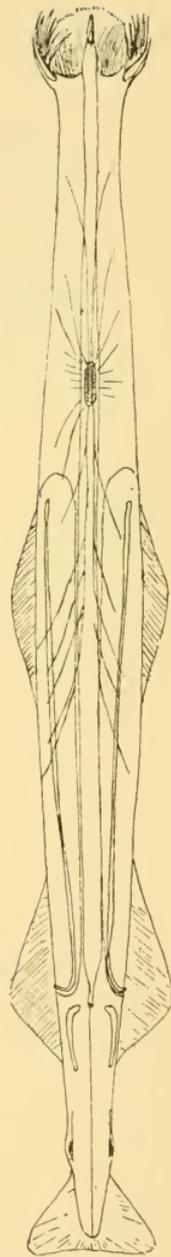


FIG. 415.
Sagitta hexaptera,
d'Orb. (†). (From
Hertwig.)

No class of multicellular animals in the ocean is represented by anything like such countless forms and individuals as that of the Crustacea; in the life of the ocean they play, according to Haeckel, a part corresponding to that of the insects in the land fauna. The Entomostraca include the most important groups, first the Copepoda, then the Ostracoda, and the Cladocera. Among the larger Crustacea, the Schizopoda, the Amphipoda, and the Decapoda are also very important, but in abundance and specific variation they can never be compared to the groups of smaller crustaceans.

The Copepoda, as a rule, attain only a few millimetres in length, and are adapted to feed on the small plants of the oceanic flora in the upper layers of all oceans. It may safely be asserted that they are the chief consumers of these minute plants, and in turn serve as food for larger animals.

Giesbrecht¹ discusses the geographical distribution of 299 species of Copepoda, and divides the area of their distribution into three regions: (1) a warm region between 47° N. and 44° S., (2) a northern region, and (3) a southern region. The warm region comprises all the oceans, the warm-water species throughout the world being more alike than the species of warm and cold regions in the same ocean. Of the 299 species, no less than 254 belong exclusively to the warm region; there are besides a few widespread forms and others peculiar to the northern or southern region. About 85 per cent of the species belong to the warm region, 5 per cent to the northern, and 2 per cent to the southern region.

As characteristic of the warm region Giesbrecht mentions the following genera: *Augaptilus*, *Calocalanus*, *Copilia*, *Euchirella*, *Hemicalanus*, *Monops*, *Pleuromma*, *Pontella*, *Pontellina*, *Sapphirina*. Peculiar to the northern area are: *Acartia biflosa*, *Calanus hyperboreus*, *C. cristatus*, *Centropages hamatus*, *Euchaeta norvegica*, *Pseudocalanus elongatus*, and perhaps *Temora longicornis*. Some forms are common to the warm region and one of the cold regions, such as *Anomalocera patersoni* and *Centropages typicus*, while *Calanus finmarchicus* and *Oithona similis* occur in all the three regions.

The warm and cold water forms differ in structure, the body, legs, and antennæ of the warm water forms being generally provided with wonderful feather or fan-shaped attachments, which greatly enlarge the

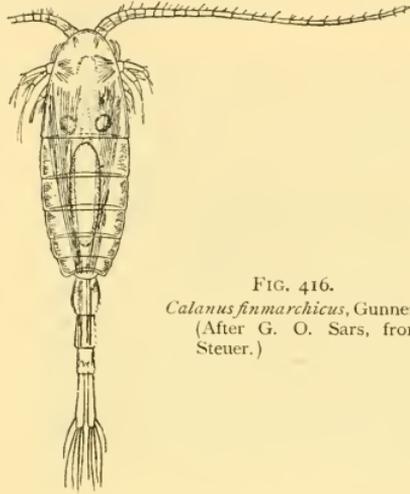


FIG. 416.
Calanus finmarchicus, Gunner.
(After G. O. Sars, from
Steuer.)

¹ Giesbrecht, "Systematik und Faunistik d. pelag. Copepoden," *Fauna und Flora des Golfes von Neapel*, Bd. 19, 1892.

surface of the animals and facilitate their floating, while in northern waters the species are devoid of such appendages. It is thus interesting to compare the widespread species *Calanus finmarchicus* (Fig. 416), which occurs in greatest abundance in boreal areas, with the tropical *Augaptilus filigerus* (Fig. 417), which has elaborate appendages, reminding one of peacocks' feathers. We find the same difference between *Oithona plumifera* and *Oithona similis*, and between *Euchæta marina* and *Euchæta norvegica* (Fig. 418). We find in these cases a perfect analogy with what Gran has described among the peridineæ in Chapter VI.; for instance, *Ceratium platycorne* (see Fig. 228, p. 324) in warm water en-

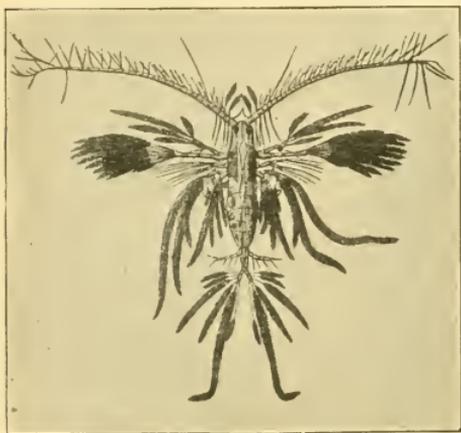


FIG. 417.
Augaptilus filigerus, Claus.
(After Zacharias, from Steuer.)

larges its surface, while in cold water the horns are much more slender, the lower specific gravity caused by the higher temperature rendering floating appliances necessary for both animals and plants (see also Chapter X.).

The Copepoda occur in all depths, and some authors have attempted to define certain bathymetrical regions, each with its own characteristic forms, but the observations available are insufficient to enable us to form definite ideas on the subject; much new light will doubtless be thrown on the matter when the reports of the "Valdivia" and "Michael Sars" Expeditions come to be published. The discussion as to whether the surface forms of cold regions are found in the deep water of warm regions is interesting.

The "Valdivia" Expedition captured *Euchirella venusta* and *Calanus finmarchicus* in a haul with a closing net between 1600 and 1850 metres

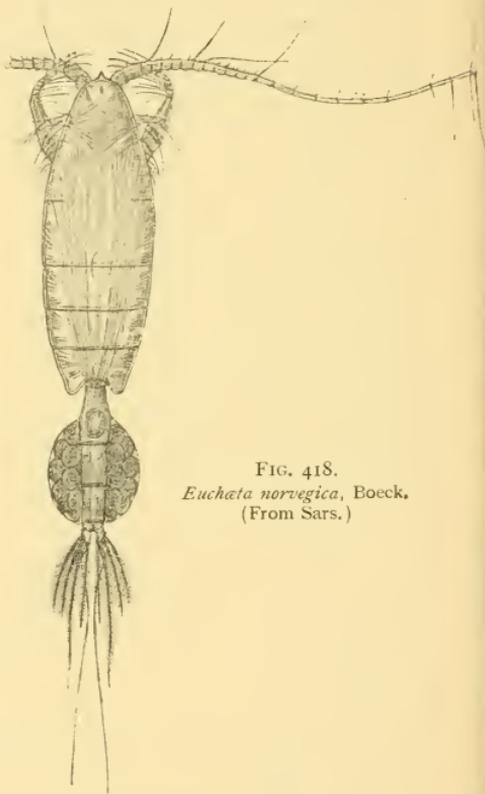


FIG. 418.
Euchæta norvegica, Boeck,
(From Sars.)

in subtropical seas where the surface temperature is very high, and Dahl mentions this latter form as living in deep water in the Sargasso Sea.

Numerous investigations on the Copepoda of the Norwegian Sea have in recent years been made by the "Michael Sars," the material having been worked up mainly by Damas, whose results will be mentioned in the sequel. From the Atlantic cruise of 1910 the "Michael Sars" also brought home a large collection of Copepoda captured both in horizontal hauls and in closing nets, and this material is at present being described by Nordgaard and Lysholm, but their results are not yet ready for discussion. G. O. Sars has, however, been good enough to determine the Copepoda for me in a few selected samples, and these determinations are so interesting that I give in the following table the number of species found at various depths:—

NUMBER OF SPECIES OF CRUSTACEANS, CHIEFLY COPEPODA, TAKEN IN
CLOSING NETS AT THE STATIONS SPECIFIED

Depth of the Hauls.	Station 50.	Station 63.	Station 80.	Station 92.	Station 113.
0 to 200 or 300 metres .	22	25	16	18	21
200 or 300 to 500 metres .	22	32	27	12	18
500 to 1000 metres .	51	27	34	33	11

The most northerly station (113) is relatively poor in species, especially in the deep cold layers, the richest station being the most southerly one (50), and remarkably enough the richest sample is the deepest one in 500 to 1000 metres, which contained twice as many species as the surface sample.

The Ostracoda are considered by Haeckel to be the most important group of Crustacea next to the Copepoda, being represented by a great number of species. The "Challenger" collected 221 species, of which 52 were taken in depths greater than 500 fathoms, 19 beyond 1500 fathoms, and 8 beyond 2000 fathoms. Many ostracoda possess the power of emitting intense phosphorescent light, and Haeckel narrates how on his voyages to Ceylon he saw the entire sea like a continuously twinkling ocean of light as far as the eye could reach; the microscope proved most of these luminous animals to be ostracoda, with some medusæ, salpæ, and worms. Ostracoda.

Some of the surface ostracoda are very widely distributed, like *Conchocia elegans*, which occurs all the way from the Norwegian Sea to the Antarctic. In northern waters we may find also *C. borealis* and *C. obtusata*. In Antarctic waters we find *C. antipoda*, closely resembling *C. obtusata* of the north. As abyssal forms we may note the large individuals (attaining 1 cm. in length) of the genus *Gigantocypris* (see Fig. 419), recorded by the "Valdivia" from the Indian Ocean and from the Atlantic between lat. 14° N. and 42° S., previously

known from the Pacific.¹ The "Michael Sars" took this genus in deep water at several stations in the North Atlantic.

Cirripedia. The Cirripedia are the only group of crustaceans which in the adult stage abandon the pelagic life of youth and become sessile, fixing themselves to the bottom like many other invertebrates. Some are fixed to the rocks of the littoral region (the balani), or to pumice stones and nodules from the great depths of the ocean, while others are attached to whales and turtles, or (like the Lepadidæ) to floating objects carried along by currents. One species (*Lepas fascicularis*) forms considerable floating clusters composed of several individuals. A peculiar group (for example, *Sacculina* from the tail of decapod crustacea) is entirely

parasitic and transformed to such a degree that the crustacean nature of the animal is hardly recognisable.

The Cirripedia from the Atlantic cruise of the "Michael Sars" have been examined by P. P. C. Hoek, who found the following species of the genus *Lepas* :—

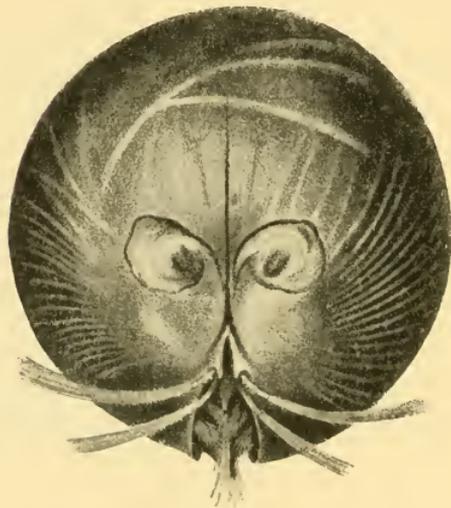


FIG. 419.
Gigantocypris agassizii, G. W. Müller (♂).
(From Müller.)

Lepas anatifera (see Chapter III., p. 100, Fig. 87), taken at Station 61 (on a floating log), and off St. John's.

Lepas anserifera, Station 67 (on Sargasso weed), Station 69 (on a small log).

Lepas pectinata, Stations 10, 25, 31, 69, 86, 91 and 92 (fixed to birds' feathers, cork, fucus, pumice-stone, and to *L. fascicularis*).

Lepas hilli, Station 56 (on a turtle).
Lepas fascicularis, Stations 25, 91, 92.

All these species are known from other oceans, especially the Pacific, and are principally warm-water forms. Of other Cirripedia the following species were captured :—

Pacilasma carinatum, Station 53 (on the bottom).

Conchoderma virgatum, Station 56 (on a turtle).

Scalpellum velutinum, Stations 24 and 53 (on the bottom).

„ *dicheloplax*, Station 10 (on the bottom).

„ *atlanticum*, Station 23 (on the bottom).

Schizopoda. G. O. Sars described 57 species of Schizopoda from the "Challenger" Expedition,² of which 32 were taken only at the surface, 6 between 32 and 300 fathoms, 4 between 300 and 1000 fathoms, 11 between 1000 and 2000 fathoms, and 4 beyond 2000 fathoms. Most of these were

¹ See G. W. Müller, *Wiss. Ergeb. "Valdivia" Expedition*, Bd. 8, 1906.

² See Zool. Chall. Exp., Part XXXVII., 1885.

represented by few specimens, though widely distributed. Hardly any of the "Challenger" species described by G. O. Sars are found in the Norwegian Sea.

The Schizopoda play a great part in northern waters, where the numerous species occur in enormous numbers, sometimes near the bottom and sometimes near the surface; the fishermen term them "Krill." They

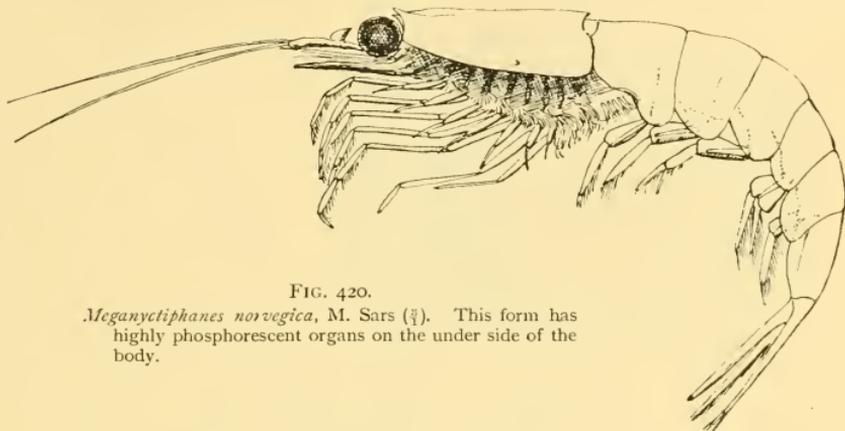


FIG. 420.
Meganyctiphanes norvegica, M. Sars (†). This form has highly phosphorescent organs on the under side of the body.

are mostly colourless, transparent, with large red spots around the mouth, and have generally the appearance of small prawns with black stalked eyes. The most important species are *Meganyctiphanes norvegica* (Fig. 420) and *Thysanoëssa longicaudata*. The closing-net samples determined by Sars included some Schizopoda, Amphipoda, and Isopoda (see list, pp. 654-655).

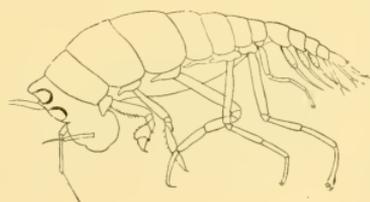


FIG. 421.
Scypholanceola agassizii, Woltereck.
(From Woltereck.)

The great majority of the species of Amphipoda inhabit the warm oceans, where they occur mostly in the upper 400 metres of water. Woltereck has described some very remarkable deep-water forms belonging to the genera *Lanceola* and *Scypholanceola* (Fig. 421).

The members of the latter genus have light-reflecting eyes, the retina of which is entirely transformed and provided with peculiar cornet-shaped reflectors. They were previously considered rare, but according to Woltereck, who is describing our material, they were taken in great quantities during the cruise of the "Michael Sars." Another deep-sea form is the large transparent *Cystosoma* with splendid red eyes, which was taken in both our southern and northern sections in depths exceeding 500 metres (Fig. 422). One of the most striking types is the genus *Phronima*, of the family Hyperidæ. Most of the Hyperidæ make themselves a house of the empty mantle of a *Salpa* or *Doliolum*, and lay their eggs in the

barrel-shaped abode (see Fig. 423). *Phronima* was taken in great quantities in the surface waters during our southern and northern sections across the Atlantic.

In the Norwegian Sea two forms are very important: *Parathemisto oblivia* (Fig. 424), which lives in the open sea, frequently even in very cold water, and also in the Norwegian fjords; and *Euthemisto libellula*, which sometimes attains a length of $4\frac{1}{2}$ cm., and lives in the icy waters of the

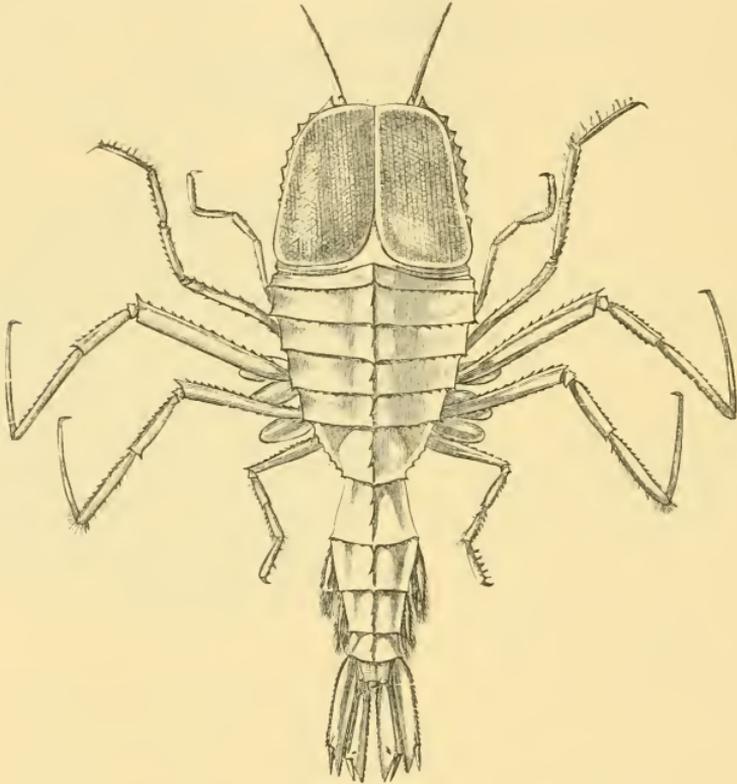


FIG. 422.

Cystosoma neptuni, Guérin-Ménéville. (After Wyville Thomson.)

Polar Sea. Both these forms were taken also in the Atlantic, but only in boreal areas (see list, pp. 654-655). A form which lives at great depths in the Norwegian Sea is *Cyclocaris guilelmi*, taken by the Prince of Monaco off the Lofotens and described by Gran.

Isopoda. While capturing turtles at Station 56 we observed a great number of deep-blue Isopoda belonging to the species *Idotea metallica*.

Decapoda. The Decapoda include nearly all the large types of crustaceans, like prawns, lobsters, crayfish, crabs, etc. The first deep-sea expeditions captured a considerable number of decapod crustaceans in the trawls at

great depths, and they were consequently supposed to be bottom-dwellers. Subsequently the Prince of Monaco, and later the "Valdivia," took in pelagic tow-nets a number of forms belonging chiefly to the family Sergestidæ, and to the genera *Acanthephyra*, *Notostomus*, and *Eryoneicus*, all of which were thus proved to lead a pelagic life. The "Valdivia" took *Sergestes* in a haul with a closing net from 5000 to 4000 metres, and Chun states in his narrative of the cruise that whenever the vertical nets reached deep water this genus never failed to appear in the hauls.

During the Atlantic cruise of the "Michael Sars" we obtained large red prawns in such abundance (several litres per haul) as to prove that these animals play a more important part in pelagic life than was previously supposed. Our catches are also of special interest, because their study has thrown new light upon the vertical distribution of the different species. We may here mention some of the most important forms recorded by Oscar Sund, who is describing this group.

Of pelagic decapoda more than forty species were taken during our expedition, but the great bulk is made up of about a dozen species, each of which has a wide geographical range, being regularly caught at all stations over vast areas. Most of these common species, which will be dealt with later on, present peculiarities in their biology and distribution.

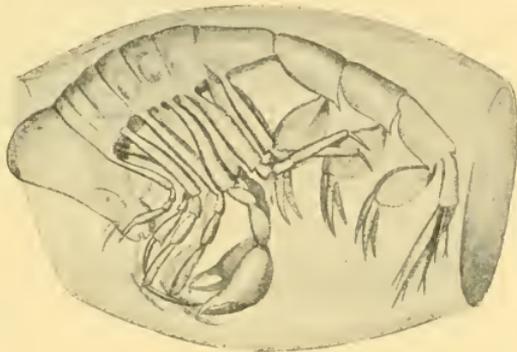


FIG. 423.
Phronima. (From Steuer.)

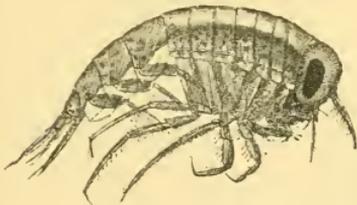


FIG. 424.
Parathemisto oblivia, Krøyer ($\frac{1}{4}$).
(From Sars.)

The genus *Acanthephyra* of the Hoplophoridae (see Plate III. Chapter X.) includes large red prawn-like forms, of which no less than eight different species were taken. On the section between Newfoundland and Ireland the two species *A. purpurea* and *A. multispina* were in special abundance.

Before the cruise of the "Michael Sars" only fifteen individuals belonging to the genus *Notostomus*, representing no less than thirteen species, had been recorded. We procured nineteen individuals in the North Atlantic belonging to five species, of which four are new to

Most of the pelagic decapoda belong to the more primitive divisions of the group, viz. Sergestidæ, Peneidæ, Pasiphæidæ, and Hoplophoridae, but a truly pelagic Pandalid (*Plesionika nana*, n. sp.) was taken at most of the stations from Spain to Newfoundland.

science. One of these new species is represented by a specimen 17 cm. long (see Fig. 425)—one of the largest pelagic prawn ever taken. *Notostomus* was taken only in the deepest hauls, which only extended down to 1500 or 2000 metres; perhaps hauls in still deeper water might have

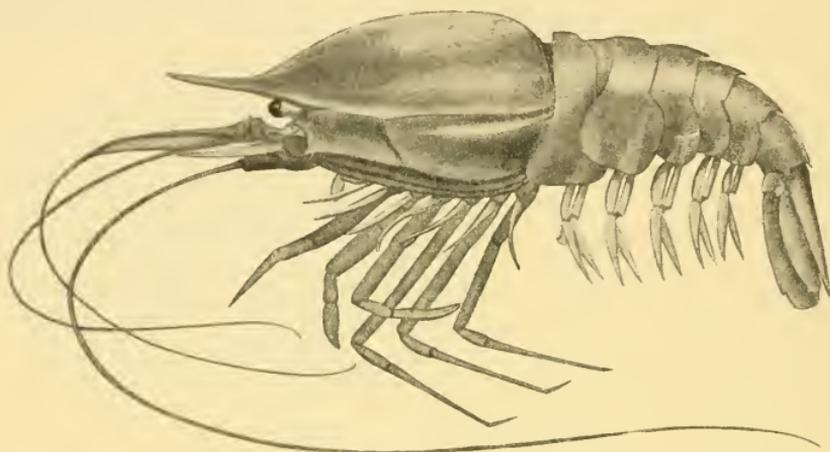


FIG. 425.
Notostomus, n. sp. Nat. size, 17 cm.

yielded more of them. Still larger are the bottom-living Peneidæ, of which a whole tubful were taken south of the Canaries in our trawl (Station 41, 2605 metres), some of them 30 to 40 cm. long, with feelers 4 or 5 feet long.

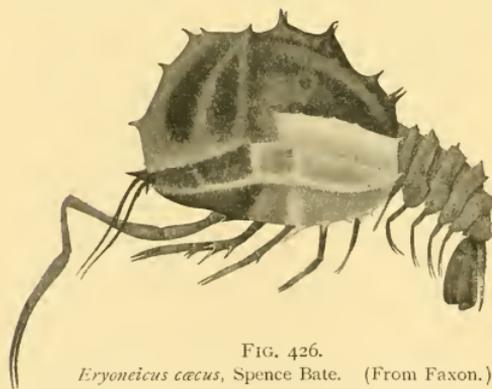


FIG. 426.
Eryoneicus cæcus, Spence Bate. (From Faxon.)

One of the most remarkable genera is *Eryoneicus*, of which twelve species are known, easily recognisable by their inflated balloon-like bodies (see Fig. 426). They are allied to *Pentacheles*, *Polycheles* (Fig. 427), etc., and Sund, after examining the twenty-four specimens collected by the "Michael Sars," expects to be able to show that

they are really the larvæ of these abyssal bottom-living decapoda. Thus, what might be regarded as a new species of *Eryoneicus* is in reality a larval stage of a previously known decapod, *Polycheles sculptus*.

During the first cruise of the "Michael Sars" in the Norwegian Sea I succeeded in capturing the two species *Pasiphæa princeps* and *Hymenodora glacialis* (Fig. 428) in deep hauls. *Pasiphæa* probably lives sometimes on the bottom, sometimes in midwater, and is common in Norwegian

fjords along with numerous species of *Pandalus*, "the deep-water prawns," which are now the object of important fisheries. *Hymenodora* is known even from the ice-region, and was met with by Scoresby during his arctic voyages.¹

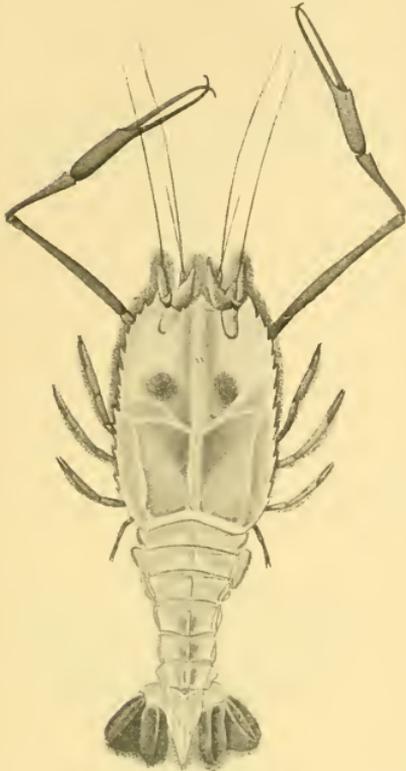


FIG. 427.

Polycheles sculptus pacificus, Fax. (From Faxon.)

the Norwegian Sea. The shell is about the size of a pin's head, and can

Though the Mollusca are widely distributed and represented by a vast number of different forms on the ocean-floor, the pelagic forms are comparatively few, but as regards abundance of individuals few groups of pelagic animals can compare with the winged snails or Pteropoda, which are divided into two groups: Thecosomata (or shelled pteropods) and Gymnosomata (or naked pteropods).

The Thecosomata are important on account of the part they play both in the plankton and in the bottom-deposits (see Chapter IV.). They include the family Limacinidæ having a spiral shell, of which the well-known *Limacina helicina* occurs in immense quantities in the Arctic (the seas around Spitsbergen and Greenland), while *Limacina balea*, the "Flueaat" of Norwegian fishermen, is a boreal species, and *Limacina retroversa* (Fig. 429) is a more southern form occurring also in

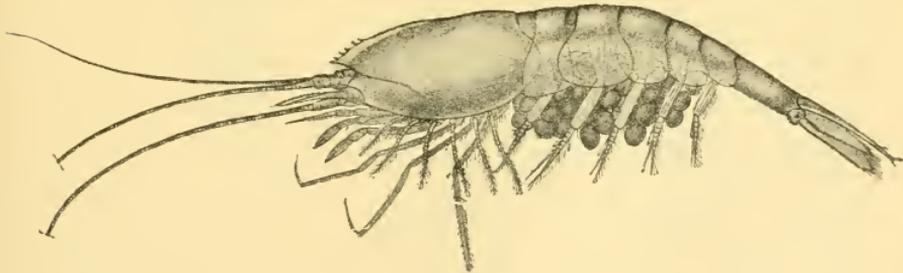


FIG. 428.

Hymenodora glacialis, Buchholz. (From G. O. Sars.)

¹ In the pelagic life of the ocean the Insecta are represented only by several species of Hemiptera (*Halobates* and *Halobatodes*), which are found skimming over the surface in the tropical regions.

barely be seen in the sea with the naked eye. The two last-mentioned forms are found in warm currents on the coast of Norway, and their presence is feared by the fishermen, because they very often spoil the herring which feed on them; the shells are very slowly digested and the stomach-contents putrify when the herrings are salted, and then the whole herring decomposes. Among the many warm-water species *Limacina bulimoides* is characteristic. The Cavolinidæ include numerous forms with cornet-shaped shells. *Clio pyramidata* (Fig. 430) and *Diacria trispinosa* are very important forms, occurring in vast numbers, and their shells are very numerous in the deposits. *Creseis*

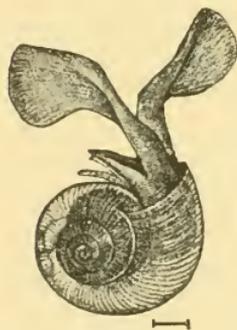


FIG. 429.
Limacina retroversa, Fleming.
(From Sars.)

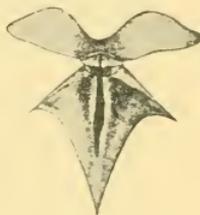


FIG. 430.
Clio pyramidata, L.
(From Boas.)

acicula (Fig. 431) and *Cavolinia gibbosa* (Fig. 432) are characteristic forms.

The "whale's food," *Clione limacina* (Fig. 433), is specially abundant in northern waters, and is better known than most of the Gymnosomata. It is 3 or 4 cm. long, perfectly transparent, with red shadings and black stomach. In the Polar Sea it may be seen swimming among the ice-floes, but it occurs also in the Norwegian Sea, in the Norwegian fjords, and in the Atlantic south of Iceland.

The majority of the pteropoda (both species and individuals) are restricted to warm water: in the Atlantic the northern limit for the warm-water forms may be roughly drawn from the Bay of Biscay to New York, and the southern limit from Brazil to the Cape. This area is the real home of *Clio pyramidata*, *C. cuspidata*, *Creseis acicula*, the Cavolinidæ, the Cymbulidæ, *Pneumoderma violaceum*, *Limacina inflata*, *L. lesueurii*, *L. bulimoides*. As with the radiolaria and copepoda, many

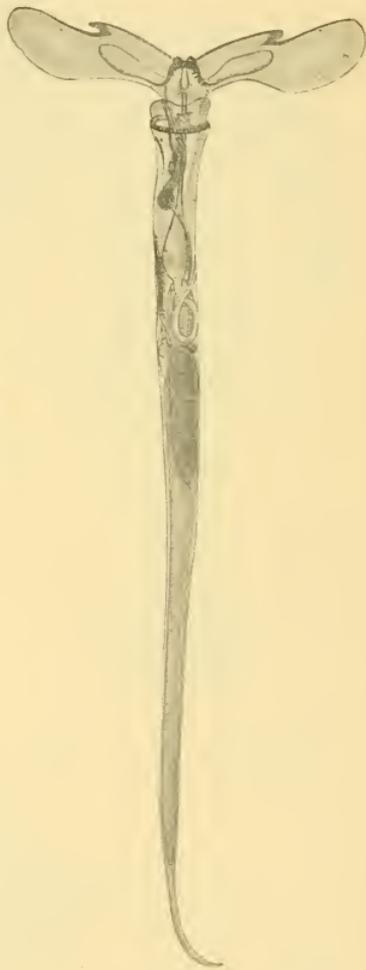


FIG. 431.
Creseis acicula, Rang.
(From Meisenheimer.)

of these warm-water species of pteropoda are also known from the Indian and Pacific Oceans, where their geographical distribution is similar to that in the Atlantic. North of lat. 45° or 46° N. we meet with only a few of the warm-water forms, *Creseis acicula* and *Clio cuspidata* having been taken in isolated specimens up to 60° N. Typical denizens of this region are *Clio pyramidata* and *Diacria trispinosa*, which appear to be as numerous as under the equator. The northern forms *Limacina helicina* and *L. balea*, as well as *Clione limacina*, also occur in the northern part of the Atlantic. In the Antarctic we find species which are very similar to the northern ones.

Meisenheimer,¹ who reported on the pteropoda of the "Valdivia" Expedition, is of opinion that the horizontal and vertical distribution of the pteropoda depends mainly on the temperature. Most of the species require a high temperature, and for this reason the majority live in the surface layers. Only exceptionally do they occur as deep as 1000 metres, and this is specially the case in the Mediterranean, where high temperatures prevail

to very considerable depths. During our Atlantic cruise we found some real deep-sea forms: *Peraclis diversa*, *Limacina helicoides*, and *Clio falcata*, which occurred only between 500 and 1500 metres.

During the Atlantic cruise of the "Michael Sars" pteropoda were taken in thousands, and this material has been examined by Bonnevie, who records the following species:—

The Thecosomata include:—Limacinidæ: *Limacina balea*, *L. retroversa*, *L. bulimoides*, *L. inflata*, *L. lesueuri*, *L. helicina*, *L. helicoides*, *Peraclis reticulata*, *P. triacantha*, *P. diversa*, and *Procymbulia* sp. Cavolinidæ: *Clio pyramidata*, *C. cuspidata*, *C. falcata*, *Creseis acicula*, *Styliola subula*, *Hyalocylix striata*, *Cuvierina columnella*, *Diacria trispinosa*, *D. quadridentata*, *Cavolinia inflexa*, *C. gibbosa*, *C. longirostris*, *C. tridentata*, *C. uncinata*. Cymbulidæ: *Cymbulia peronii*.

The Gymnosomata comprise, besides *Pneumodermopsis macrochira* and *Clione limacina*, several new species not yet described.

Of other Mollusca I may mention the beautiful surface forms:

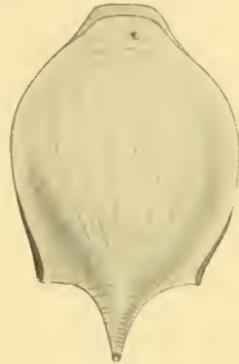


FIG. 432.
Cavolinia gibbosa, Rang.
(From Meisenheimer.)

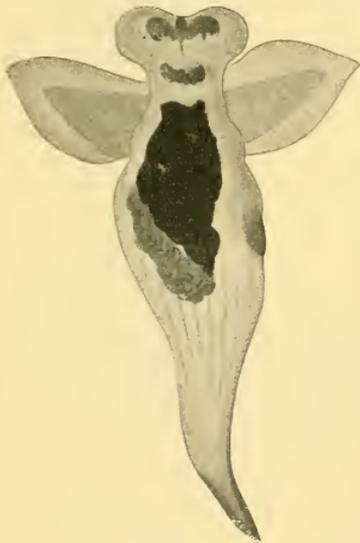


FIG. 433.
Clione limacina, Phipps. (From Vanhöffen.)

¹ Meisenheimer, *Wiss. Ergeb. "Valdivia" Expedition*, Bd. 9, 1905.

Ianthina, *Carinaria* (see Fig. 122, p. 154), *Pterotrachea* (see Fig. 123, p. 154), and *Glaucus*, which were taken in abundance in the southern section of our Atlantic cruise.

Cephalopoda.

Of the large group of Cephalopoda (squids and cuttle-fishes) previous expeditions obtained very few in their small tow-nets, those captured being generally taken in the bottom trawls, and it was uncertain whether they lived at the bottom, or in intermediate depths, or near the surface. It has long been recognised, however, that many Cephalopoda are true pelagic animals, and in the sixties of last century Japetus Steenstrup applied the term "Decapodes pelagici" to the group *Ægopsidæ*. The Prince of Monaco not only captured Cephalopods in his pelagic trawls, but also obtained them from the stomachs of whales which he shot, his material being reported on by Joubin.¹ During the "Valdivia" Expedition the large vertical nets captured a wealth of new forms belonging especially to small types, and Chun in his narrative draws attention to the remarkable Cranchiidæ and the little *Spirula*. Chun has recently published the first part of his report on the "Valdivia" collections of Cephalopoda, dealing with the *Ægopsidæ*.²

It was a special pleasure to me that Chun undertook to describe the Cephalopoda obtained during our Atlantic cruise, and his report, which has just been completed, is available for this preliminary record of the results. His determinations are given in the list on pp. 595-597, and comprise 43 species in all, 3 or 4 of which are new to science, besides some larval forms, the identity of which is uncertain.

The Cephalopoda are generally divided into two groups according to the number of tentacles, those with ten arms or tentacles being termed Decapoda, and those with eight tentacles Octopoda; the Decapoda are subdivided into *Ægopsidæ* and *Myopsidæ*. The *Myopsidæ* and all the Octopoda have a membrane covering the eye, but in the *Ægopsidæ* this is perforated.

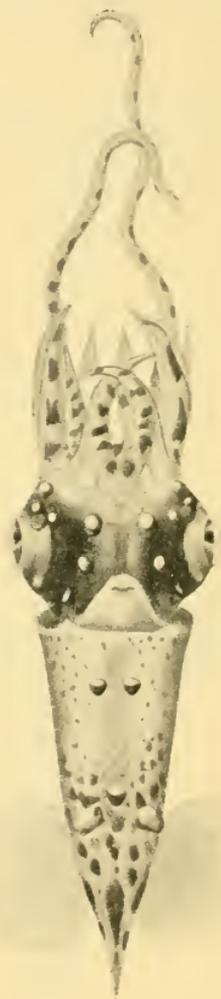


FIG. 434.
Pterygioteuthis giardi, Fischer (♀).
(From Chun.)

¹ Joubin, "Céphalopodes provenant des campagnes de la Princesse-Alice," *Campagnes scientifiques du Prince de Monaco*, Fasc. xvii., 1900.

² Chun, *Wiss. Ergeb. "Valdivia" Expedition*, Bd. 18, 1910.

Most pelagic squids belong to the (Egopsidæ, which present a wealth of forms ranging from minute fantastically shaped deep-sea species to the giant squids.

The Enoploteuthidæ obtained by us are small forms previously known from the Atlantic and Indian Oceans. The general occurrence of *Pterygioteuthis giardi* (see Fig. 434) seems to justify the conclusion that it is a very common pelagic species, inhabiting the open ocean far from land; it is provided with light-organs. The larvæ belonging to this



FIG. 435.
Larva of Enoploteuthidæ (1^o). (From Chun.)

family are very abundant in the North Atlantic (see Fig. 435).

Of the family Onychoteuthidæ many undetermined larvæ have been taken by the "Michael Sars," which are of great interest as proving the occurrence of this group; a larval form taken by the "Valdivia" is shown in Fig. 436. *Onychoteuthis banksii* occurs from the Mediterranean to the Kattegat and Skagerrack and along the entire coast of Norway. *Octopodoteuthis sicula* and *Calliteuthis reversa* are minute forms, the former known from the north-eastern part of the Atlantic, while the latter is widely distributed in the surface waters of the Indian and Pacific Oceans, and has



FIG. 436.
Young of *Teletoteuthis caribæa*.
Les. ($\frac{2}{3}$). (From Chun.)



FIG. 437.
Calliteuthis reversa, Verrill ($\frac{2}{3}$). (From Chun.)

light-organs (see Fig. 437). *Ctenopteryx siculus*, *Brachioteuthis riisei*, and the three species of *Doratopsis* are small and live presumably in the upper water-layers. *Doratopsis exophthalmica* (Fig. 438) is noticeable on account of its remarkable eyes (see Fig. 439).

The families Ommatostrephidæ, Gonatidæ, and Chiroteuthidæ

include mostly large forms, belonging to a biological group of squids (comprising the family of giant squids, Architeuthidæ), the members of which are among the pirates of the ocean, and in their turn fall a prey to the large squid-hunting whales. *Illex illecebrosus* and *Ommatostrephes todarus* are northern forms, of great importance on the banks of Newfoundland, and along the coasts of Iceland and Norway, as *Gonatus fabricii* (see Fig. 98, p. 113) is the squid of the "bottle-nose grounds" in the Norwegian Sea. *Todaropsis eblanæ* and *Ommatostrephes sagittatus* extend nearly as far north as the southern borders of the Norwegian Sea.



FIG. 438.

Doratopsis exophthalmica, Chun (¶). (From Chun.)

Mastigoteuthis, *Grimalditeuthis*, and *Chiroteuthis* are large squids, some of which were captured by the Prince of Monaco around the Azores, Madeira, and Canaries. *Grimalditeuthis richardi* described by Joubin, proves to be identical with *G. bonplandi* (see Fig. 440) taken by the "Michael Sars." A new species is described by Chun under the name of *Mastigoteuthis hjorti*. We succeeded in catching adults as well as larvæ of the Ommatostrephidæ and Gonatidæ; Chun has described the interesting larva of *Ommatostrephes* (see Fig. 441), taken in the southern



FIG. 439.

Head of *Doratopsis lippula*, Chun.

section of our Atlantic cruise, in which the two long tentacles are united into a tube.

In the Cranchiidæ we have an entirely different group of wonderful deep-sea forms, which probably undertake extensive vertical migrations; some of these, for instance *Corynomma speculator*, *Toxeuma belone* (Fig. 442), and *Bathothauma lyromma* (Fig. 443), were taken in the Indian Ocean by the "Valdivia."

Among the Myopsidæ I mention first the interesting form *Spirula australis* (see Fig. 60, p. 81), of which only three specimens had previously been taken: one in the Pacific by the "Challenger," one off North America by the "Blake," and one in the Indian Ocean by the

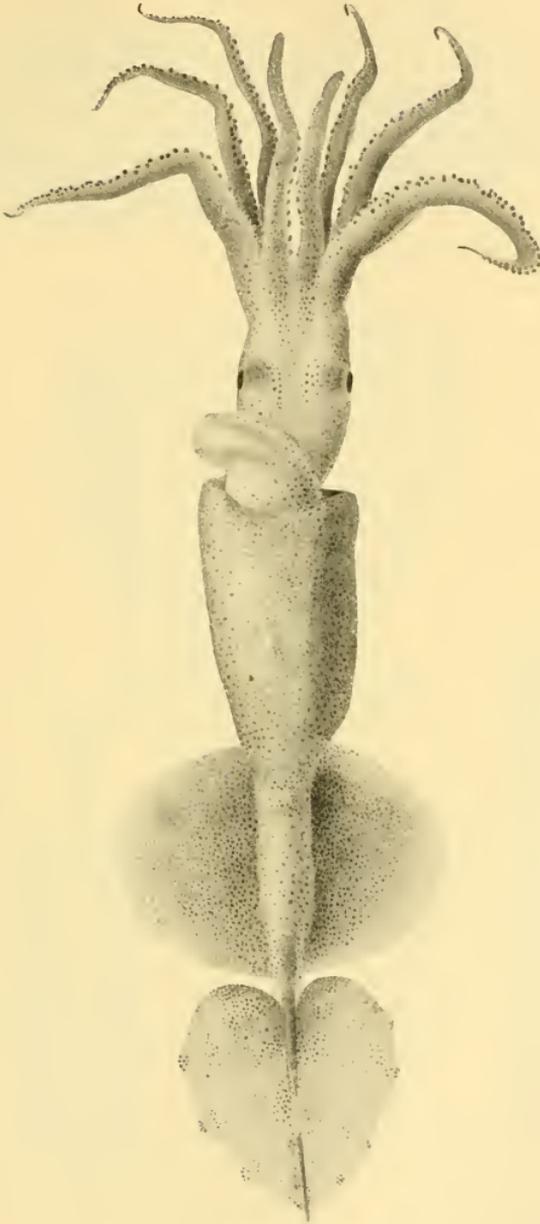


FIG. 440.
Grimalditeuthis bonplandi, Vérany. Half nat. size. (From Joubin.)

“Valdivia.” The “Michael Sars” captured no less than seven specimens,

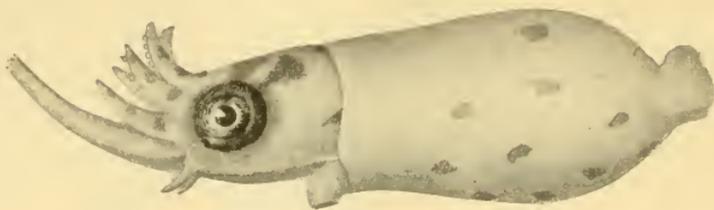


FIG. 441.
Larva of *Ommatostrephes* (1^o). (From Chun.)



FIG. 442.
Toxeuma belone, Chun. About
nat. size. (From Chun.)



FIG. 443.
Bathothauma lyromma, Chun. Two-thirds nat. size.
(From Chun.)

in different interesting stages of development, around the Canaries and

on the track to the Azores. In all probability this form is bathypelagic. Of other Myopsidæ the genera *Sepiola*, *Rossia*, *Loligo*, and *Sepia* have been captured only in trawls along the bottom. The same remark applies to the genera *Octopus* and *Cirrotheuthis*, belonging to the Octopoda. A large new species, named by Chun *Octopus (Polypus) lothei*, was taken in the trawl south of the Canaries in 2600 metres of water. Interesting pelagic forms of Octopoda were also met with; for instance: *Tremoctopus*, *Eledonella*, *Bolitæna*, *Opisthoteuthis*, *Vampyrotheuthis*, and *Cirrothauma*. The two last mentioned are probably the most interesting. *Vampyrotheuthis infernalis*, a fantastic deep-sea form, had previously been taken by the

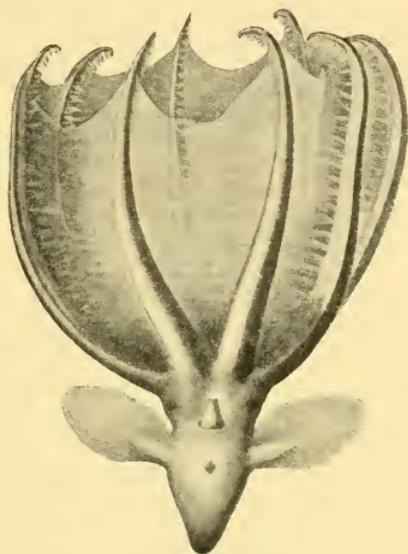


FIG. 444.

Cirrothauma murrayi, Chun. About half nat. size. (From Chun.)

“Valdivia.” *Cirrothauma murrayi* (Fig. 444) is a new species taken at great depths in our northern section. It is as fragile as a Ctenophore, and of a jelly-like consistency, its structure being exceedingly interesting and unlike that of any previously known squid. It is, besides, the only blind squid known, and has therefore been exhaustively treated by Chun in his report on our material.

I. CEPHALOPODA DECAPODA

A. EGOPSIDÆ

ENOPLOTEUTHIDÆ

Abrialiopsis morisii, Vérany, Station 23.

Pterygioteuthis giardi, Fisch., Stations 15, 29, 35, 45, 49, 51, 52, 53, 54, 56, 62, 64, 67, 81, 87.

Larvæ of Enoploteuthidæ, Stations 45, 47, 48, 51, 53, 56, 58, 62, 67, 81, 82, 84.

ONYCHOTEUTHIDÆ

Larvæ of Ægopsidæ, mostly Onychoteuthidæ, Stations 10, 29, 32, 49, 51, 52, 57, 64, 82, 88.

VERANYIDÆ

Octopodoteuthis sicula, Rüppell, Station 90.

HISTIOTEUTHIDÆ

Calliteuthis reversa, Verrill, Stations 42, 49, 51, 52, 58, 62, 70, 80, 81, 82, 84, 92.

OMMATOSTREPHIDÆ

Illex illecebrosus, Les., Stations 33, 39, Newfoundland Bank.

Todaropsis eblana, Bal., Station 33.

Ommatostrephes sagittatus, Lam., Station 115.

Larvæ of Ommatostrephidæ (*Rhynchoteuthis*), Stations 48, 56, 67.

GONATIDÆ

Gonatus fabricii, Lichtenst., Stations 70, 80, 81, 94.

BATHYTEUTHIDÆ

Ctenopteryx sicuus, Rüppell and Vérany, Stations 56, 88.

TRACHELOTEUTHIDÆ

Brachioteuthis riisei, Steenstrup, Stations 45, 51, 52, 53, 62, 64, 67, 84, 88.

CHIROTEUTHIDÆ

Mastigoteuthis flammea, Chun, Stations 29, 64.

Larvæ probably of the preceding, Stations 35, 51, 53, 84.

Mastigoteuthis grimaldii, Fisch. (Joubin), Stations 64, 67, 81, 82.

Mastigoteuthis hjorti, n.sp., Stations 52, 62, 63 (?).

Grimalditeuthis bonplandi, Vérany, Station 53.

Doratopsis vermicularis, Vérany, Station 64.

Doratopsis lippula, Chun, Station 51.

Doratopsis exophthalmica, Chun, Station 90.

Young stages probably of the preceding, Stations 53, 88, 94.

Young stages of the genus *Doratopsis*, Stations 23, 53, 56, 58, 81, 90.

CRANCHIIDÆ

Cranchia scabra, Leach, Stations 51, 52.

Leachia cyclura, Les., Stations 23, 64.

Desmoteuthis pellucida, Chun, Stations 10, 45, 67, 98, 101.

Corynomma speculator, Chun, Stations 51, 64.

Teuthovenia megalops, Prosch., Stations 10, 45, 51, 58, 63, 64.

Toxexuma belone, Chun, Stations 49B, 51, 53, 67.

Galiteuthis suhmii, Hoyle, Station 64.

Bathothauma lyromma, Chun.

B. MYOFSIDÆ

SPIRULIDÆ

Spirula australis, Lam., Stations 34, 35, 42, 44, 45.

SEPIOLIDÆ

Heteroteuthis dispar, Rüppell, Stations 42, 56, 58.

Sepiolo rondelettii, d'Orbigny, Stations 39, 96.

Rossia caroli, Joubin, Station 70.

LOLIGINIDÆ

Loligo media, L., Stations 14, 20.

Loligo forbesi, Steenstr., Station 39.

SEPIIDÆ

Sepia d'Orbignyi, Férussac, Station 33.

Sepia officinalis, L., Station 37.

II. CEPHALOPODA OCTOPODA

PHILONEXIDÆ

Tremoctopus atlanticus, d'Orbigny, Stations 51, 53, 62.

Argonauta sp., Stations 45, 49B.

Larvæ, either of *Tremoctopus* or *Argonauta*, Stations 95, 98, 101.

POLYPODIDÆ

Octopus (Polypus), n.sp., Station 58.

Octopus (Polypus) lothei, n.sp., Station 41.

BOLITÆNIDÆ

Eledonella pygmaea, Verrill, Stations 45, 53, 62.

Bolitæna diaphana, Hoyle, Stations 35, 53, 56, 64, 92.

CIRROTEUTHIDÆ

Opisthoteuthis agassizii, Verrill, Station 4.

Cirrotheuthis umbellata, Fischer, Stations 25, 53, 70.

Vampyroteuthis infernalis, Chun, Stations 51, 57.

Cirrothauma murrayi, n.sp., Station 82.

The Tunicata have been so termed from the gelatinous mantle or tunic surrounding their body, which is composed of a peculiar substance, "tunicin," supposed to be closely related to cellulose. All Tunicata have pelagic larvæ, which have long attracted the interest of zoologists, because their central nervous system (medullar tube), sense organs, and axial skeleton present a striking likeness to the lower vertebrates or to the early embryonal stages of the vertebrates. Among the Tunicata there is a large group, the Ascidians, which at the close of larval

life fix themselves to the bottom and become sessile, like the Hydro-medusæ, forming colonies by budding. They are thus meropelagic, whereas all other Tunicata are holopelagic and perfectly independent of the bottom. These latter are the only ones to be dealt with here, viz. Appendicularians, Salpæ, and the genera *Doliolum* and *Pyrosoma*.



FIG. 445.
Oikopleura labradoriensis,
Lohm (about $\frac{1}{8}$ "),
(From Lohmann.)

The Appendicularia resemble greatly the larvæ of Ascidians, and present a remarkable likeness to early vertebrate types. As a rule they are transparent and perfectly devoid of colour. Their body (see Fig. 445) is clumsy in shape and contains all the organs of nutrition and propagation, with a long elastic tail which serves solely the purpose of locomotion. Lohmann has studied the biology of this group,¹ and his results will be referred to later. The Appendicularians live mostly in the upper 200 metres of the ocean, though in tropical waters they occur deeper; in fact in the Sargasso Sea the German Plankton Expedition found more of them below than above 200 metres. As with most surface forms the species are most abundant in warm waters, like *Appendicularia sicula*, *Fritillaria venusta*, and *Oikopleura parva*, while *Oikopleura vanhöffeni* and *O. labradoriensis* are northern forms.

The Salpæ are free-swimming, barrel-shaped, transparent animals, well-known to all sea-faring people (Fig. 446). They are often seen crowding the surface-waters of the ocean in countless numbers. Among investigations of recent years we may cite the report on the "Valdivia" collection by Apstein.² In hauls with closing nets the "Valdivia" found the majority of Salpæ in depths less than 200 metres.

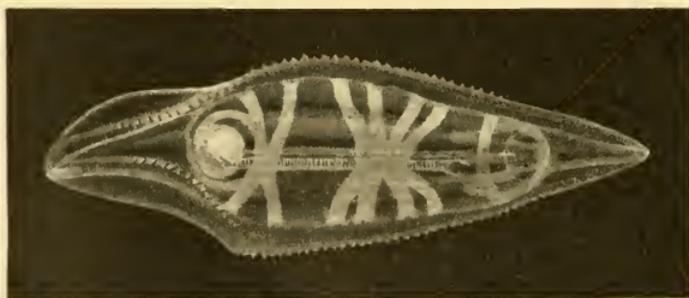


FIG. 446.
Salpa fusiformis forma *aspera*, Cham. Nat. size.

¹ Lohmann, *Ergeb. Plankton-Expedition*, Bd. 2, 1896.

² Apstein, *Wiss. Ergeb. "Valdivia" Expedition*, Bd. 12, 1906.

Only exceptionally, and chiefly in the Antarctic, forms were found between 1500 and 1000 metres that in warm waters live at the surface. The Salpæ are individually most abundant in warm water, and in the Atlantic we do not find a single species which is peculiar to the area north of lat. 45° N. Apstein tells us that three species have been found in the northern region, viz. *Salpa fusiformis*, *S. mucronata*, and *S. zonaria*, but they really belong to warm waters and have been carried north by currents (see Fig. 447). The genus *Cyclosalpa* comprises typical warm-water forms.

The genus *Doliolum* is also, according to Neumann's¹ treatise on the "Valdivia" collection, chiefly a warm-water form exceedingly sensitive to changes of temperature. *Doliolum krohni*, *D. tritonis*,

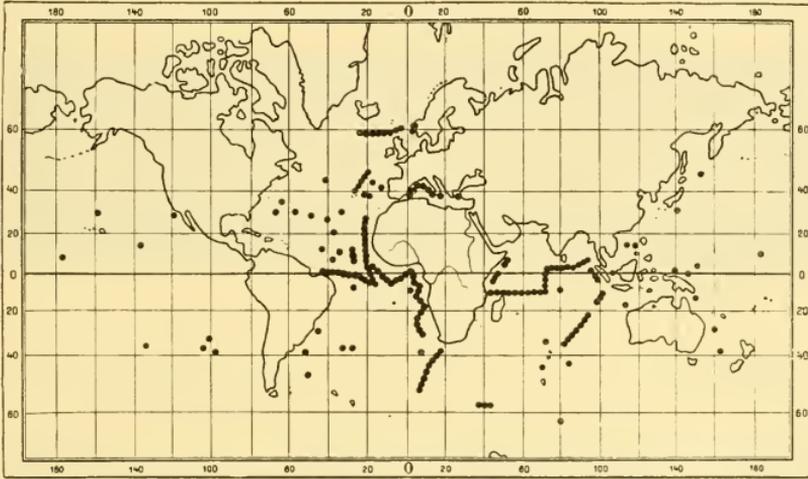


FIG. 447.—DISTRIBUTION OF *SALPA FUSIFORMIS*.
(From Apstein.)

D. mülleri, and *D. gegenbauri* are the species which go farthest north in the Atlantic.

The genus *Pyrosoma* (Fig. 448) has from the earliest days of oceanography attracted the interest of man, to a great extent on account of the strong phosphorescent light emitted, the name meaning "fire-animal." The individuals are aggregated into cylindrical colonies, which may attain an enormous size (several yards long). Some occur in the surface-waters, some in deep water.

In the narrative of the "Challenger" cruise, Sir John Murray, describing the voyage from the Bermudas to the Azores, writes as follows:—"On the 25th (of June) a very large colony of a new species of *Pyrosoma* was captured in the trawl. The cylinder was 4 feet 2 inches in length and 10 inches in diameter, closed at one end, and as in the

¹ Neumann, *Wiss. Ergeb. Valdivia-Expedition*, Bd. 12, 1906.

smaller forms, the colony was spotted with red, the red spots being the visceral nuclei of the several animals. The specimen was kept in a tub of water till after dark, when it gave off brilliant phosphorescent light on being disturbed. The officers amused themselves by writing their names along this living cylinder with one finger, the track of which remained as a bright line of light for some seconds. Salpæ were the commonest animals in the surface waters; there were several kinds, and many long bands of them in the chain form were taken in the surface nets. Brilliant phosphorescence was observed at night during calm weather."¹ During the Atlantic cruise of the "Michael Sars" great quantities of Salpæ, *Doliolum* and *Pyrosoma*, were captured. The collections have been examined by Bjerkan, to whom I am indebted for the following list, which shows that many of the species are widely distributed in the North Atlantic. Excluding the Appendicularia, which have not yet been

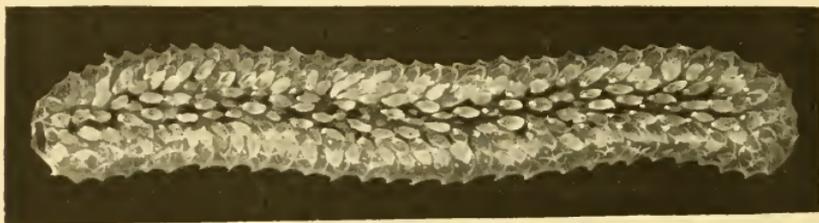


FIG. 448.

Pyrosoma spinosum, Herdman. Nat. size.

investigated, seventeen species were taken during the cruise, of which seven were taken to the north as well as to the south of the Azores.

Cyclosalpa pinnata, Forsk., Stations 56, 57, 58, 59, 86, 88.

Cyclosalpa floridana, Apstein, Stations 22, 25, 29.

Salpa maxima, Forsk., Stations 29, 33, 34, 35, 42, 43, 52, 56, 62, 66, 86, 88.

Salpa fusiformis, Cuv., Stations 10, 19, 31, 39, 51, 52, 53, 56, 58, 67, 81, 82, 84, 86, 87, 88, 90, 92, 94, 97, 98, 100, 101, 102.

Salpa fusiformis forma *aspera*, Cham.,² Stations 10, 15, 19, 24, 25, 29, 32, 51, 58, 62, 67, 84, 87, 88, 90, 92.

Salpa amboinensis, Apstein, Stations 19, 23, 49, 56, 58.

Salpa mucronata, Forsk., Stations 32, 43, 44, 45, 59, 56, 57, 58, 59, 67, 83, 87.

Salpa confederata, Forsk., Stations 31, 40, 42, 43, 51, 69, 81, 84, 86, 88.

Salpa zonaria, Pall., Stations 10, 15, 22, 23, 25, 29, 42, 43, 56, 62, 66, 67, 71, 80, 81, 82, 84, 88, 97, 102.

Salpa tilesii, Cuv., Station 10.

Salpa henseni, Traustedt, Stations 56, 58.

Doliolum tritonis, Herdman, Stations 88, 90, 92, 94, 98, 100, 101.

Doliolum sp., Stations 23, 25, 29, 32, 34, 44, 48, 49, 56, 67, 84.

Pyrosoma spinosum, Herdman, Stations 10, 39, 51, 62, 64, 67, 81, 84, 87, 88, 90.

Pyrosoma giganteum, Lesueur, Stations 29, 48, 87, 88.

Pyrosoma atlanticum, Péron, Stations 42, 47, 56, 58.

Pyrosoma, n.sp., Stations 49, 56, 88.

¹ Narrative Chall. Exp., vol. i, p. 170, 1885.

² Previously forma *echinata* (Herdman).

As indicated in Chapter VII., zoologists have until lately been unable to decide what species of fishes live along the bottom, and what species belong to the intermediate and surface waters. In recent years our knowledge has greatly increased. The "Valdivia" Expedition took no less than 151 species in pelagic fishing appliances.¹ Many of these have raised considerable interest on account of their curious shapes, especially the so-called "deep-sea fishes," which were supposed to live in the great depths of the ocean.

During the cruise of the "Michael Sars" probably about 10,000 specimens of pelagic fishes were taken, exclusive of the many larvæ and young stages. This abundant material has not yet been worked up, and complete lists, even of the adult fishes, are not available. Of the Scopelidæ (including the genus *Myctophum*), the genus *Melanphaës* and different Stomiatiidæ, only a limited number of species have been dealt with, many of the species being new, while the larvæ and young fish have as yet only been divided into certain groups. Nevertheless, the following list is of interest, as it indicates a great advance

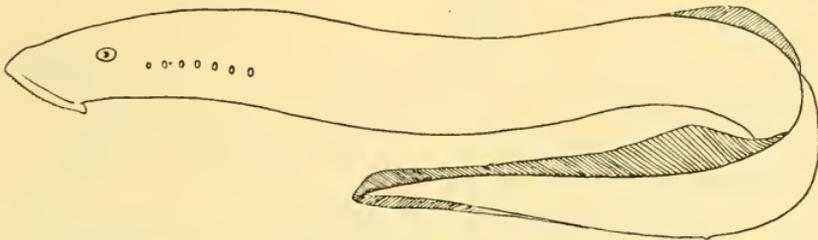


FIG. 449.

Petromyzon marinus, L. (From Goode and Bean.)

in our knowledge of the fishes of the North Atlantic; though the collections of the "Michael Sars" are deficient as regards the coastal and northern waters of the Atlantic, much information has been gained regarding the pelagic fishes of the Norwegian Sea and the North Sea.

The present list records 95 species, all, except one specimen of the lamprey, *Petromyzon marinus* (see Fig. 449), taken on the banks of Newfoundland, belonging to the Teleostei, or bony fishes.

The sub-order Malacopterygii comprises many of the most important forms from coastal waters as well as from the ocean.

The Clupeidæ (or herrings) are economically the most important of all pelagic fishes, and belong wholly or chiefly to the coast waters (neritic). In southern waters (Bay of Biscay, off the coasts of Spain, Portugal, and Africa) the principal species are the anchovy (*Engraulis encrasicolus*, see Fig. 450), *Clupea alosa*, and the sardine or pilchard (*Clupea pilchardus*, see Fig. 451), while in northern waters the herring (*Clupea harengus*) and the sprat (*Clupea sprattus*) predominate.

The Salmonidæ have many pelagic representatives. The light-coloured salmon and sea-trout are generally considered to be pelagic when away from the rivers and the coasts. The list of bottom-fish in

¹ Brauer, *Wiss. Ergeb.* "Valdivia" Expedition, Bd. 15, 1906.

Chapter VII. includes the deep-sea genera *Argentina* and *Alepocephalus*, and it is somewhat surprising to find the small curious forms of the pelagic genus *Opisthoproctus* referred to the same family; but there are

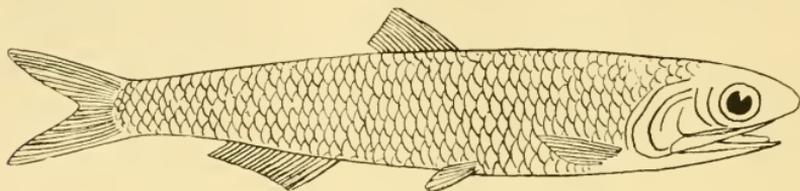


FIG. 450.
Engraulis encrasicolus, Cuv. (From Day.)

really certain features connecting it with *Alepocephalus*. The Opisthoproctidæ are small fishes, only a few centimetres long, laterally com-

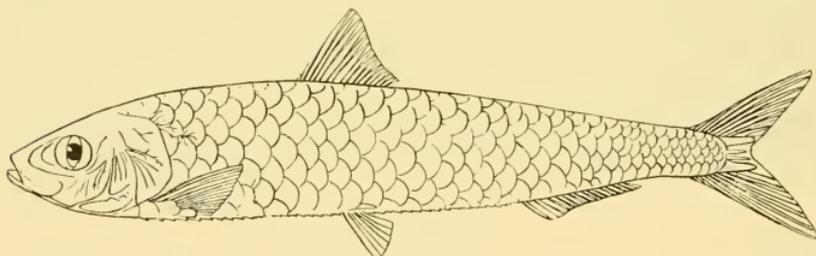


FIG. 451.
Clupea pilchardus, Walb. (From Smitt.)

pressed, with large thin scales, telescopic eyes, a remarkable flattening of the belly, forming a peculiar sole, and with a small adipose fin as in all

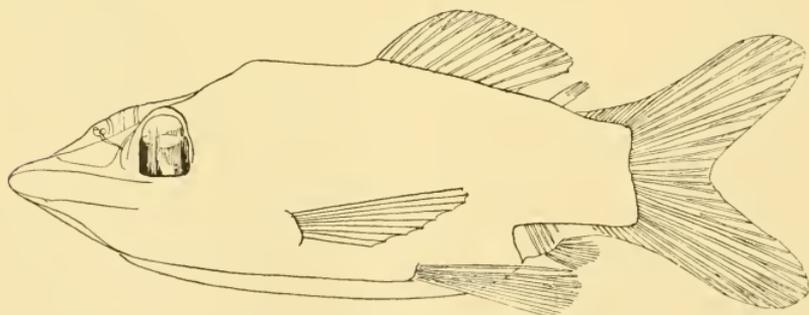


FIG. 452.
Opisthoproctus grimaldii, Zugmayer. Nat. size, 2 cm.

other Salmonidæ. One species, *Opisthoproctus soleatus*, was taken previous to our cruise in the Atlantic, and the other species (*O. grimaldii*, see Fig. 452) was taken subsequently near Gibraltar.

The families Stomiatiidæ and Sternoptychidæ present many points of resemblance, and comprise many fishes which were previously looked upon as genuine deep-sea forms. They vary greatly in shape, some being long and slender, others short and laterally compressed, and the

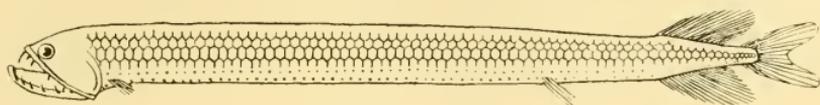


FIG. 453.
Stomias boa, Risso. Nat. size, 16 cm.

mouth is large with a great number of teeth. Both families are characterised by abundant light-organs, the only difference between them lying in the fact that the Sternoptychidæ have only one kind of

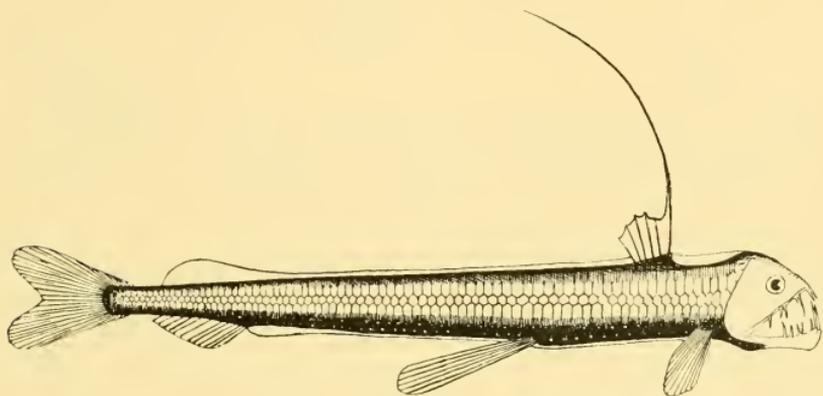


FIG. 454.
Chauliodus sloanei, Bl. and Schn. Nat. size, 6 cm.

light-organ, while the Stomiatiidæ have below or behind the eye large and powerful light-organs, very often coloured, quite different in structure from the small ones on the body.

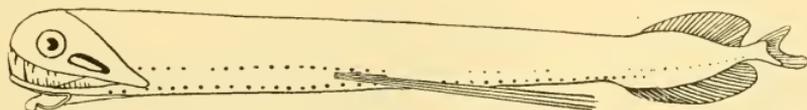


FIG. 455.
Photostomias guernei, Coll. Nat. size, 17 cm.

The Stomiatiidæ occurring most commonly in the Atlantic are *Stomias boa* (see Fig. 453) and *Chauliodus sloanei* (see Fig. 454), both taken in the tow-nets of the "Michael Sars" at nearly all oceanic stations. They both occur in all oceans, and some of the rarer forms, like *Macrostomias longibarbus*, *Malacosteus indicus*, and *Astronesthes niger*, are also known from other oceans. An interesting species,

Photostomias guernei, is shown in Fig. 455. The list includes several new forms, which have not yet been described, showing that the Stomiidæ are more abundant in the Atlantic than was previously supposed.

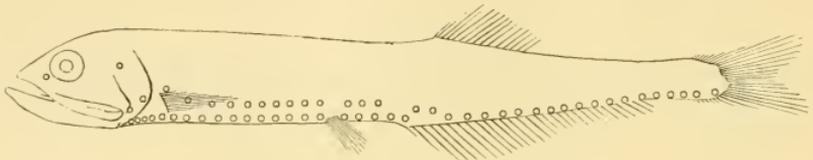


FIG. 456.
Gonostoma denudatum, Rafin. Nat. size, 3.5 cm.

The Sternoptychidæ occur in vast numbers, some of the forms being among the most abundant of all pelagic fishes in the ocean, like

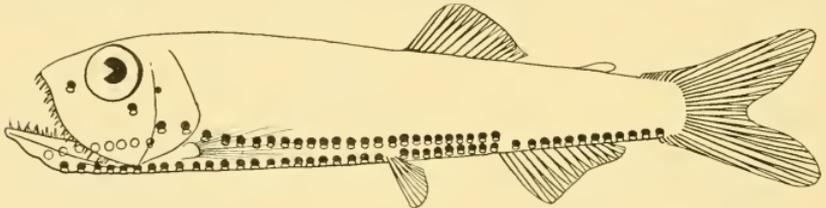


FIG. 457.
Vinciguerria lucetia, Garm. Nat. size, 3.9 cm.

the genus *Cyclothone*; in the North Atlantic the two species *C. microdon* and *C. signata* (see Plate I. Chapter X.) are specially abundant. Nearly

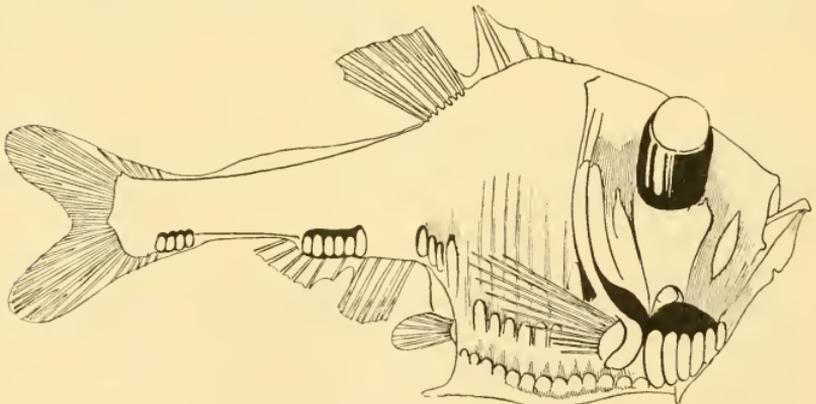


FIG. 458.
Argyropelecus hemigymnus, Cocco. Nat. size, 3.5 cm.

allied to *Cyclothone* is the genus *Gonostoma*, the species *Gonostoma grande* and *G. rhodadenia*¹ being biologically very interesting (see Plate II.

¹ On Plate II, this species is named *G. elongatum*.

Chapter X.). *Gonostoma denudatum* is shown in Fig. 456. The genera *Vinciguerria* (see Fig. 457), *Ichthyococcus*, and *Valenciennellus* resemble each other considerably, and have large and numerous light-organs; their geographical distribution is very wide. Very peculiar are the compressed silvery forms of the genera *Argyropelecus* (see Fig. 458) and *Sternoptyx*, which have highly-developed light-organs. Most of them occur in all oceans, the species in the list having been taken at many stations in the North Atlantic, while some of them are also known from the Norwegian Sea.

The sub-order Apodes includes the eel-like fishes devoid of ventral

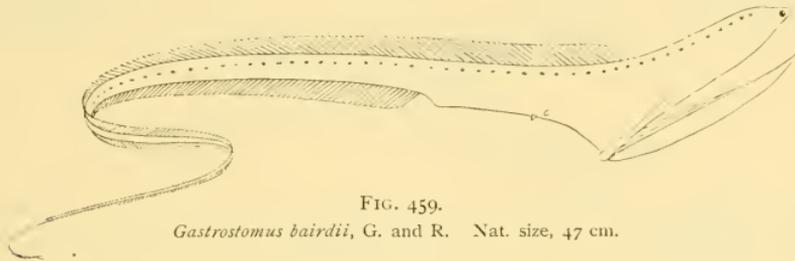


FIG. 459.

Gastrostomus bairdii, G. and R. Nat. size, 47 cm.

fins. From coastal waters the eel, the conger, and the Murænidæ are best known. In deep waters the Synphobranchidæ, included in the list of bottom-fishes, are very important; some of them are perhaps deep-living pelagic fish, but our knowledge on this point is still imperfect. The three species of the Nemichthyidæ and the two species of the Saccopharyngidæ are undoubtedly pelagic forms. *Gastrostomus bairdii* is shown in Fig. 459. *Serrivomer sector* was taken at numerous stations, one specimen of the large and remarkable *Nemichthys*



FIG. 460.

Cyema atrum, Günth. Nat. size, 11.5 cm.

scolopaceus was captured south of the Azores, and the peculiar *Cyema atrum* (see Fig. 460) was taken at three stations in the southern part of our track. To this sub-order belong the larval forms termed Leptocephali, which are all larvæ of Anguillidæ, Murænidæ, Nemichthyidæ, Synphobranchidæ, and Saccopharyngidæ.

The sub-order Haplomi includes the Scopelidæ, one genus of which, *Myctophum*, is represented by numerous species (Brauer mentions more than seventy); these play a greater part in the surface fauna of the ocean than all other pelagic fishes. Our list records only those species determined up to the present time, and there are doubtless many more. Of greatest interest to us are *Myctophum glaciale*, *M. punctatum*, which

(together with *M. elongatum*) are known from the Norwegian Sea, but most of the species belonging to this genus are warm-water forms. *M. rafinesquei* is shown in Fig. 461. Several genera belonging to the Scopelidæ are recorded in the list of bottom-fishes, *Bathysaurus*,

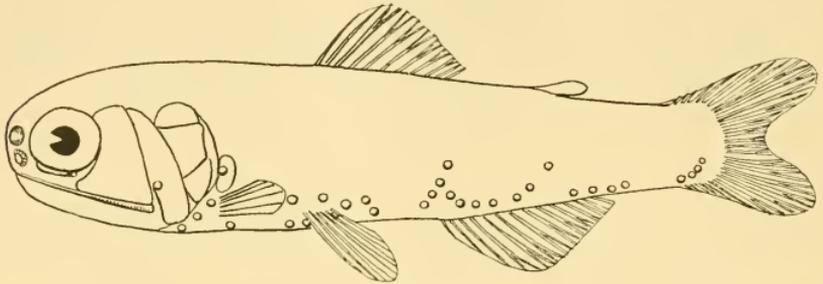


FIG. 461.

Myctophum (Diaphus) rafinesquei, Cocco. Nat. size, 7 cm.

Bathypterois, etc., which will probably prove to be bathypelagic forms, but the present state of our knowledge renders this merely a conjecture. Of interest is the remarkable form *Omosudis lowei* taken on a long line between the Canaries and the Azores (Station 49; see Fig. 462). This sub-order

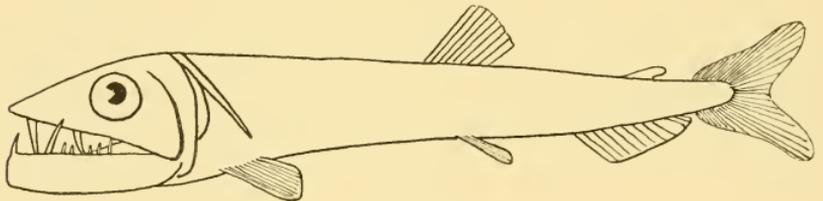


FIG. 462.

Omosudis lowei, Günth. Nat. size, 15 cm.

includes the Cetomimidæ, one genus of which was previously known and one was discovered by us; both genera contain blind forms (see Chapter X.).

The sub-order Catosteomi contains the Syngnathidæ, the needle-fish



FIG. 463.

Syngnathus pelagicus, Osbeck. Nat. size, 12 cm.

and the pipe-fish. The pipe-fishes (*Siphonostoma typhle* and *Syngnathus acus*) are common along the coasts of Northern Europe. Of the needle-shaped species, *Syngnathus pelagicus* (see Fig. 463) is a typical Sargasso form (see Plate V. Chapter X.), while *Nerophis æquoreus* lives mainly in the north-eastern part of the Atlantic, where it occurs in all the hauls

with surface tow-nets. The beautiful little *Hippocampus* (see Fig. 71, p. 89) was taken between the Canaries and the Azores.

The sub-order Percosoces contains several important and interesting surface-fish. To the family Scombresocidæ belong the gar-pike (*Belone*), the genus *Scombresox*, and the flying-fish of the genus *Exocoetus*. *Scombresox saurus* attains a length of 50 cm., and resembles the gar-pike, but does not approach so near the coasts, nor does it extend so far north; it is known from the Atlantic coasts of North America, Northern Europe and Africa. Day records a capture of 100,000 individuals in one haul off the British shores. Only very young specimens were taken by the "Michael Sars" (see Chapter X.), but these are very interesting, because they prove that the species occurs pelagically right across the Atlantic. Flying-fishes were constantly observed on our southern

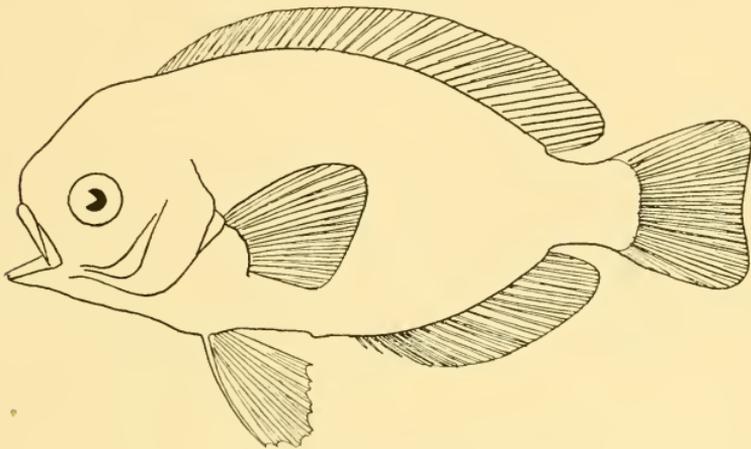


FIG. 464.

Lirus maculatus, Günth. Nat. size, 9.5 cm.

track, and some of the specimens which flew on board have been referred to *Exocoetus spilopus*. Between 40 and 50 species of this genus are known from tropical and sub-tropical waters. Very interesting are our captures of minute young flying-fish (see Chapter X.). The only fish belonging to the sub-order Percosoces from great depths is *Chiasmodes niger* (see Fig. 514, p. 721), taken by the "Michael Sars" in the Sargasso Sea. It was previously known from the eastern and western sides of the Atlantic, and from the Indian Ocean. The fish has very powerful teeth, and can swallow a fish much larger than itself, the digestive tract being marvellously tensile (see Chapter X.). *Lirus maculatus* (see Fig. 464) and *L. ovalis* belong to the family Stromateidæ. Along with Acanthopterygians, like *Polyprion americanus*, these fishes gather around wreckage and other floating objects. They live in tropical or sub-tropical surface waters, and biologically resemble the large lump-fish or sun-fish. All the forms mentioned were captured from a boat, either with a hoop-net or, in the case of *Mola rotunda*, with a harpoon.

The sub-order Acanthopterygii does not play the important part

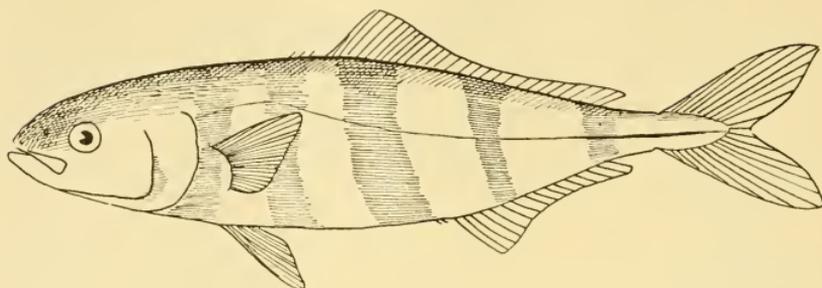


FIG. 465.
Naucrates ductor, L.

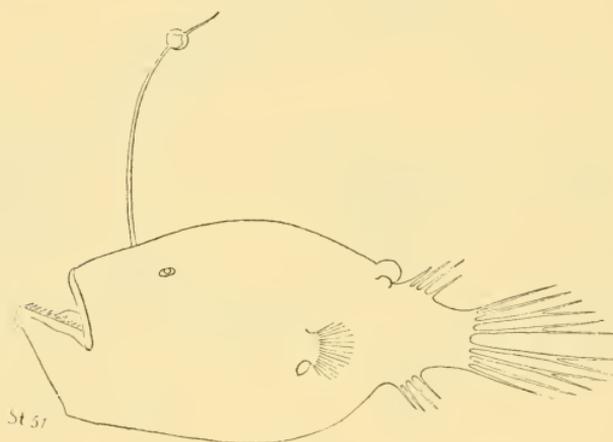


FIG. 466.
Ceratias couesi, Gill. Nat. size, 3 cm.

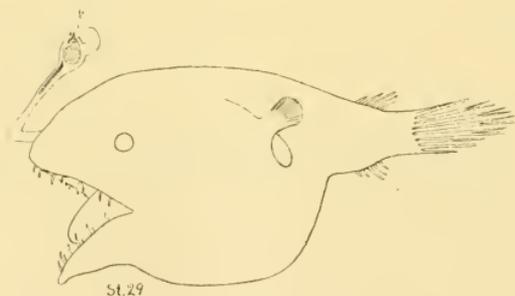


FIG. 467.
Oneirodes, n.sp. No. 2. Nat. size, 3 cm.

among the oceanic pelagic fish that it does among the bottom-fishes (see Chapter VII.). One group, however, is very important, viz. the Scombri-

formes or mackerels. The Scombridæ are represented by many species in tropical and sub-tropical waters, the most important in the North Atlantic being the mackerel (*Scomber scomber*), the tunny (*Thynnus thynnus*), the bonito (*Thynnus pelamys*), and *Pelamys sarda*. The adult fishes are widespread, but most of them probably seek the coasts in spawning time. The natural history of all these important and interesting species has been very little investigated, and very little material was obtained during the cruise of the "Michael Sars." We obtained far

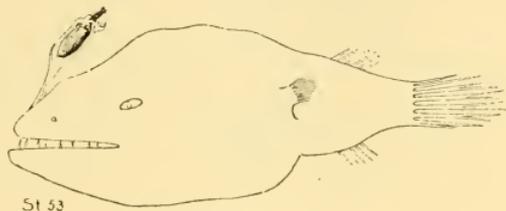


FIG. 468.

Oneirodes, n.sp. No. 3. Nat. size, 2 cm.

more information concerning the Carangidæ or horse-mackerels, of which young individuals were taken abundantly so far from land that their oceanic habitat may be considered as proved. To this family also belongs the famous pilot-fish (*Naucrates ductor*, see Fig. 465), some specimens of which were taken. Allied forms are *Zeus faber* and *Capros aper*, of which only adult individuals were taken in our trawls, but which nevertheless must be supposed to be capable of living in mid-water. The

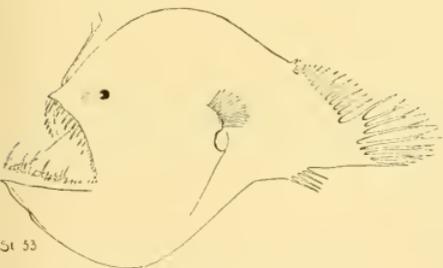


FIG. 469.

Melanocetus johnsoni, Günth. Nat. size, 4.5 cm.

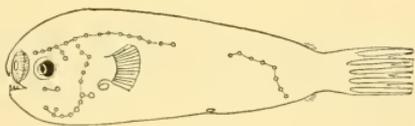


FIG. 470.

Aceratias macrorhinus indicus, A. Br.
Nat. size, 2.8 cm.

young of *Capros aper* and of several other Acanthopterygians were taken in the surface waters far from land. Bathypelagic forms are very scarce among the Acanthopterygians. Our list records only two species of the genus *Melanphaês*, but many of our specimens have not yet been determined. *M. mizolepis* shows a wide distribution in the North Atlantic, and is known from the Indian Ocean.

The sub-order Pediculati is well known from shallow water through the angler (*Lophius piscatorius*), the eggs of which we found floating off the banks of Newfoundland. Genuine deep-sea forms are the members of the Ceratiidæ, containing the genera *Ceratias*, *Oneirodes*, *Melanocetus*

(see Figs. 466-469). They are small, generally black, forms, with a mouth of gigantic size provided with powerful teeth. They have attracted special attention from the nasal tentacle carrying at its end a peculiar

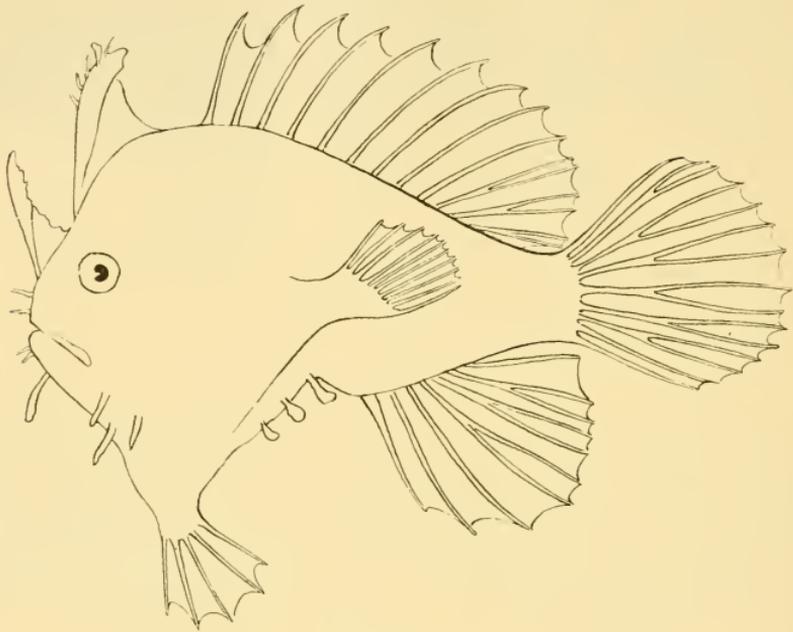


FIG. 471.

Antennarius marmoratus, Günth. Nat. size, 3.3 cm.

lantern-like light-organ. Of the eight species of Ceratiidæ taken during our cruise, no less than five are supposed to be new to science; one species (*Melanocetus krechii*) is represented by a single specimen

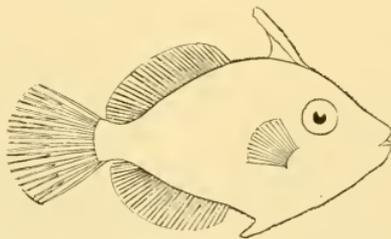


FIG. 472

Monacanthus. Nat. size, 2 cm.

from the Indian Ocean. Such facts show that our knowledge of the fauna of the ocean still leaves much to be desired. Remarkable small forms of the genus *Aceratias* (see Fig. 470) also belong to this sub-order. One of these was previously known from the Indian Ocean only; the

other was taken off the Congo. *Antennarius marmoratus* (see Fig. 471) presents in its shape some likeness to the Ceratiidæ and to *Lophius*, but is in fact a small surface form peculiar to the Sargasso Sea (see Plate V. Chapter X.), where the genus *Monacanthus*, belonging to the sub-order Plectognathi (see Fig. 472 and Plate V.), also occurs.

PELAGIC FISHES

TAKEN BY THE "MICHAEL SARS" IN 1910 IN THE ATLANTIC
NORTH OF LAT. 26° N.

Class—CYCLOSTOMATA

Order—PETROMYZONTES

PETROMYZONTIDÆ

Petromyzon marinus, L., 1910 (see Fig. 449).

Class—PISCES

Sub-Class—TELEOSTOMI

Order—TELEOSTEI

Sub-Order—MALACOPTERYGII

CLUPEIDÆ

Engraulis encrasicolus, Cuv., 1910, Station 36 (see Fig. 450).

Clupea alosa, L., 1910, Station 36.

Clupea pilchardus, Walb., 1910, Station 36 (see Fig. 451).

SALMONIDÆ

Opisthoproctus soleatus, Vaill., 1910, Stations 49, 52, 64 (see Fig. 72, p. 89).

Opisthoproctus grimaldii, Zugmayer, 1910, Stations 23, 49 (see Fig. 452).

STOMIATIDÆ

We give here Brauer's¹ classification of the Stomiatiidæ and Sternoptychidæ.

Stomias boa, Risso, 1902, Faroe-Shetland Channel; 1910, Stations 10, 19, 29, 34, 42, 51, 53, 56, 62, 63, 64, 67, 80, 82, 84, 87, 88, 90, 92, 94, 98, 101 (see Fig. 453).

Chauliodus sloanei, Bl. and Schn., 1910, Stations 10, 25, 29, 34, 35, 42, 45, 49, 50, 51, 52, 53, 56, 62, 63, 64, 80, 81, 82, 84, 88, 90 (see Fig. 454).

Photostomias guernei, Coll., 1910, Stations 34, 45, 49, 51, 53, 58, 81, 82 (see Fig. 455).

Eustomias obscurus, Vaill., 1910, Station 29.

¹ "Die Tiefsee Fische," *Wiss. Ergeb. Valdivia-Expedition*, Bd. 15, 1906.

- Eustomias*, n.sp., 1910, Stations 45, 81.
Macrostomias longibarbus, A. Br., 1910, Stations 23, 52.
Melanostomias, n.sp., 1910, Stations 49, 87.
Dactylostomias, n.sp., 1910, Stations 42, 45, 49, 51, 52, 53, 56, 58, 62.
Echiosstoma (species undetermined), 1910, Station 62.
Idiacanthus ferox, Günth., 1910, Stations 34, 42, 45, 49, 51, 53 (see Fig. 67, *b*, p. 86).
Malacosteus indicus, Günth., 1910, Station 48.
Malacosteus niger, Ayres, 1910, Station 51.
Malacosteus choristodactylus, Vaill., 1910, Stations 45, 51, 58.
Astronesthes niger, Rich., 1910, Stations 51, 52, 53, 64, 67 (see Fig. 80, p. 93).
Astronesthes (species undetermined), 1910, Stations 42, 87, 88.

STERNOPTYCHIDÆ

- Gonostoma rhodadenia*, Gilb., 1910, Stations 49, 51, 52, 53, 58, 101.
Gonostoma grande, Coll., 1910, Stations 45, 53, 56, 62, 64, 81, 88, 92, 94, 98.
Gonostoma denudatum, Rafin., 1910, Stations 58, 62 (see Fig. 456).
Cyclothone signata, Garm., 1910, Stations 10, 22, 25, 27, 28, 34, 35, 40, 42, 45, 47, 48, 49, 50, 51, 52, 53, 56, 62, 63, 66, 67, 80, 81, 82, 88, 90, 92, 94, 101.
Cyclothone signata alba, A. Br., 1910, Stations 34, 52, 56, 62, 64, 66, 67, 81, 92, 101.
Cyclothone livida, A. Br., 1910, Stations 34, 35.
Cyclothone microdon, Günth., 1910, Stations 10, 19, 25, 27, 29, 34, 35, 42, 45, 47, 48, 49, 50, 51, 52, 53, 56, 62, 63, 64, 67, 80, 81, 82, 90, 92, 94, 101.
Cyclothone microdon pallida, A. Br., 1910, Stations 28, 35, 56, 63, 81, 98, 101.
Cyclothone acclinidens, Garm., 1910, Stations 51, 67.
Vinciguerrria lucetia, Garm., 1910, Stations 20, 29, 34, 39, 42, 45, 50, 51, 52, 53, 56, 62, 64, 69, 81, 88 (see Fig. 457).
Ichthyococcus ovatus, Cocco, 1910, Stations 23, 58.
Valenciennellus tripunctulatus, Esm., 1910, Stations 23, 29, 34, 35, 42, 45, 48, 51, 52, 53, 56, 58, 62.
Argyropelecus affinis, Garm., 1910, Stations 34, 45, 48.
Argyropelecus hemigymnus, Cocco, 1910, Stations 10, 15, 19, 23, 29, 34, 35, 42, 45, 49, 51, 52, 53, 56, 58, 62, 64, 66, 67, 88, 92, 98 (see Fig. 458).
Argyropelecus offersi, Cuv., 1910, Stations 10, 23, 56, 58, 88, 92.
Argyropelecus aculeatus, Cuv. and Val., 1910, Stations 23, 29, 34, 42, 52, 53, 58, 62, 67.
Sternoptyx diaphana, Herm., 1910, Stations 23, 29, 34, 45, 48, 49, 51, 52, 53, 56, 62, 66, 67, 81, 82.

Sub-Order—APODES

NEMICHTHYIDÆ

- Serrivomer sector*, Garm., 1910, Stations 45, 49, 51, 52, 56, 64, 67.
Nemichthys scolopaceus, Richards, 1910, Stations 51, 58.
Cyema atrum, Günth., 1910, Stations 45, 53, 62 (see Fig. 460).

SACCOPHARYNGIDÆ

- Gastrostomus bairdii*, Gill and Ryd., 1910, Stations 35, 53, 62, 64, 67, 80, 81 (see Fig. 459).
 New genus, 1910, Station 53 (see Fig. 83, *b*, p. 97).

Sub-Order—HAPLOMI

SCOPELIDÆ

- Omosudis lowei*, Günth., 1910, Station 49 (see Fig. 462).
Myctophum (*Myctophum*) *rissoi*, Cocco, 1910, Stations 29, 56.
Myctophum (*Myctophum*) *glaciale*, Reinh., 1902, Faroe-Shetland Channel, Faroe Bank; 1910, Stations 10, 15, 19, 70, 80, 82, 90, 102.
Myctophum (*Myctophum*) *benoiti*, Cocco, 1910, Station 28.
Myctophum (*Myctophum*) *benoiti hygomi*, Lützk., 1910, Stations 29, 49.
Myctophum (*Myctophum*) *punctatum*, Rafin., 1910, Stations 25, 29, 53, 80, 92.
Myctophum (*Myctophum*) *affine*, Lützk., 1910, Stations 52, 53.
Myctophum (*Myctophum*) *humboldti*, Risso, 1910, Stations 20, 53.
Myctophum (*Myctophum*) *cocconi*, Cocco, 1910, Stations 20, 25, 29, 53, 56, 58, 62, 64.
Myctophum (*Myctophum*) *chærocephalum*, Fowl., 1910, Stations 50, 53.
Myctophum (*Diaphus*) *gemellari*, Cocco, 1910, Stations 49, 53, 56.
Myctophum (*Diaphus*) *rafinesquei*, Cocco, 1910, Stations 62, 84 (see Fig. 461).
Myctophum (*Lampanyctus*) *maderense*, Lowe, 1910, Station 34.
Myctophum (*Lampanyctus*) *warmingi*, Lützk., 1910, Station 51.
Myctophum (*Lampanyctus*) *micropterum*, A. Br., 1910, Stations 51, 62.
Myctophum (*Lampanyctus*) *gemmifer*, G. and B., 1910, Station 58.

CETOMIMIDÆ

- Cetomimus storeri*, G. and B., 1910, Station 35 (see Fig. 497, p. 681).
 New genus, 1910, Station 64 (see Fig. 498, p. 682).

Sub-Order—CATOSTEOMI

SYNGNATHIDÆ

- Syngnathus pelagicus*, Osbeck, 1910, Sargasso Sea, Stations 51, 53, 64 (see Fig. 463).
Nerophis æquoreus, L., 1910, Stations 10, 56, 58, 84, 86, 87, 88, 90, 92, 94, 98.
Hippocampus ramulosus, Leach, 1910, Station 48 (see Fig. 71, p. 89).

Sub-Order—PERCESOCES

SCOMBRESOCIDÆ

- Scombrox saurus*, Walb., 1910, Stations 25, 27, 37, 46, 47, 48, 49, 50, 51, 52, 56, 64, 66, 90.
Exocoetus spilopus, Val., 1910 (see Fig. 61, p. 82).

CHIASMODONTIDÆ

- Chiasmodon niger*, Johns., 1910, Station 52 (see Fig. 514, p. 721).

STROMATEIDÆ

- Lirus medusophagus*, Cocco, 1910, Stations 23, 25.
Lirus maculatus, Günth., 1910, Station 49 (see Fig. 464).
Lirus ovalis, Cuv. and Val., 1910, Stations 49, 56.
Lirus perciformis, Mitchell, 1910, Station 61.

Sub-Order—ACANTHOPTERYGII

Division—PERCIFORMES

BERYCIDÆ

Melamphaës mizolepis, Günth., 1910, Stations 67, 80, 81, 82, 92.*Melamphaës*, n.sp., 1910, Stations 51, 67.

CYPHOSIDÆ

Cyphosus bosaii, Lacép., 1910, Station 61.

SERRANIDÆ

Polyprion americanus, Bl. and Schn., 1910, Station 56.

CAPROIDÆ

Capros aper, Lacép., 1910, Stations 1, 3, 20, 39, 56, 58.

Division—SCOMBRIFORMES

CARANGIDÆ

Caranx trachurus, L., 1910, Stations 1, 3, 14, 20, 36, 39, 49, 52, 56, 58 (see Fig. 86, p. 98).*Temnodon saltator*, Cuv. and Val., 1910, Station 36.*Seriola*, sp.juv., 1910, Station 66.*Naucrates ductor*, L., 1910, Station 49 (see Fig. 465).

TRICHIURIDÆ

Lepidopus caudatus, Euphras., 1910, Station 43.

Division—ZEEORHOMBI

ZEIDÆ

Zeus faber, L., 1910, Stations 1, 20.

Division—SCLEROPAREI

SCORPÆNIDÆ

Sebastes dactylopterus, de la R., 1910, Station 21.

Sub-Order—PEDICULATI

CERATIIDÆ

Ceratias couesi, Gill., 1910, Station 51 (see Fig. 466).*Ceratias*, n.sp., 1910, Station 42 (see Fig. 59, p. 81).*Oncirodes*, n.sp. No. 1, 1910, Stations 64, 81, 84 (see Fig. 90, p. 104).*Oncirodes*, n.sp. No. 2, 1910, Station 29 (see Fig. 467).*Oncirodes*, n.sp. No. 3, 1910, Station 53 (see Fig. 468).*Oncirodes megacevos*, Holt and Byrne, or n.sp. No. 4, 1910, Stations 52, 62 (see Fig. 81, p. 95).*Melanocetus johnsoni*, Günth., 1910, Station 53 (see Fig. 469).*Melanocetus krechii*, A. Br., 1910, Stations 45, 53.

ACERATIIDÆ

Aceratias mollis, A. Br., 1910, Stations 45, 49, 51, 64.

Aceratias macrorhinus indicus, A. Br., 1910, Stations 45, 49, 51, 56, 67 (see Fig. 470).

ANTENNARIIDÆ

Antennarius marmoratus, Günth., 1910, Stations 64, 66, 67 (see Fig. 471).

Sub-Order—PLECTOGNATHI

Division—SCLERODERMI

BALISTIDÆ

Monacanthus sp., 1910, Station 67 (see Fig. 472).

Division—GYMNODONTES

TETRODONTIDÆ

Tetrodon spengleri, Bl., 1910, Station 37.

MOLIDÆ

Mola rotunda, Cuv., 1910, Station 87 (see Fig. 102, p. 119).

2. DISTRIBUTION OF PELAGIC ANIMALS

The foregoing remarks and lists show that our knowledge of the distribution of pelagic animals in the ocean is now considerable, especially as regards small forms, which are easily captured in closing nets, and whose habitat may therefore be localized with accuracy. As to larger organisms the difficulties increase in proportion to their size. Thus only five of the 151 pelagic species of fishes taken during the "Valdivia" Expedition were captured in closing nets, but the bathymetrical distribution of certain species was approximately determined by lowering large vertical nets to different depths and comparing the catches. By studying the material thus obtained, Brauer¹ succeeded in ascertaining the bathymetrical distribution, or at least the upper limit, of several common species.

In Chapter II. I have described our methods of capturing pelagic animals by means of large closing nets and by simultaneously towing eight or ten nets at different depths, and in Chapter III. I have given particulars of some of the catches thus secured. My object in this chapter is to show in some detail the knowledge now available as to the vertical and horizontal distribution of pelagic animals and animal-communities

¹ Brauer, *loc. cit.*

in the waters examined by the "Michael Sars," viz. the North Atlantic and the Norwegian Sea.

To commence with, it will be advisable to consider the details of our fishing methods. The method of simultaneously towing many appliances at different depths cannot be supposed to give such exact results as hauls with closing nets, because the tow-nets function not only while being towed along, but are also liable to do so while being lowered and raised. To counteract the errors arising in this way we generally towed our nets all night long, or for lengthened periods sometimes extending to twelve hours. The distance thus covered in towing the nets was infinitely greater than the distance traversed by the nets in being lowered and raised, and the sources of error were presumably proportionally diminished.

In order to judge of the results obtained in this way we may examine the catches of individuals belonging to a definite species at all depths and at all stations. Of the well-known species *Argyrolepecus hemigymnus* we took during our cruise a total of 286 individuals, at the various depths indicated in the following table:—

Vertical distribution of <i>Argyrolepecus</i> .	Surface	0 individuals.
	At a depth of 50 metres	0 "
	" 100	"	0 "
	" 150	"	62 "
	" 300	"	155 "
	" 500	"	48 "
	" 750	"	0 "
	" 1000	"	6 "
	" 1250	"	0 "
	" 1500	"	11 "
" 2000	"	4 "	

The bulk occurred at depths between 150 and 500 metres; no individuals were caught above 150 metres, and only about 7 per cent were taken at depths lower than 500 metres. If we assume, then, that these 7 per cent were captured during the process of hauling in the appliances, and that none of them live at depths below 500 metres, we will have an idea of the accuracy of our method.

We see, further, that by far the greater number were caught at a depth of 300 metres, where we generally had out a $\frac{3}{4}$ -metre silk net, whereas at 150 metres and at 500 metres the appliance used was, as a rule, a young-fish trawl, that would have had a far greater capacity for catching these fishes. It seems, accordingly, that a preponderating majority of the individuals of this species

are very strictly limited to an intermediate layer situated at a depth of about 300 metres. A closer investigation showed that the individuals captured at a depth of 150 metres were all caught at night. This may be due either to an upward nocturnal wandering or to chance, though on this question the small amount of our material makes it unsafe to hazard an opinion; in subsequent investigations, however, it will be worth while taking this fact into consideration. Among the individuals captured at 500 metres there must, at any rate, be a few that were taken in the process of hauling in the young-fish trawl through the intermediate layer above, though the majority probably lived at that depth—a deduction supported by the fact that far fewer specimens were found in the young-fish trawl towed at 1000 metres, which may have been captured while hauling in.

This instance is a good illustration of our method with its advantages and deficiencies. Clearly the method is trustworthy only in cases where many specimens have been caught. At the same time, it is the only effective method of capture known at present, and it is therefore interesting to inspect the results obtained.

The distribution of different animal-communities in the ocean rarely coincides with what seem to be natural distributional areas. The fact is that the occurrence of animals is largely influenced by such conditions as depth and temperature. In Chapter VII. we have seen that the limit between the southern and the northern bottom-fishes did not coincide with the border-line between the Atlantic Ocean and the Norwegian Sea, but ran from Ireland or the Channel to Iceland, and thence to the coast of the United States. In the case of pelagic animals we may also distinguish between southern or Atlantic communities and northern communities, the border-line between these two communities very nearly coinciding with the line separating the corresponding communities of bottom-fish.

A. THE ATLANTIC PELAGIC COMMUNITIES

There is a striking difference between the pelagic faunas of the open ocean and of the coast banks. In the open sea we find different pelagic communities according to the different conditions presented at various depths, and by way of introduction it may be useful to inspect the aggregate catches of a

definite group of pelagic animals taken at a genuine oceanic station far from land in deep water. I have for this purpose prepared the following list recording all the fishes taken at Station 53, to the south of the Azores, during the night of the 8th-9th of July, but I regret being unable in the case of the young fish to indicate the species, which would have added greatly to the interest of the list:—

PELAGIC FISHES, STATION 53

- SURFACE, TOW-NET: Scopelidæ: *Myctophum coccoi*, *M. punctatum*, *M. chærocephalum*, *M. affine*, *M. humboldti*, etc.; Stomiatidæ: *Stomias boa*, 13 *Astronesthes niger*.
- 50 METRES, TOW-NET: Great numbers of larvæ and young fish, some with telescopic eyes, 4 small larvæ of the common eel (*Leptocephalus brevirostris*, 4.8-5.7 cm. long); many Scopelidæ: 12 *Stomias boa*, *Chauliodus sloanei*, 3 *Dactylostomias* n.sp. No. 1, *Idiacanthus ferox*.
- 100 METRES, TOW-NET: Scopelidæ: *Myctophum (Diaphus) gemellari*, 3 *Stomias boa*, *Vinciguerria lucetia*, *Argyropelecus*.
- 150 METRES, YOUNG-FISH TRAWL: A few fish-larvæ, 2 *Leptocephalus* n.sp., some *Argyropelecus*, 2 *Stomias boa*, *Photostomias guernei*, *Gonostoma rhodadenia*, new genus of Saccopharyngidæ.
- 300 METRES, YOUNG-FISH TRAWL: Young fish with telescopic eyes; Scopelidæ (*Myctophum coccoi*, etc.); 5 *Cyclothone signata*, *Cyclothone microdon*, 10 *Vinciguerria lucetia*, 13 *Valenciennellus tripunctulatus*, 16 *Argyropelecus hemigymnus*, *Argyropelecus aculeatus*, *Sternoptyx diaphana* (young fish from 8.5 cm. in length).
- 550 METRES, TOW-NET: 14 *Cyclothone signata*, 7 *Cyclothone microdon*, 14 *Chauliodus sloanei*, 3 *Sternoptyx diaphana*.
- 800 METRES, YOUNG-FISH TRAWL: 22 *Cyclothone signata*, 121 *Cyclothone microdon*, *Gonostoma rhodadenia*, *Gonostoma grande*, *Stomias boa*, 2 *Vinciguerria lucetia*, 2 *Idiacanthus ferox*, *Astronesthes niger*, 4 *Gastrostomus bairdii*.
- 1300 METRES, LARGE NET: *Leptocephalus*, 16 *Cyclothone signata*, 357 *Cyclothone microdon*, 7 *Gonostoma grande*, *Photostomias guernei*, 5 *Chauliodus sloanei*, 2 *Idiacanthus ferox*, *Cyema atrum*, 3 *Gastrostomus bairdii*, *Melanocetus johnsoni*, *Melanocetus krechi*, *Oneirodes* n.sp. No. 3, 3 *Aceratias macrorhinus indicus*.

These catches may be classified into three main regions:— (1) a region extending downwards from about 500 metres, characterised by the occurrence of *Cyclothone* and various black or dark coloured fishes, and of many peculiar invertebrates, red prawns being prominent; (2) a region ranging between 150 and 500 metres, characterised by a peculiar community of silvery or grayish fishes, belonging to the families Sternoptychidæ and Stomiatidæ; and (3) the surface region comprising the upper 150 metres, characterised by transparent or blue coloured animals and juvenile forms, especially the members of the large family Scopelidæ.

In describing the pelagic communities of the open Atlantic it is therefore natural to treat each of these three regions separately, and to consider the pelagic communities of the coast banks as a fourth biological region.

Bathypelagic Communities in Depths greater than 500 Metres.—The most abundant fishes in this region are two Sternoptychidæ of the genus *Cyclothone*, viz. *C. signata* and *C. microdon*.

Of these two species we caught altogether over 7500 individuals, which were all measured and arranged according to their length and the instrument in which they were captured, so as to obtain information regarding the occurrence of the different sizes at different depths. Fig. 473 shows, in the case of both species, the results of the catches made between Newfoundland and Ireland.

Cyclothone microdon was found during the cruise of the "Michael Sars" in the North Atlantic at every station where an appliance was towed in depths below 500 metres. Above 500 metres it was met with only occasionally, and at a depth of 300 metres we came across only one individual. In depths from 500 metres down to 1500 metres its quantitative occurrence appears to be fairly uniform.

In our northern as well as in our southern section we found approximately the same number of individuals in each of the three young-fish trawls which we towed simultaneously at depths of 500 metres, 1000 metres, and 1500 metres. At depths below 1500 metres we made only a few hauls, though, on the other hand, we carried out some vertical hauls, which allow of a comparison between the quantity met with above and below 1500 metres. At Station 63 (in the northernmost portion of the Sargasso Sea) we secured ten individuals in a haul from a depth of 4500 metres up to 1500 metres, and twenty-seven individuals in a haul from 1350 metres up to 450 metres. Accordingly, seeing that the first haul was made through a distance more than three times as great as the second, we get the result that there were nine times more individuals in the intermediate layer from 1350 metres up to 450 metres than below 1500 metres. A more complete analysis of the different depths from 1500 metres down to the bottom of the sea (about 5000 metres) would have been very desirable, but unfortunately we were unable to spare time for it. It may be that there is a layer at the lowest depths where there are no individuals, and I, for my part at any rate, cannot

Vertical
distribution of
Cyclothone.

Cyclothone microdon.
1300 Individuals from Stations 80-101
Newfoundland to Ireland.

Cyclothone signata.
780 Ind from Stations 80-101
Newfoundland to Ireland.

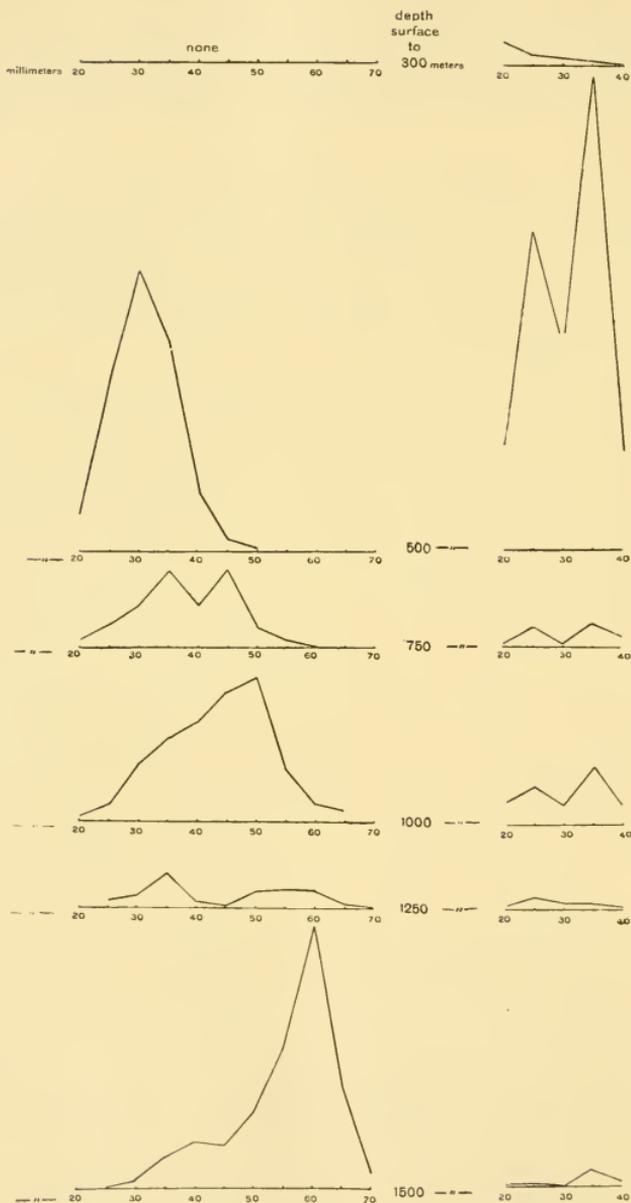


FIG. 473.

help believing that the profoundest deep is far more poorly supplied than the intermediate layer.

If we next examine the size-distribution at the different depths, we shall see that it is perfectly clear that the smaller sizes are met with much higher up than the larger ones, which latter are mainly to be found at a depth of 1500 metres. In the northern section we find that at a depth of 500 metres the greatest number of individuals were 30 mm. in length,

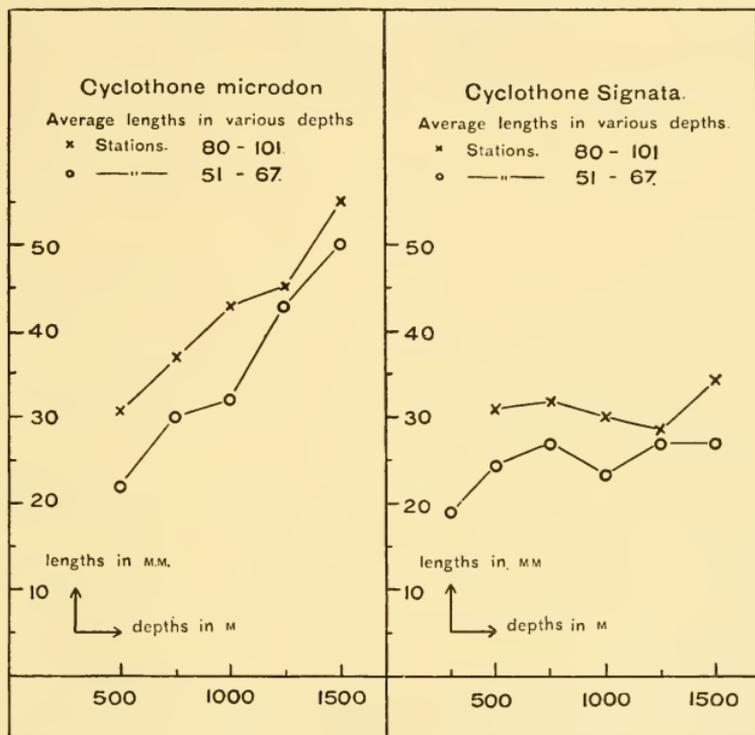


FIG. 474.

whereas at 1500 metres the majority attained 60 mm. At a depth of 500 metres we came across only two that were over 50 mm. in length. The smaller and younger individuals of a length of 20-30 mm. live, accordingly, to a preponderating extent, 1000 metres higher up in the water-layers than the majority of the largest and oldest individuals.

Another remarkable fact which strikes us when we study our catches is that the average size of the individuals is much less in the southern than in the northern section at the same

depth, as shown by the graph (Fig. 474). We see, for instance, that in the southern section, if we want to get individuals of an average size of 30 mm., we must fish 250 metres farther down than we would in the northern section.

The vertical distribution of *Cyclothone signata* is very different from that of *C. microdon*. We have captured many individuals at a depth of 300 metres, at any rate, in our southern section. The bulk, however, were found at a depth of 500 metres. In the hauls made at greater depths, the quantity diminished so rapidly that we may assume that a large portion of the fishes were caught during the process of hauling in, and that there is only a comparatively thin layer below 500 metres in which they live. In a vertical haul from a depth of 4500 metres to 1500 metres we caught no individuals of this species, but, on the other hand, we secured three individuals in a haul from 1350 metres to 450 metres.

Cyclothone signata is, accordingly, found in an intermediate layer with a maximum in the number of individuals at about 500 metres. In the case of this species, too, we note that the younger individuals are mainly to be found high up in the water (notice particularly the southern stations), and that the same size is to be found deeper in the southern section than in the northern (see Figs. 473 and 474).

Vertical
distribution of
AcanthePHYra.

We have a remarkable parallel to the vertical distribution of these two species of fish in the case of the species of red prawns. These latter, along with the black fishes, form a populous and characteristic "community." We have come across no fewer than about forty species of pelagic prawns, of which we shall here refer only to *AcanthePHYra multispina* and *A. purpurea*.

AcanthePHYra multispina shared with *Cyclothone microdon* the peculiarity that the largest and oldest individuals were found in the nets towed at the greatest depths, say, at 1000-1500 metres (see Fig. 475). At depths between 500 and 750 metres we met with medium-sized specimens, and in the upper layers, from 50 to 150 metres, we found the larvæ. These larvæ were taken in quantities, whereas formerly only a single individual collected by the Prince of Monaco, described by Coutière as *Hoplocaricyphus similis*, but now identified as a larva of *AcanthePHYra multispina*, was known.

AcanthePHYra purpurea resembles *Cyclothone signata*, in that its distribution is chiefly confined to an intermediate layer between 500 and 750 metres in depth. Our appliances

captured so few individuals at greater depths that we may safely assume that even these were caught during the process of hauling in. A vertical haul at Station 63, from a depth of 4500 to 1500 metres, yielded five individuals of *A. multispina*, but none of *A. purpurea*; while another haul from 1350 to 450 metres gave us two *A. multispina* and thirty-three *A. purpurea*. The larvæ of the latter occur in the higher layers of water, just as is the case with *A. multispina*.

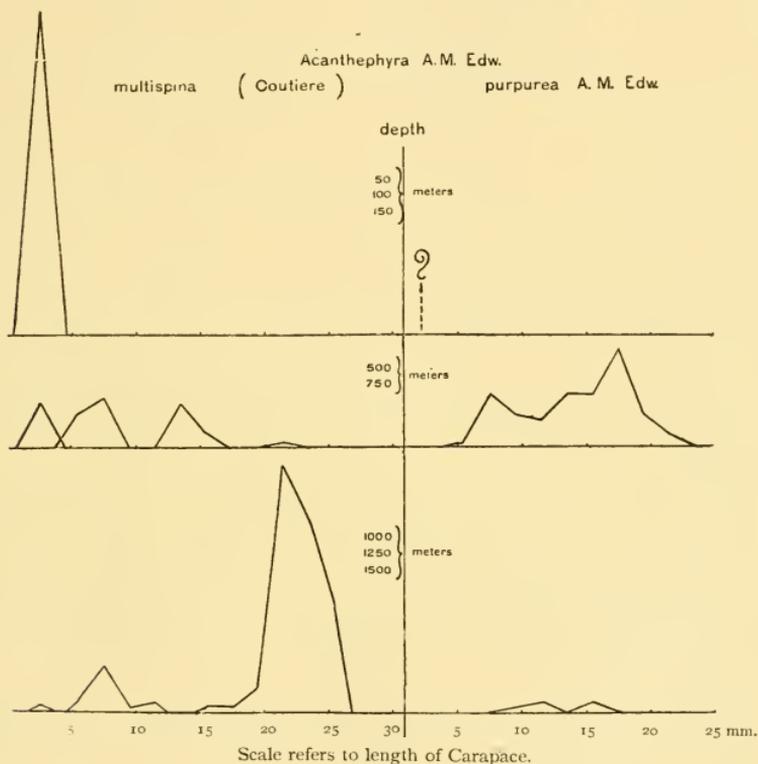


FIG. 475.

What has just been said illustrates the conditions on the northern section from Newfoundland to Ireland, and if we examine the material from the stations farthest south in the Sargasso Sea, we are confronted with exactly the same difference that we encountered in the case of the species of *Cyclothone*, namely, that the same forms descend to greater depths in the south than they do in the north; the larger individuals of *Acanthephyra purpurea*, for instance, occur at depths

between 500 and 750 metres in the northern section, whereas in the south they were seldom captured by the net towed at 500 metres, though present in large numbers at a depth of 1000 metres.

Bathypelagic region.

The results of these investigations clearly show that the dark-coloured fish, the deep-red prawns, and other organisms are limited to the deep parts of the ocean beyond 500 metres. This bathypelagic region may, however, be subdivided into various layers. We thus recognise a layer varying according to geographical position between 500 and 800 metres containing the light-coloured species of *Cyclothone* and the bright-red prawn with orange-coloured eggs (*Acantheephyra purpurea*). The layer from 800 or 1000 metres downwards may require to be still further subdivided, for certain forms like the larger *Acantheephyra* with red eggs (*A. multispina*). *Notostomus* and several fishes and squids have been taken only in the deepest hauls at 1500 or 2000 metres, but we must point out that the deeper parts of the Atlantic were not investigated by us, our efforts being devoted mainly to the upper layers between 1500 metres and the surface. We shall, therefore, consider the layers below 500 metres as a whole, referring to some characteristic forms from this bathypelagic region, examining their horizontal and vertical distribution, and discussing the laws which seem to govern their occurrence.

We have seen that Haecker, in dealing with the vertical distribution of the Radiolaria, recognised a Pandora region from 400 to 1000 metres, and an abyssal region from 1500 to 5000 metres; and this division coincides very well with the two regions characterised, respectively, by the occurrence of *Cyclothone signata* and *C. microdon* and by the two species of prawns.

Among the medusæ a similar correlation is found, *Periphylla hyacinthina* being most abundant at 500 metres, and *Atolla bairdi* at 1000 metres.

No nemertines were taken in depths less than 700 or 800 metres, and the fifteen specimens belonging to the genus *Planctonemertes*, taken at five separate stations, were taken beyond 1500 metres.

The ostracod *Gigantocypris* was taken at eleven stations, but only one individual occurred at 500 metres, the remainder occurring in deeper water. *Pyrosoma spinosum* was always taken beyond 750 metres, most of the specimens coming from 1500 metres.

Three species of pteropoda (*Peraclis diversa*, *Limacina helicoides* and *Clio falcata*) live below 500 metres, but according to Bonnevie, the first of these seems to avoid the cold bottom water, while the second species seems to prefer this water and the third seems indifferent. All three forms are dark-coloured, and their structure differs from that of the surface forms, being of a more archaic type.

All the large groups of squids include bathypelagic species, of which the following may be mentioned:—

Oegopsidæ: *Calliteuthis reversa*, *Mastigoteuthis flammea*, *M. grimaldi* and *M. hjorti*, *Grimalditeuthis bonplandi*, *Toxema belone*.

Myopsidæ: larvæ of *Spirula*.

Octopoda: *Eledonella pygmea*, *Vampyroteuthis infernalis*, *Cirrothauma murrayi*.

Many peculiar species of fish were found at and beyond 750 metres, for instance: *Malacosteus indicus* and *M. niger*, *Gastrostomus bairdii*, *Cyema atrum*, *Gonostoma grande*, *Melamphaës mizolepis*, *Cetomimus storeri* and a closely allied new genus. Of eight species of Ceratiidæ seven have been taken only beyond 500 metres. *Aceratias macrorhinus indicus* may also be mentioned.

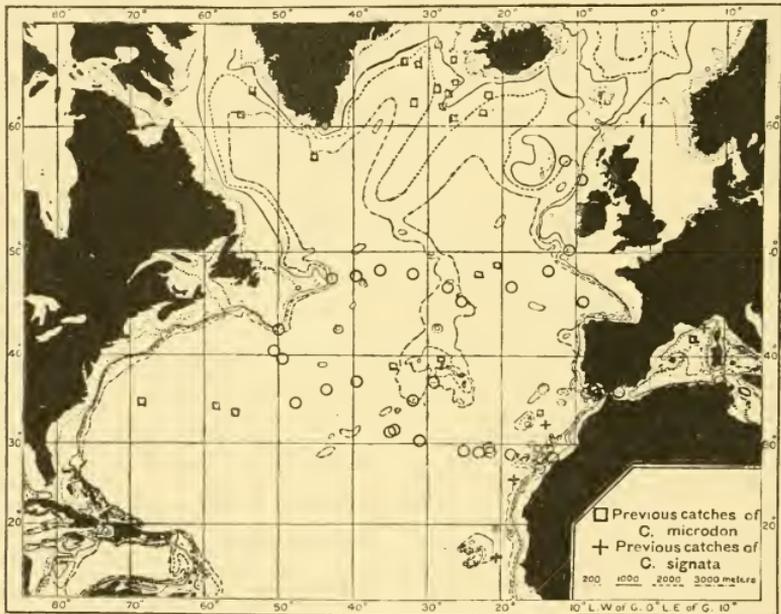
Proceeding to consider the horizontal or geographical distribution of these forms, we commence with the most abundant species of fish, *Cyclothone signata* and *C. microdon*. The chart (Fig. 476) shows the localities where these species have been taken previous to and during the "Michael Sars" Expedition, and it is seen that the records are so numerous that these fishes may be said to occur all over the area examined, wherever a fishing appliance was lowered to a depth of 500 metres. They are found everywhere, from the Wyville Thomson Ridge in the north to beyond the Azores in the south, and from the slopes of Africa and Europe to the slopes of America; but the distribution of the two species is not identical. *Cyclothone microdon* has been captured by previous expeditions¹ on both sides of Greenland, in Davis Straits, in Denmark Straits, and also south of Iceland, whereas *C. signata* is unknown in these localities; and outside the Atlantic *C. microdon* occurs in the Pacific, in the Indian Ocean, and in the Antarctic south of lat. 50° S., whereas *C. signata* is much more restricted in its southern distribution, having been taken at only one locality to the south of lat. 40° S.

Horizontal
distribution of
Cyclothone.

The peculiar vertical and horizontal distribution of the two

¹ This information is derived from a chart in Brauer's paper on the deep-sea fishes of the "Valdivia" Expedition.

forms in question seems explicable when compared with the distribution of temperature. In Chapter VII. we noted that the temperature along the ocean-floor is very uniform, and consequently the abyssal bottom-fish, like *Macrurus armatus* and *M. filicauda*, have a very wide distribution. Throughout the abyssal region of the Pacific, Atlantic, and Indian Oceans the temperature varies only between 1° and 3° C., and only far south in the Antarctic do we meet with temperatures below 0° C. The water-layer from 5000 or 6000 metres up to 1500



○Cyclothone Signata and microdon
caught by "Michael Sars"

FIG. 476.

metres is practically homogeneous as to temperature, and if it were possible for a fish to swim so far, keeping constantly at a depth of 1500 metres, it might travel from India to Australia, then westwards past the Cape, and northwards through the Atlantic as near to Iceland as the depth would permit, encountering all the way no greater variations in temperature than from 3° to 5° C. Even at a depth of 1000 metres conditions are very uniform, for only in the Indian and North Atlantic Oceans do the temperatures rise to 7° or 8° C.,

neglecting the somewhat higher temperatures found off the entrances to the Red Sea and the Mediterranean, but the temperatures at 1000 metres usually vary only from 4° to 6° C. The habitat of *Cyclothone microdon* is below 1000 metres, the temperatures generally varying between 3° and 6° C., and the wide range of this species must evidently be directly connected with the wide areas occupied by these temperatures. On the other hand, the area of distribution of *C. signata* at about 500 metres shows great differences in temperature in different parts of the ocean. In the Indian and Atlantic Oceans, where *C. signata* is found, temperatures at this depth are generally above 10° C., sometimes even above 15° C. In the sea between Newfoundland and Iceland, as well as south of lat. 40° S., temperatures are below 5° C., and in these localities *C. signata* is absent.

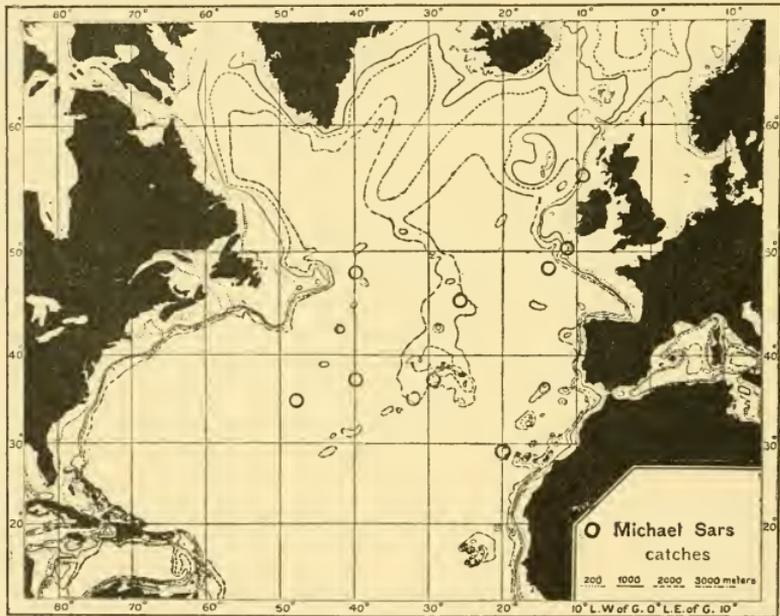
These facts, especially the conditions touching the wide distribution of the bathypelagic *C. microdon*, assume more general importance considering that we found many bathypelagic species in the North Atlantic, which have been taken in the deep water of other oceans. As instances of such forms I may mention the widely distributed medusæ *Atolla* and *Periphylla*, which were taken by us in the Northern Atlantic at nearly all the localities and depths where *C. microdon* and *C. signata* were taken. The genus *Gigantocypris*, taken at three stations in our southern and at six stations in our northern section, had previously been captured by the "Valdivia" in the Indian Ocean. Three species of squids, taken by us in deep hauls in the North Atlantic, were caught by the "Valdivia" in the Indian Ocean, viz. *Calliteuthis reversa*, *Mastigoteuthis flammea*, *Toxuma belone*. Bathypelagic fishes common to both these oceans are: *Malacosteus indicus*, *Cyema atrum*, *Melamphaës mizolepis*, *Cetomimus storeri*, *Melanocetus krechi*, *Ceratius couesi*, besides *Aceratias macrorhinus indicus*. These squids and fishes are, however, represented by very few specimens, in some cases only one from each ocean. The fact that we caught several new species of the family Ceratiidæ, as well as such interesting forms as *Gastrostomus bairdii* and *Gonostoma grande*, proves that a great field of research is still open to systematic zoologists. The chart (Fig. 477) shows the distribution of *Gonostoma grande*.

Bathypelagic forms.

All the forms mentioned live, as far as we know, always in deep water, except perhaps the early stages, which in some cases occur closer to the surface, but certain cold-water

species found in depths below 500 or 1000 metres may in other localities nearer the polar regions reach the surface.

During the Atlantic cruise of the "Michael Sars" numerous arctic or northern forms were found in deep water in company with the genuine or permanent deep-sea animals, especially in our northern section from Newfoundland to Ireland. We succeeded in proving the continuous occurrence of such forms from the cold water-layers off the Banks of Newfoundland down to great depths, just as these cold water-layers have



Gonostoma grande

FIG. 477.

proved to be directly connected with the deep layers of the ocean (see pp. 658-659).

Pelagic Communities in Depths between 150 and 500 Metres.—At the upper limit of the bathypelagic region in about 500 metres certain fish, entirely different from the bathypelagic species, make their appearance along with *Cyclothone signata*. These fish are as a rule laterally compressed, with a mirror-like silvery skin; when coloured, the back is generally blackish brown, and the resplendent mirror-like sides of the body blue or violet. The eyes are large,

very often telescopic, and the body is provided with a number

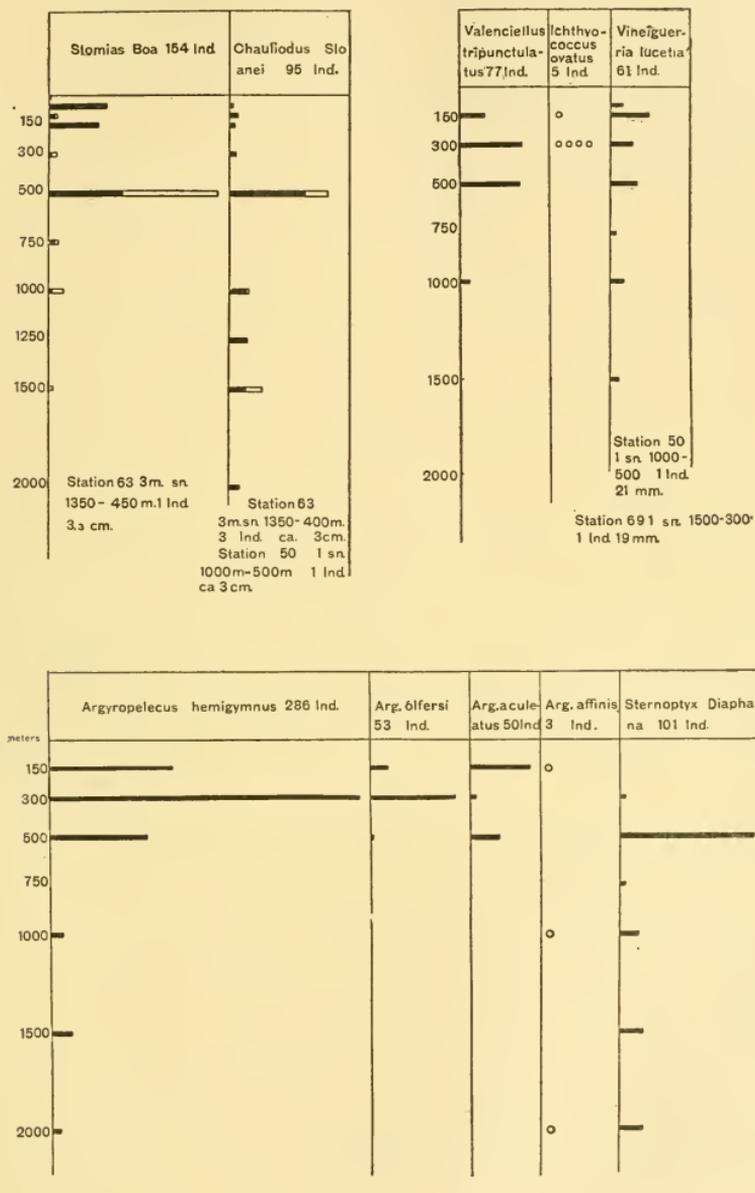


FIG. 478.

of light-organs varying in size. These forms have their lower

limit at about 500 metres, where they are found together with the upper representatives of the bathypelagic fauna, just as on the continental slopes the Macrurid bottom-fauna is mingled with the deepest living species belonging to the coast banks. Fig. 478 shows the vertical distribution of certain of these pelagic fishes, and we see that *Sternoptyx diaphana*, *Stomias boa*, and *Chauliodus sloanei* were taken most abundantly at 500 metres, while the species of the genera *Argyropelecus*, *Valenciennellus*, and *Vinciguerria* were mostly taken at 300 metres; the upper limit for all these species seems to be about 150 metres below the surface. As regards the geographical distribution of these species, we find that, excepting *Stomias boa*, they occur in the Indian Ocean to the north of lat. 40° S., and in the Atlantic between lat. 44° N. and 40° S., though *Argyropelecus olfersi*, *A. aculeatus*, and *A. hemigymnus* have been found on the coasts of Norway, and *Stomias boa* has been taken in the Faroe-Shetland channel during one of our cruises in the "Michael Sars."

During our Atlantic cruise in 1910, *Argyropelecus affinis* and *A. aculeatus*, *Valenciennellus tripunctulatus*, *Ichthyococcus ovatus*, and *Serrivomer sector* were only taken at our southern stations, and did not appear at any of the stations between Newfoundland and Ireland, while *Argyropelecus hemigymnus*, *Sternoptyx diaphana*, *Stomias boa*, and *Chauliodus sloanei* were caught both at northern and southern stations, but only *Stomias boa* occurred in numbers of any consequence at the northern stations. Thus, of 286 specimens of *Argyropelecus hemigymnus* taken during the cruise only 17 were captured on our northern track; of 101 specimens of *Sternoptyx diaphana* only 2 were taken north of the Azores; of 95 specimens of *Chauliodus sloanei* only 10 were taken north of the Azores. On the other hand, out of our total of 154 specimens of *Stomias boa* 91 were taken on the northern track, and this species appears to be the only abundant one north of lat. 45° N.

The temperature throughout the region occupied by these fishes, between lat. 40° S. and 45° N., and between 500 and 150 metres, exceeds 10° C. We found the distribution of the fishes of the Atlantic coast banks to be limited by this temperature in a northerly direction as well as vertically. A limit of this kind can only be roughly fixed, and is subject to variations, but the isotherm of 10° C. seems on the whole to coincide with the localities where the organisms in question occur in numbers of importance. Within the region great

variations apparently occur, for at a depth of 200 metres the temperature exceeds 17° C. in the Sargasso Sea, in the Mexican Gulf it is above 20° C., in the Indian Ocean it varies between 13° and 20° C., while in the southern Atlantic it is only a little above 10° or 12° C. The fauna living at this depth is thus subject to temperatures varying between 10° and 20° C., corresponding with what we found in the case of the fishes of the Atlantic coast banks from south of the Canaries to the south-western coast of Britain.

All the silvery fishes of the region between 150 and 500 metres are small, and the same remark applies to all the other organisms of the community. They consist almost exclusively of small crustaceans (copepoda, ostracoda, amphipoda), sagittidæ, pteropoda, and small medusæ. Besides these we commence to find the larvæ of squids and fishes, which, however, become more numerous in the layer above 150 metres.

Pelagic Communities in Depths less than 150 Metres.—In reviewing the pelagic oceanic forms I mentioned that they belong mainly to the warm belt on both sides of the equator between lat. 40° N. and 40° S., where both species and individuals are most numerous. Foraminifera, radiolaria (acantharia), copepoda, medusæ, siphonophora, pteropoda, and salpæ all occur in abundance, and the number of species rapidly decreases as soon as we leave tropical waters. This is also the case with the typical and most abundant surface fishes, the scopelidæ, which occur in numerous tropical and subtropical forms, while only a few species are found in the northern part of the North Atlantic.

The beautiful siphonophores *Physalia* and *Veleva* were first seen by us during our short visit to the Mediterranean and in the Spanish Bay. On the way from the Canaries to the Azores and thence westward to Station 64 they were frequently seen, sometimes accompanied by *Agalmopsis* and *Cestus veneris*, besides various surface mollusca. On the other hand, none of these forms were observed on our northern track between Newfoundland and Ireland.

Distribution
of Siphono-
phora.

The shelled pteropods (Thecosomata) are vertically limited to a comparatively thin layer, extending in our northern section down to only 50 or 100 metres, and in the southern section to 250 metres, four-fifths of all the individuals taken occurring within these limits. No less than 3500 individuals comprising 22 species were preserved by us, and of these only about 500 specimens comprising 16 species came from the northern section.

Distribution
of Pteropoda.

In the southern section, again, the majority were taken in the western half towards the Sargasso Sea, west of the longitude of the Azores, where these forms occurred in great abundance.

Distribution
of Salpidæ.

The distribution of salpæ is somewhat different. Certain forms occur only in the south, for instance, *Cyclosalpa floridana*, *Salpa amboinensis*, and *S. heuseni*; but the majority were taken to the north and south of the Azores, for example, *Cyclosalpa pinnata* and *Salpa maxima*. The medusa *Pelagia perla* is similarly distributed. All these surface animals occur in this central region of the North Atlantic in such countless numbers as to be immediately noticeable, and it struck me at the time that this peculiar distribution north and south of the Azores might be correlated with the submarine ridge on which these islands are situated. The currents are probably influenced by the configuration of the bottom, and the distribution of the pelagic organisms, even in the surface waters, may possibly be thereby affected, as we have often observed during previous cruises of the "Michael Sars" in the Norwegian Sea. A third group of salpæ, viz. *Salpa fusiformis*, *S. mucronata*, *S. confæderata*, and *S. zonaria*, while certainly most abundant north and south of the Azores, occurred frequently in other localities, especially in our northern section. *Salpa fusiformis* was doubtless the principal form among these, and was the only one observed at all the stations to the south-west of Ireland, between Rockall and the west coast of Scotland, and towards the Faro-Shetland channel. Fig. 479 illustrates the distribution of *Salpa zonaria*, which was found abundantly in the northern part of the Atlantic.

Distribution
of Cephalo-
poda.

Most of the squids taken at the surface occurred south of the Azores, especially larval forms, and included larvæ of Onychoteuthidæ, *Octopodoteuthis sicula*, Cranchiidæ (*Cranchia scabra*, *Teuthowenia megalops*, *Galiteuthis suhmi*), *Heteroteuthis dispar*, *Tremoctopus atlanticus*, and *Argonauta*. Certain northern forms like *Gonatus* may be supposed to be wholly boreal.

Distribution
of Scopelidæ.

Among oceanic surface fish the Scopelidæ are probably most abundant. They were taken in thousands, but only a few have as yet been determined. Of these, *Myctophum rissoi*, *M. benoiti*, *M. affine*, *M. humboldti*, *M. coccoi*, *M. chærocephalum*, *M. gemellari*, *M. maderense*, *M. warmingi*, *M. micropterum*, and *M. gemmifer* were taken only in the south; while *M. glaciale*, *M. punctatum*, and *M. rafinesquei* were also taken in our northern section. The Scopelidæ were usually accompanied by numerous young fish, of which I may mention

the fry of the horse mackerel, the young of *Scombrosox saurus* (a near relation of the gar-pike), and of the flying fish (*Exocoetus*). These forms were with one exception observed only in our southern section.

A peculiar group of fishes are the Sargasso fish, which live on or around the Sargasso weed. We found *Antennarius marmoratus*, *Syngnathus pelagicus*, *Hippocampus ramulosus*, and *Monacanthus*, together with a peculiar Sargasso fauna, including small crabs (*Planes minutus*) and small prawns of several kinds

Sargasso
fishes.

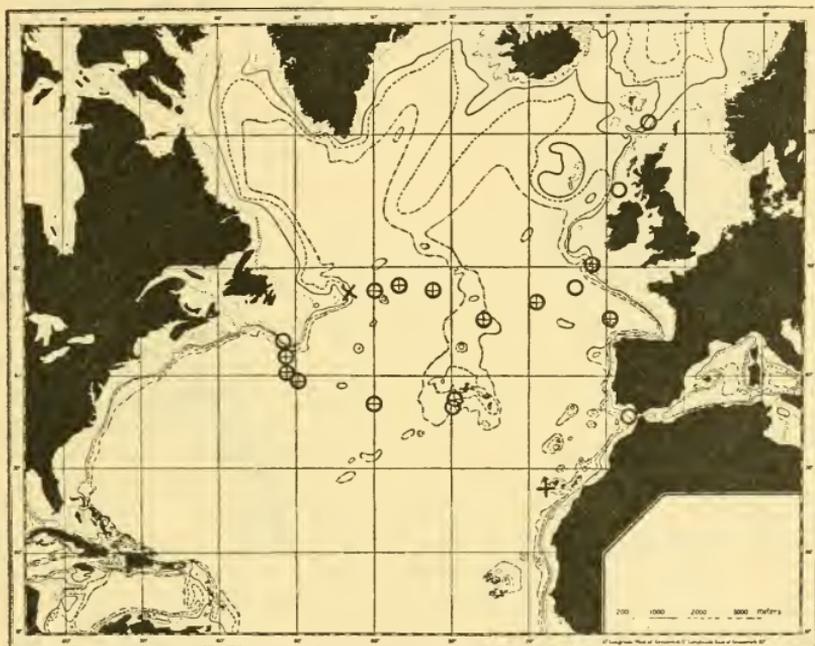


FIG. 479.—DISTRIBUTION OF *SALPA ZONARIA*.

(see Plates V. and VI., Chapter X.). But besides the Sargasso fish various remarkable forms occur in the surface waters of the ocean, such as the "wreck-fish," *Lirus medusophagus* and *L. ovalis*, *Polyprion americanus*, and the pilot fish (*Naucrates ductor*), taken by us to the south of the Azores, where salpæ and large medusæ were present in such numbers, as well as the enormous sunfish (*Mola*), harpooned due north of the Azores.

A community nearly as peculiar as the Sargasso fauna exists in the north-eastern corner of the area investigated by us, extending from the Azores to Ireland and thence to Rockall

Transitional
area between
the Atlantic
and the
Norwegian
Sea.

and the Faroe-Shetland channel. Johs. Schmidt first drew attention to this community. *Salpa fusiformis*, the larval actinia *Arachnactis albida* (the distribution of which is shown in Fig. 480), the barnacles *Lepas pectinata* and *L. fascicularis*, young stages of the thread-like fish *Fierasfer*, *Nerophis æquoreus*, larvæ of the common eel and scopelidæ (*Myctophum glaciale* and *M. punctatum*) occur here in great numbers. Excepting the salpæ, the barnacles and the leptocephali, which also occur in the warm Atlantic, all these forms live in what may be

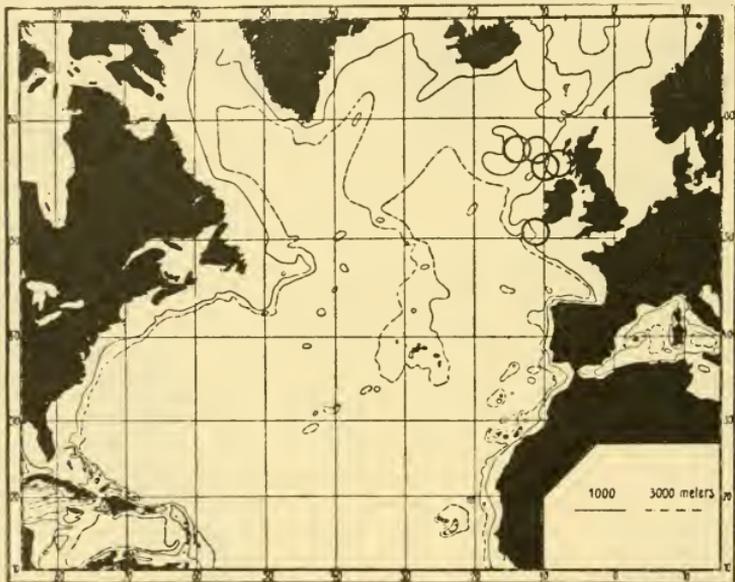


FIG. 480.—DISTRIBUTION OF *ARACHNACTIS ALBIDA*.

called a transitional area between the Atlantic and the Norwegian Sea.

The conditions of temperature in this bathymetrical region are shown in Figs. 159, p. 227, and 160, p. 228 (surface temperature for February and August), and in Fig. 312, p. 445 (temperature at 100 metres). Comparing these charts with the current chart in Chapter X., we obtain a good impression of the currents of the North Atlantic. The warm Gulf Stream, originating in the Gulf of Mexico, follows the east coast of the United States towards the Banks of Newfoundland, where it divides into several branches. A northern branch appears to run towards Davis Strait, partly as an undercurrent. An eastern branch runs towards the Azores and, spreading out like a fan,

merges finally into the Canary stream and the enormous whirlpool of the Sargasso Sea. A North European branch, after reaching the British Isles, continues to the Norwegian Sea and the North Sea. We may consequently distinguish various surface regions in the North Atlantic: (1) the genuine Gulf Stream; (2) the eastern Azores current; (3) the Canary current; (4) the Sargasso Sea; (5) the North European Gulf Stream.

The last mentioned, which we crossed on our northern track, receives a certain admixture of cold water from the Labrador current, besides many animals from northern waters. It appears from these considerations that the limit to the genuine warm-water forms of the Atlantic follows a line parallel to the axis of the true Gulf Stream water, the faunas to the north and south of this line differing to some extent.

Pelagic Communities on the Coast Banks of the Atlantic.—The chief aim of our cruise was to examine the pelagic life of the open ocean, and our catches on the coast banks were therefore casual. On the coast of Africa, at Cape Bojador, quite close to the shore we caught the young of the anchovy (*Engraulis encrasicolus*), *Clupea alosa*, the sardine (*Clupea pilchardus*), the horse mackerel (*Caranx trachurus*), and *Scombrosox saurus*. Together with the mackerel, the bonito, the tunny, and the gar-pike, these fish are the most important pelagic species on the coast banks. To these may be added the great sharks: the blue shark (*Carcharias glaucus*), probably the species most commonly captured by sea-faring people; the hammer-head (*Zygæna malleus*), which the trawlers get among the hake on the coast of Morocco; and several others.

Fishes of the African coast.

As far as we know, these fishes belong mainly to the coast waters; at all events the herring, mackerel, tunny, and gar-pike spawn in the coast waters or their vicinity. On the other hand, we found on our cruise the eggs and young of *Scombrosox* so far from land that they may safely be said to spawn in the open ocean, as is probably the case with *Caranx*. Many of these fishes are probably widespread in the ocean, even if they do appear in the coast waters.

When journeying some years ago on the west coast of France I was informed that a peculiar bonito and tunny fishery had recently originated in the Atlantic, carried out with deck cutters which went as far as 150 miles off the coast of France, the voyages lasting eight to twelve days. The fishing commences in July and continues all the autumn, and is a kind

Fishery in the open ocean.

of harling, like the mackerel fishery in the North Sea. It is carried on only during the day, some of the fish weighing over thirty pounds. This is the only fishery I know of in the open ocean over deep water and away from the coast banks, and the species captured visit the coast banks, at all events, some time during the year.

Among pelagic fishes, however, the sardine is the most important to the fisheries on the Atlantic coast banks, and it is captured in the same area as the Atlantic bottom fish, *i.e.* from the Channel along the coasts of Spain and Portugal and Africa. The sardine, the bonito, and the tunny are here probably the only Atlantic pelagic species of economic importance.

B. THE NORTHERN PELAGIC COMMUNITIES

In the ocean we find no sharply defined border between the animal-communities belonging respectively to the tropics and the polar seas; on the contrary, there are numerous transitions between the extreme conditions of life peculiar to the tropics and the polar regions. It is therefore difficult to classify the communities, and this difficulty is intensified by the fact that most records note merely the occurrence or non-occurrence of certain organisms and not their quantitative occurrence—a vital point in discussing questions of distribution. If I attempt to separate the genuine Atlantic from the northern pelagic animal-communities, it is because I feel that in this way we shall actually gain a better conception of their main features. I believe that a division of this kind will coincide generally with the limit drawn between the areas of distribution peculiar to the southern and northern bottom fish on the Atlantic coast banks, *viz.* the isotherm of 10° C. at 100 metres, running from the Channel, south of Ireland, skirting the south coast of Iceland, and thence to the United States.

Among northern communities it is impossible to separate oceanic and coastal communities so sharply as among Atlantic communities, probably because northern communities are chiefly restricted to comparatively small areas, and the substances carried from the land vary in quantity and quality, giving rise to corresponding variations in the food supply. Neither is the vertical distribution so easily defined as in the Atlantic, certain species having a very different vertical distribution in different areas.

It is extremely important for a true conception of the

communities of northern waters to distinguish between the various types of areas of distribution. In accordance with all previous descriptions of the animal life of northern waters, we may recognise three typical faunas, viz. (1) the arctic, (2) the boreal, and (3) the temperate Atlantic.

The arctic communities include those forms which are propagated and attain their maximum abundance in waters belonging to the ice-covered area at temperatures below 2°C .

The temperate Atlantic communities comprise those forms which occur mainly in the warm layers of the Atlantic, and only at certain seasons or in small quantities occur in the north. Most of these forms are entirely oceanic.

The boreal communities include those forms having their maximum frequency in waters at temperatures between 4° and 8°C . It is the boreal region which specially interests us, but the nature of boreal communities can only be fully grasped when we know the "strange elements"—the Atlantic and arctic "visitors."

The boreal region includes several areas, each limited by natural borders, one of which lies between the west coast of Britain and South Iceland, extending to the Faroe-Shetland channel, the upper layers being occupied by the North European branch of the Gulf Stream. Another area is the Norwegian Sea, separated from the first-mentioned by the submarine ridges between Shetland and Faroe and Iceland; a third area is found round Greenland, Davis Straits, and the Newfoundland banks.

We will discuss the Norwegian Sea first, because this area has been most thoroughly investigated.

The Norwegian Sea.—The borders of the ice may be considered as indicating roughly the limits of distribution of pelagic arctic communities. It is therefore interesting to examine the ice-limits as shown by the charts published by the Danish Meteorological Institute. Fig. 481 represents some of these ice-limits for different months of the years 1902, 1903, and 1906, showing considerable variations from season to season and from year to year. Vast areas of the Barents Sea and White Sea are closed in winter and open in summer, as also the sea off Spitsbergen, and the Greenland Sea between Jan Mayen and Greenland. The Polar Sea north of Spitsbergen is in certain years ice-covered all the year round, but sometimes a

Arctic animal communities.

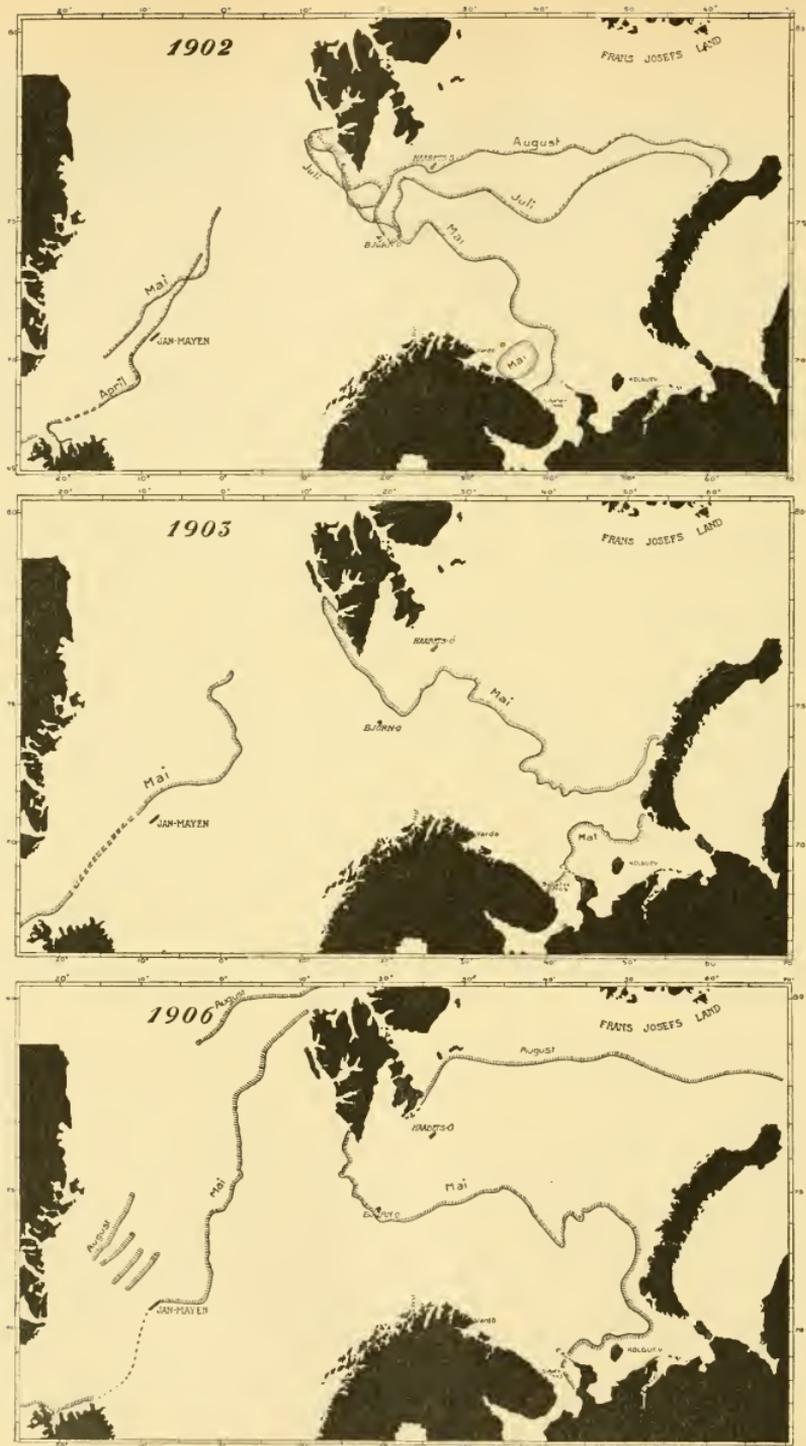


FIG. 481.—ICE BOUNDARIES FROM THE CHARTS OF THE DANISH METEOROLOGICAL OFFICE.

bay of open water runs for an unknown distance towards the north.

The vertical distribution of the cold water in the Norwegian Sea along a line from Greenland past Jan Mayen to Vesteraalen is shown in Fig. 310, p. 436, which indicates that the great body of water in the Norwegian Sea has a temperature below 2° C., and that warm water is found only in the eastern part of the sea towards Norway to a depth of 500 or 600 metres.

The investigations of the "Michael Sars" have been limited mainly to the area covered by this warm water, but a thorough investigation of the arctic Greenland Sea has been made by the Duke of Orleans in his expeditions on board the "Belgica," in which Koefoed took part, and had the opportunity of making collections with the same appliances as were employed on board the "Michael Sars." The "Belgica" and "Michael Sars" material has been dealt with jointly by Koefoed and Damas, upon whose treatise¹ I have drawn for information about some of the most important arctic forms.

Damas and Koefoed divide the Copepoda of the Greenland Sea into several biological groups: (1) forms which live mainly in the surface waters, such as *Calanus finmarchicus* and *C. hyperboreus*, *Pseudocalanus elongatus* and *P. gracilis*, *Oncaea conifera* and *O. notopus*, *Oithona similis*; (2) forms living mostly in mid-water, but occasionally appearing at the surface, a typical form being *Euchæta norvegica*; (3) mid-water forms which never occur at the surface, especially *Euchæta glacialis*; and (4) deep-sea forms, like *Euchæta barbata*, *Chiridiella macrodactyla*, and others.

At the surface the commonest form is *Calanus hyperboreus*, one of the largest of copepods, attaining a length of 9 mm. At the ice it is found 5 to 10 metres below the surface in enormous numbers. Thus in July a few hauls with closing nets in lat. 75° 55' N. long. 9° W., depth 1275 metres, gave:—

In a haul from	10 to	0 metres,	1000 specimens.		
"	"	100 to 20	"	2	"
"	"	400 to 210	"	4	"

It is mainly an arctic form, and occurs in the Polar basin, in the Greenland Sea, and in the colder parts of the Norwegian Sea. Its propagation takes place principally in the shallow parts of the Greenland Sea, on the coast banks and not where the water is deep, whence the young are carried out into deeper water by currents. The wealth of animal life in the Arctic is

¹ Damas and Koefoed, *loc. cit.*

largely due to the enormous abundance of this species, which constitutes the food of the arctic whales.

Vertical
distribution of
Copepoda in
the Norwegian
Sea.

In the boreal parts of the Norwegian Sea most of the arctic species occur in the deeper layers in accordance with the hydrographical conditions, as shown by the following abstract from a table given by Damas and Koefoed:—

	0-50 metres.	50-100 metres.	100-200 metres.	200-500 metres.	500-1000 metres.
<i>Calanus finmarchicus</i> . . .	×	×	×	×	×
<i>Calanus hyperboreus</i> . . .			×	×	×
<i>Pseudocalanus elongatus</i> . . .	×	×	×	×	×
<i>Microcalanus pusillus</i> . . .					×
<i>Euchaeta norvegica</i> . . .			×	×	×
<i>Euchaeta glacialis</i> . . .					×
<i>Chiridius armatus</i> . . .			×	×	×
<i>Chiridius obtusifrons</i> . . .				×	×
<i>Amalophora magna</i> . . .					×
<i>Oncaea conifera</i> . . .				×	×
<i>Oithona plumifera</i> . . .		×		×	×
<i>Oithona similis</i> . . .	×	×	×	×	×

According to this table a peculiar bathypelagic fauna appears to exist in the Norwegian Sea, whether the surface layers be warm or cold. We find, however, many transitions between the typically arctic and the typically boreal forms, and the most intimate knowledge of their distribution and life-history is necessary to enable us fully to characterise the various species.

Among the pteropoda *Limacina helicina* is typically arctic; it spawns on the coast banks of Greenland at a temperature of 0° C., and between the ice-floes, the young being gradually distributed into deeper water.

As already indicated, there are certain medusæ which must be considered as arctic coast forms (see Fig. 398, p. 570), such as *Hippocrene superciliaris*, *Codonium princeps*, *Catablema campanula*. Of oceanic medusæ *Aglantha digitalis* is found in the upper layers, and *Crossota norvegica* in the deepest layers of the Norwegian Sea, both being characteristic forms.

The siphonophore *Diphyes arctica*, the sagittidæ *Krohnia hamata*, *Sagitta gigantea* and *S. arctica*, the ostracod *Conchæcia borealis*, the schizopoda *Meganyctiphanes norvegica*, *Boreophausia inermis* and *Thysanoëssa longicaudata*, the amphipoda *Euthemisto*

libellula and *Parathemisto oblivia*, the prawns *Hymenodora glacialis* and *Pasiphæa princeps* are partly arctic, partly boreo-arctic, and partly boreal in their occurrence, but in the present state of our knowledge it is impossible to define sharply the general laws of their distribution. In the year 1900 I made a number of closing-net hauls in the Norwegian Sea, which showed that there was a peculiar pelagic fauna in the deep cold layer below the Gulf Stream, including the following large forms: *Cyclocaris guilelmi*, *Hymenodora glacialis*, *Pasiphæa princeps*, and large *Sagittæ* (*S. gigantea*).

Of holopelagic fish there is not a single arctic species. The coast fishes of Greenland, Spitsbergen, and other Arctic shores may certainly be captured in the surface waters above the coast-banks, but their life-cycle is not wholly pelagic. In regard to one species only, *Gadus saida* (the polar cod), there may be some doubt, for it lives everywhere along the ice independent of depth, but it seems most feasible to classify it among the Arctic shore-fishes. In the case of this fish the ice apparently replaces the shore, a condition peculiar to many other arctic forms.

Highly important is the Capelan or Caplin (*Mallotus villosus*), which lives in the Arctic or in the extreme north of the boreal area, where it appears at all events once a year to deposit its spawn on the coast banks. We may thus term it a meropelagic fish of "boreo-arctic" character.

The black *Paraliparis bathybi* has been taken by the "Michael Sars" in mid-water in the Norwegian Sea, but whether this species is mainly a bathypelagic or a bottom fish cannot be decided from the available records.

It has long been known that Atlantic species sometimes appear in the coast waters of Norway, and Nordgaard¹ has published an interesting review of historical details of this kind. Thus in 1821 salpæ were observed by a certain Norwegian priest, and between the 'twenties and 'forties of last century when Michael Sars was engaged in his pioneer work on the west coast of Norway, he found many Atlantic forms, like *Salpa mucronata* and *S. fusiformis*, well known by the fishermen and termed "Silderæck," a portent of successful herring fishery. Sars described from the west coast of Norway some new species of Siphonophores and a larval Actinian having their main distribution in the Atlantic, such as *Galeolaria*

Atlantic
animal
communities.

¹ Kgl. Videnskapers selskaps skrifter, Trondhjem, 1910.

biloba and *G. truncata*, *Agalmopsis elegans*, *Physophora hydrostatica* (*borealis*), and *Arachnactis albida*. Since then many records of Atlantic forms occurring on the coast of Norway have been published, and Collett¹ has collected many such records referring to fishes. Similar information has been gathered in Sweden, Denmark, and Germany. I give here some of these records, without any claim to completeness.

Of Foraminifera, the majority of which are oceanic forms, *Globigerina bulloides* is always found in the Gulf Stream off the coast of Norway.

Surface Radiolarians (*Acantharia*), and also Atlantic deep-sea species of the same group, sometimes occur, for instance, *Challengeridæ*, *Medusettidæ*, and *Arachnosphæridæ*. Jørgensen has greatly contributed to our knowledge on this group of animals. In the Skagerrack, Atlantic Radiolarians have also been found by Aurivillius.

As prominent among Atlantic Medusæ taken in the Norwegian Sea and fjords we may mention *Atolla bairdi* and *Periphylla hyacinthina*. In May 1911 I investigated the Sognefjord, having a depth of 1000 to 1200 metres, towing simultaneously a number of pelagic fishing appliances at various depths, and captured more than 1000 *Periphylla hyacinthina* of all sizes; they occurred at all depths below 75 metres, 100 large and 300 small individuals being taken at 750 metres. Of southern jelly-fish *Cyanea lamarcki* and *Rhizostoma octopus* have been taken on the Norwegian coast; the former is a coast form and probably came from the southern North Sea. Among the Siphonophores *Physophora hydrostatica* is most abundant, but the other forms recorded by Michael Sars also occur.² Damas has drawn attention to the importance of this immigration.

Arachnactis albida is frequently found and is a characteristic Atlantic species.

Nordgaard has recorded Atlantic Copepoda from Lofoten (*Pleuromma robusta*), and the barnacle, *Lepas fascicularis*, has frequently been found. The southern pteropod *Clio pyramidata* also occurs. *Salpa fusiformis* and *S. mucronata* occur on the coast of Norway, having been recorded by many observers from the south-west coast to Trondhjem fjord (Nordgaard).

Regarding the squids some interesting information is on record. Steenstrup collected information about colossal squids

¹ Collett, *Meddelelser om Norges Fiske* (Kristiania, 1902-1905).

² See Damas in *Report on Norwegian Fishery and Marine Investigations*, vol. ii. No. 1, 1909.

from the Northern Atlantic stranded on various North European coasts, which he described as *Architeuthis dux*. The stranding of such giant squids is recorded from Nordland (where Collett heard of a specimen 12 feet long) and from Trondhjem. In my opinion it is an open question whether certain smaller squids do not passively invade the Norwegian coasts in enormous quantities from the Atlantic. During the cruises of the "Michael Sars" in the Norwegian Sea we never found the larvæ of the abundant *Gonatus fabricii*, but on our Atlantic cruise we caught them between Newfoundland and Ireland.

Our knowledge is, however, most exhaustive on the subject of the Fishes, and from Collett I have compiled the following list of Atlantic species found in Norwegian waters with their relative frequency:—

SCOMBRIDÆ (MACKERELS)

Auxis thazardus, 2 specimens.

Thynnus thynnus (the tunny), annually.

Euthynnus alliteratus, 3 specimens.

Sarda sarda, almost annually.

STROMATEIDÆ

Centrolophus pompilus, 2 specimens.

ZEIDÆ

Zeus faber (John Dory), about 16 specimens, between Christiania and Bergen.

LAMPRIDÆ

Lampris guttatus, annually one or more specimens.

BRAMIDÆ

Brama raii, 1 specimen.

Pterycombus brama, 14 specimens.

TRICHIURIDÆ

Trichiurus lepturus, 1 specimen.

XIPHIIDÆ

Xiphias gladius (the swordfish), 30 or 40 specimens during the last twenty years, Christiania fjord to Finmark.

TRACHYPTERIDÆ

Trachypterus arcticus, annually one or more specimens stranded.

Regalecus glesne, 12 specimens during sixty years.

STERNOPTYCHIDÆ

Argyropelecus offersi, about 20 specimens observed as far as Finmark.

Argyropelecus aculeatus, 1 specimen.

Argyropelecus hemigymnus, 1 specimen in Finmark.

SCOPELIDÆ

Myctophum glaciale, 4 or 5 specimens in one hundred years.

Myctophum elongatum, shoals observed during certain periods in the Trondhjem fjord.

SCOMBRESOCIDÆ

Scombrosox saurus (skipper or saury pike), found now and again as far as Finmark.

Exocoetus volitans (flying-fish), 1 specimen, Christiania fjord.

CLUPEIDÆ

Clupea pilchardus (sardine), since 1871 no specimen on record.

Clupea alosa, 30 specimens.

Clupea finta, 10 specimens recorded.

Engraulis encrasicolus (anchovy), insignificant numbers.

SYNGNATHIDÆ

Nerophis æquoreus, sporadic, as far as Tromsø.

MOLIDÆ

Mola mola (sunfish), stranded now and again; in Christiania fjord 20 specimens since the 'seventies.

Besides these several southern sharks have been found, for instance, the blue shark (*Carcharias glaucus*), which, however, is rare. *Petromyzon marinus*, which we took in the surface waters off the banks of Newfoundland, has been found up to Finmark.

These carefully gathered records show that many Atlantic fishes occur in the Norwegian seas only as very rare visitors, and seldom in great quantities. That these fishes are scarce is shown by the fact that in all the hauls made by the "Michael Sars" in the Norwegian Sea only *Myctophum glaciale* and *Nerophis* were observed. On the other hand interesting information as to the occurrence of Atlantic invertebrates has been gathered.

This list of Atlantic fish from the Norwegian Sea is of general interest because none of the species recorded are known to live in the deep region of the Atlantic below 500 metres, but are forms belonging either to the surface layers, or silvery forms from the "intermediate" layers about 300 metres. The Sternoptychidæ and the Trachypteridæ belong to the latter, while the others are typical surface forms. Not a single *Cyclothone* has as yet been captured in the Norwegian Sea.

In the Norwegian Sea the boreal region is essentially limited by the presence of arctic water, which in the Greenland

Sea in the west, at Spitsbergen in the north, and in deep water, even close to the banks of Norway and the North Sea, excludes all boreal species (see Fig. 310, p. 436).

In the boreal area, as thus limited, we find not a single species of fish, perhaps not even a single animal-form, which may be said to be entirely oceanic.¹ The only oceanic community in the Norwegian Sea would perhaps be the arctic deep-sea fauna. Among the boreal species, however, we find several gradations between the purely oceanic and the purely coast forms of life.

Of all invertebrates the minute crustacean *Calanus finmarchicus* *Calanus finmarchicus.* is undoubtedly the most important in the boreal community. If during spring or summer a hoop-net is towed along the surface in the warm part of the Norwegian Sea off the coast banks, a practically uniform catch is obtained, consisting almost exclusively of this species, indicating a "monotonous" pelagic life, as Haeckel calls it. G. O. Sars, in his reports on the "Vöringen" Expedition, drew attention to this fact and to the wealth of life peculiar to the open ocean, and this monotonous fauna has recently been investigated by Gran and Damas during the cruises of the "Michael Sars." *Calanus finmarchicus* occurs both above the coast banks and in the fjords, but in these localities its preponderance is less pronounced than in the open sea.

In the coast waters we notice many pelagic forms belonging to various groups, along with many larval forms of bottom animals, thus introducing a strange variety into the pelagic life. Want of space prevents a full discussion of this animal community, and in regard to the various groups I refer the reader to my preceding review. Besides *Calanus finmarchicus* there are many other Copepoda, especially the genera *Centropages*, *Temora*, *Acartia*, *Anomalocera*, and *Euchaeta*. Of Schizopoda *Thysanoëssa*, *Meganyctiphanes*, *Mysis*, and of Decapoda *Pasiphaea* and *Pandalus*, occur. Vast numbers of Medusæ are found at the surface and in the deep water of the fjords, in the Norwegian depression or gut, and in the Skagerrack. Two species of jelly-fish, the brown stinging jelly-fish *Cyanea capillata*, and the transparent *Aurelia aurita*, are frequent. Of Pteropoda we meet with *Clione limacina*, *Limacina retroversa*, and *L. balea*. The most important squid is *Ommatostrephes todarus*. Of fish the following species may be noted: mackerel (*Scomber scomber*), sprat (*Clupea sprattus*), herring (*Clupea harengus*), salmon

Coast water forms.

¹ According to Damas even *Calanus finmarchicus* is to some extent dependent on the configuration of the bottom (in the spawning time).

(*Salmo salar*), sea trout (*Salmo trutta*), capelan (*Mallotus villosus*).

In the southernmost part of our boreal region certain Atlantic pelagic forms are found in such numbers that they may be considered as belonging to the boreal area, though in the main they are Atlantic; so far the occurrence of these species resembles that of certain bottom fish, like the sole, the turbot, and the brill. The principal forms are: the horse mackerel (*Caranx trachurus*), *Clupea alosa*, and the anchovy (*Engraulis encrasicolus*).

Certain bottom fishes are often found in mid-water, such as the sharks which pursue the herring shoals, the common dog-fish (*Acanthias vulgaris*), the herring-shark (*Lamna cornubica*) and the large *Selache maxima*. Many fishes of the cod family lead a partly pelagic life, especially the saithe, and sometimes also the cod, haddock, and others. A specially remarkable type is the Norway haddock (*Sebastes marinus*). The pelagic eggs, larvæ, and young of economically important fishes, chiefly the cod and flounder families (*Gadidæ* and *Pleuronectidæ*) form another very important section of the pelagic communities.

When in the year 1900 I commenced my investigations with the newly built "Michael Sars," one of my main objects was to find out to what extent the fishes of the coast banks occurred in the deep mid-water of the Norwegian Sea. A large amount of information regarding this question has been accumulated, and we may now classify these animals in four groups:—

1. Larvæ and young organisms which have been carried out by currents, mainly of jelly-fish and cod, saithe and haddock.

2. Adult coast fish which have migrated; they spawn on the coast banks, but not over the deep water of the Norwegian Sea, the species observed being herring, cod, haddock, and saithe; also the squid, *Ommatostrephes todarus*.

3. Adult forms which spawn and occur in all stages of development in the coast waters, and also spawn over the deep Norwegian Sea; the only species of this kind observed is the Norway haddock (*Sebastes marinus*).

4. Atlantic animals: besides those previously mentioned we have also found the squids, *Gonatus fabricii* and *Architeuthis dux*, and the "Atlantic" whales, the "Bottle-nose" (*Hyperoodon diodon*) and the cachalot (*Physeter macrocephalus*).

Of these groups I will discuss the three last, leaving the first to be dealt with in the next chapter.

On the chart (Fig. 482) I have denoted all the localities

from which we possess definite information as to the occurrence of herrings, gadids, and *Sebastes* over deep water. Most of the

The herring.

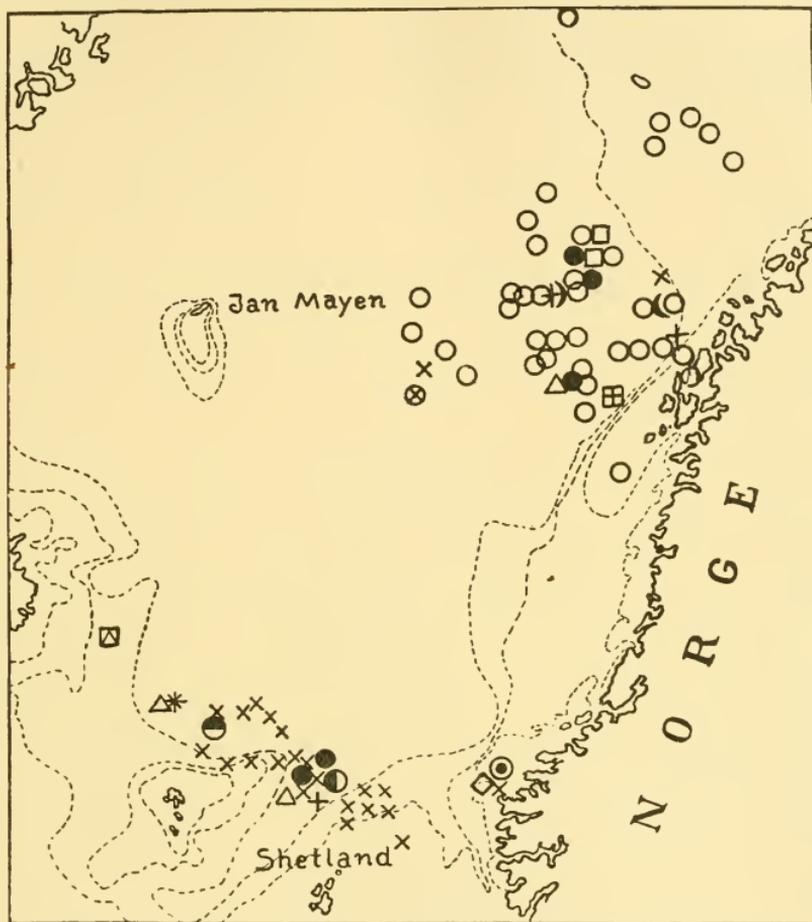


FIG. 482.—ANIMALS CAUGHT OVER GREAT DEPTHS IN THE NORWEGIAN SEA.

The isobaths represent depths of 100, 200, and 500 fathoms.

- | | | |
|----------------------|-------------------------|-----------------------|
| ○ <i>Sebastes</i> . | ⊙ <i>Cyclopterus</i> . | □ Haddock. |
| ● Cephalopoda. | × Herrings. | ⌋ <i>Anarrhicas</i> . |
| ◐ <i>Lamna</i> . | + Cod. | ⌋ Greenland shark. |
| ◑ <i>Acanthias</i> . | △ <i>Gadus virens</i> . | ◇ Mackerel. |

herrings occur from the northern slope of the North Sea towards Iceland. Only in two places elsewhere, between the Lofotens and Jan Mayen, did we succeed in capturing herrings, and

though the individuals are few they are very interesting because the localities are no less than 240 miles distant from any shore. As the herring spawns on the bottom comparatively near the shore, and the young are consequently born there, these captures illustrate the actual migrations. Several of the records obtained near the slopes of the coast banks of the North Sea, the Faroe Islands, and Iceland are specially interesting, because the fishermen always report that herrings occur in the stomachs of ling and cod captured on the slopes of the banks in summer. It will be an interesting object for future research to ascertain if herrings may be captured along the bottom on the slopes. This might be possible now that the trawl has proved a fit appliance for the capture of herrings along the bottom, and if successful would confirm the hypothesis of Sir John Murray that this part of the sea bottom, the "mud-line," is a feeding ground for these fishes.

The Gadidæ (cod, haddock, and saithe) have been taken in the surface waters over the deep parts of the Norwegian Sea far from the coast banks, but not in great numbers. The species most numerously represented in these parts seems to be the Norway haddock (*Sebastes marinus*). As will be noticed from the chart it has been taken in many localities, and these have been added to by recent investigations. *Sebastes* occurred mostly at depths of 100 to 200 metres, and we captured them by means of floating long lines, as shown in Fig. 74, p. 90, in numbers bordering on the abundance necessary for commercial fishing. Thus on one occasion we captured 65 fishes on 600 hooks with salted bait. Two young specimens of this fish were captured during the "Vöringen" Expedition, and during our cruises we have found the fry in thousands all over the Norwegian Sea—a fact pointing to the existence and propagation of a large stock of *Sebastes* in these intermediate layers.

Among the squids *Ommatostrephes todarus* plays the most important part in the animal community of the Norwegian Sea. In his book on the Mollusca of Northern Norway, G. O. Sars, referring to this form, says: "It is the commonest squid on our coasts, and among the fishermen is generally termed 'Akker,' 'sprut,' etc. They generally appear in enormous shoals, coming from the open ocean in pursuit of the herring shoals on which they gorge themselves greedily. In pursuing the herring they often run up on the beach in their excitement, and long sandy beaches are sometimes said to be covered with the carcasses of stranded squids. At Lofoten they have been

The Norway
haddock.

*Ommato-
strephes
todarus.*

fished and salted in barrels for bait in the cod-fisheries, being usually captured at dusk or during the night by the aid of minute grappels, several large hooks tied around a cylindrical piece of lead, baited with a herring and lowered to a suitable depth. The species is known outside Norway from the Skagerrack, the Faroe Islands, and Iceland, as well as from the west coast of France and the Mediterranean."

While fishing on the slopes of the coast banks one often finds this squid in the stomachs of cod, and repeatedly I have had occasion to make most interesting notes as to the occurrence of this species in the open sea far from land. One night we were hauling long lines on the Faroe slope, working with an electric lamp hanging over the side in order to see the line, when like lightning flashes one squid after another shot towards the light; on the same occasion the beaks of these animals were found in the stomachs of the captured fish. In October 1902 we were one night steaming outside the slopes of the coast banks of Norway, and for many miles we could see the squids moving in the surface waters like luminous bubbles, resembling large milky white electric lamps being constantly lit and extinguished; with a hand-line we captured several specimens. The existence of such numbers of squids in the open sea must undoubtedly be considered a very important item in the fauna.

Squids occur very abundantly also in the western part of the Norwegian Sea, where the small "bottle-nose" whale is captured by whalers during spring and summer. I have tried to obtain reliable information as to where this whaling goes on, and on the basis of this information I have prepared a chart (Fig. 483); each dot signifies a place where several whales have been observed or shot. The chart brings out the peculiar fact that all the localities are situated on the western side of the Gulf Stream water in the Norwegian Sea, *i.e.* in the transition belt between the Arctic and Atlantic currents. We gather from this chart that in April and May the "bottle-nose" is widely distributed over this part of the Norwegian Sea; in July the whaling ceases, and in September the inhabitants of the Faroe Islands get their last "bottle-nose." These whales are never, or only on extremely rare occasions, observed or shot on the coast banks, and thus they do not enter the Barents Sea, but, according to an experienced whaler, they follow the 800-fathoms line.

The "bottle-nose" whale.

I have succeeded in obtaining information as to the stomach-contents of the "bottle-nose"; these consist mainly of the

*Gonatus
fabricii.*

remains of squids, not *Ommatostrephes todarus*, but *Gonatus fabricii*, which must consequently occur in great numbers in

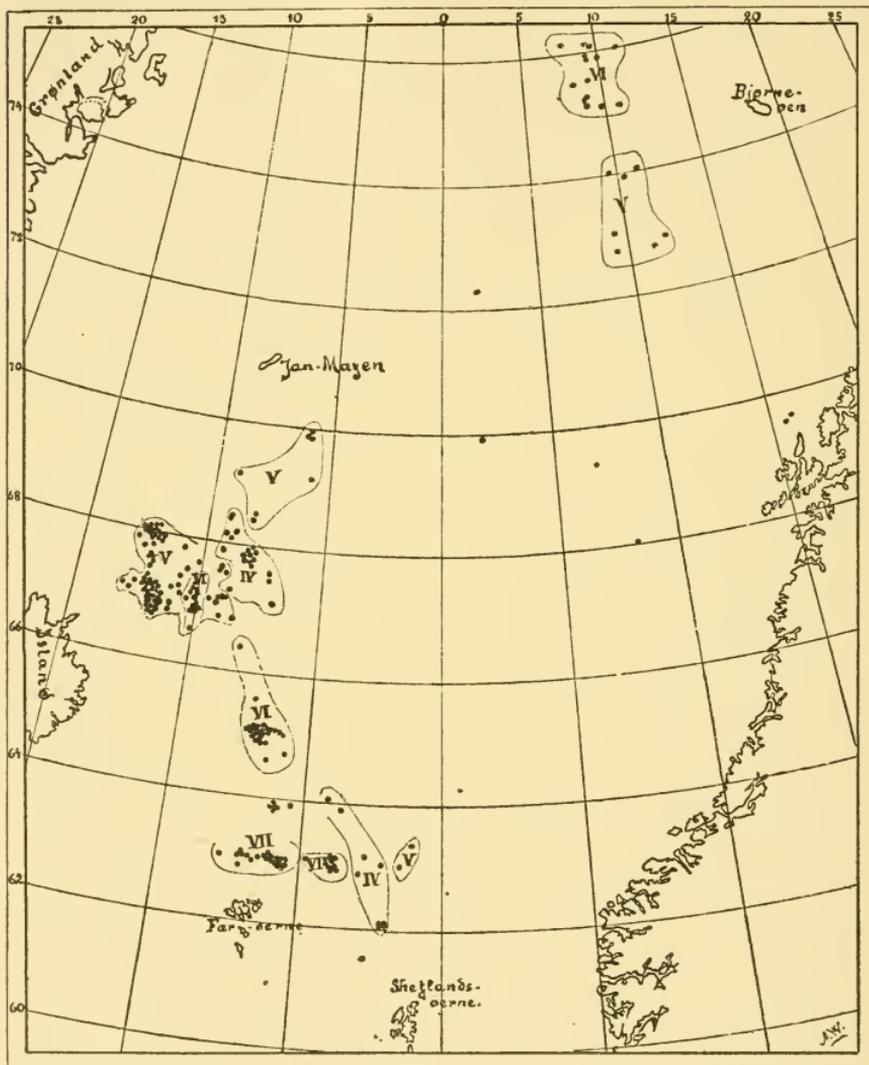


FIG. 483.—DISTRIBUTION OF "BOTTLE-NOSE" WHALE (*HYPEROODON DIODON*) IN THE NORWEGIAN SEA.

IV.—VII. indicate the months April-July.

the western part of the Norwegian Sea; farther south, in the vicinity of the Faroe Islands, herrings are also found in the stomachs. As previously mentioned, numerous larvæ of *Gonatus*

fabricii were taken on our Atlantic cruise between Newfoundland and Ireland (at Stations 70, 80, 81, and 94, covering a wide expanse of ocean); such larvæ have never been taken by us in the Norwegian Sea. As a working hypothesis we may suppose that in spring and summer *Gonatus* migrates into the Norwegian Sea from the Atlantic, just as the "bottle-nose" is universally believed to do.

The same remark probably applies to the interesting giant squid, *Architeuthis dux*, a specimen of which (see Fig. 484) was found floating at the surface to the north of the Faroe Islands

Architeuthis.

during a cruise with the "Michael Sars" in 1902. This specimen was not large, but in 1903 in Iceland I had the opportunity of making an interesting observation, showing the gigantic dimensions of these squids. On the 15th of August the "Michael Sars" arrived in Mofjord on the east coast of Iceland, and visited the local whaling station. On the shore were two freshly caught whales, one a north-caper, the other



FIG. 484.—*ARCHITEUTHIS*, FOUND DEAD NORTH OF THE FAROE ISLANDS.

a cachalot. Inspecting the cachalot I saw around its enormous jaws several long parallel stripes (see Fig. 485), consisting, as closer scrutiny revealed, of great numbers of circular scars or wounds about 27 mm. in diameter; Fig. 486 shows a piece of the skin with these scars. It occurred to me that these scars must have been left by the suckers of a giant squid, and following up this idea I found in the whale's mouth a piece of a squid-tentacle 17 cm. in maximum diameter. In the stomach of the whale many squid-beaks of various sizes were found, the largest measuring 9 cm. in length, besides some fish bones, and the men who had shot the whale told me that in its death-flurry it disgorged the arm of a squid 6 metres

long. Similar observations have been recorded from the Azores by the Prince of Monaco.

The Boreal Area outside the Norwegian Sea.—The northern North Atlantic has previously been investigated by Danish expeditions on board the "Ingolf," "Thor," and "Tjalfe" in the waters of western Europe, Iceland, and Greenland, by a German expedition on the west coast of Greenland and by British expeditions west of Britain, while Hensen's Plankton Expedition also crossed this area. On the other hand, the



FIG. 485.—CACHALOT WITH LONG STRIPES FROM STRUGGLE WITH *ARCHITEUTHIS*.

exceedingly interesting waters between Davis Strait and the United States have been very little examined.

The results of all these expeditions prove the northern North Atlantic to contain the same pelagic animals as the Norwegian Sea. According to the various bodies of water, however, the animal life varies in composition in different parts of the ocean. Thus to the west of Britain pelagic life is temperate Atlantic, mingled to some extent with boreal forms; to the south of Iceland the boreal forms predominate, though the Atlantic admixture is very important; in Davis Strait the character of the fauna is mainly Arctic, though some boreal forms still appear (the capelan, for instance, seems very characteristic). Proceeding from Labrador to the Northern States the purely

Arctic, the boreal, and the subtropical Atlantic forms are met with in succession, their distribution changing according to seasons and local conditions; the boreal waters are here squeezed between bodies of Arctic and Atlantic water, and the transitions between the different bodies of water and between the different animal-communities are very sudden.

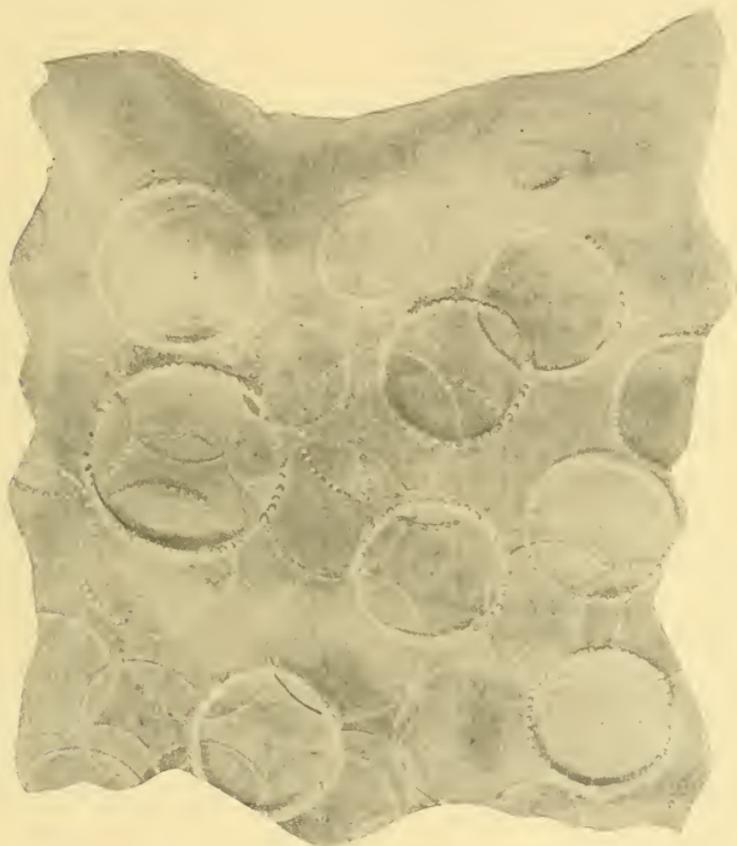


FIG. 486—SKIN OF CACHALOT WITH MARKS FROM STRUGGLE WITH *ARCHITEUTHIS*.
Nat. size.

The tow-nettings made by the "Michael Sars" in 1910 between the Sargasso Sea and Newfoundland and thence to Ireland are particularly interesting, because they comprise Arctic, boreal, and Atlantic forms mingled together in the same oceanic area, and afford a rare opportunity for observing to what extent the distribution of different forms depends on certain physical conditions.

	Station 50.			Station 63.			Station 80.			Station 92.			Station 113.			
	0 ↑ 200	210 ↑ 500	500 ↑ 1000	2 ↑ 200	200 ↑ 500	900 ↑ 1000	0 ↑ 235	235 ↑ 525	525 ↑ 950	0 ↑ 200	200 ↑ 500	500 ↑ 1000	0 ↑ 100	100 ↑ 300	300 ↑ 500	500 ↑ 1000
Limits of vertical haul (metres)→																
DECAPODA																
<i>Hippolyte</i>			+			+										
<i>Acanthephyra</i>				□		+		○	+							+
<i>Hymenodora</i>			+													
<i>Sergestes</i>				□												
<i>Pandalus</i> , larvæ													□			
<i>Munida rugosa</i> , juv.														○		
SCHIZOPODA																
<i>Stylocheiron longicorne</i>				□												
<i>Euphausia krohnii</i>					○	+		○			○	+				
" <i>gibba</i>			+													
" <i>tenera</i>			+													
" larvæ	□	○					□			□						
<i>Thysanoëssa neglecta</i>													□			
" <i>longicaudata</i>								○	+					○	○	+
" <i>minor</i>			+													
" <i>parva</i>						+										
<i>Thysanopoda acutifrons</i>															○	
" <i>obtusifrons</i>			+												○	
<i>Meganocythipes norvegica</i>															○	
<i>Nematoscetes microps</i>			+					○	+							
" <i>megalops</i>			+													
<i>Nematobranchion boops</i>															○	
AMPHIPODA																
<i>Oxycephalus</i> sp.				□												
<i>Scina borealis</i>			+		○				+							
<i>Scyphocaris anonyx</i>									+							
<i>Phronima sedentaria</i>	□	○		□	○	+				□						
<i>Hyperia medusarum</i>					○				+						○	
<i>Parathemisto obliqua</i>															○	
<i>Euthemisto libellula</i>							□	○	+							
<i>Lycæa</i> sp.	□									□						
<i>Platyscelis</i> sp.			+		○											
ISOPODA																
<i>Eurycope gigantea</i>									+							
<i>Munnopsis</i> sp.									+							
CALANOIDA																
<i>Calanus minor</i>				□	○									□	○	○
" <i>finmarchicus</i>							□	□		○	+				○	+
" <i>helgolandicus</i>						+				○	+		+			
" <i>hyperboreus</i>										○	+				○	+
" <i>gracilis</i>	□	○	+	□	○	+	□	□		□						
" <i>robustus</i>	□	□														
<i>Eucalanus elongatus</i>	□	○	+	□	○	+	□	□	+	□	○	+				
" <i>attenuatus</i>	□	□														
" <i>cornutus</i>	□	○	+	□	○					□	□	+				
" <i>nasutus</i>	□	□		□	□						○	+	□			
" <i>monachus</i>	□	□	+			+						+				
Nauplii, etc.										□						+
<i>Pseudocalanus elongatus</i>							□	○	+							
<i>Spinocalanus magnus</i>														+		
<i>Scottocalanus securifrons</i>			+													
<i>Onchocalanus rostratus</i>																
<i>Megacalanus longicornis</i>													+			
<i>Euchæta norvegica</i>							□	○	+			+	□	○	○	+
" <i>barbata</i>									+							+
" <i>marina</i>	□															
" <i>glacialis</i>				□		+				□					○	+
" sp. juv.																
" <i>acuta</i>			+	□	○	+				□						
<i>Undeuchæta minor</i>			+								○					
" <i>major</i>			+						○		+					
" sp.																
<i>Chirundina stressi</i>			+											+		
<i>Euchirella messinensis</i>			+			+										
" <i>rostrata</i>				□		+	□	○	+							
" <i>venus</i>				□												
" <i>venusta</i>				□	○											
" <i>brevis</i>	□															
<i>Lophothrix frontalis</i>																
" <i>latipes</i>			+													
<i>Cephalophanes refulgens</i>			+													
<i>Pleuromma xiphias</i>		○	+			+										
" <i>abdominalis</i>		○	+													
" <i>gracilis</i>		○		□	○	○				○	○					
" <i>robusta</i>		○								○	○					
<i>Metridia curticauda</i>			+													
" <i>lucens</i>													□	○	○	
" <i>normani</i>			+			+							□	○	○	
" <i>longa</i>													□	○	○	+

G. O. SARS' LIST OF CRUSTACEA (continued).

Limits of vertical haul (metres)→	Station 50.			Station 63.			Station 80.			Station 92.			Station 113.			
	0 ↑ 200	210 ↑ 500	500 ↑ 1000	2 ↑ 200	200 ↑ 500	900 ↑ 1000	0 ↑ 235	235 ↑ 525	525 ↑ 950	0 ↑ 200	200 ↑ 500	500 ↑ 1000	0 ↑ 100	100 ↑ 300	300 ↑ 500	500 ↑ 1000
CALANOIDA, continued—																
<i>Lucicutia flavicornis</i>	□		+	□	○		○								+	
<i>curta</i>			+												+	
<i>brevis</i>															+	
<i>atlantica</i>															+	
<i>Amalophora affinis</i>			+			+			+						+	
<i>magna</i>																
<i>obtusifrons</i>						+		○								
<i>Ætideus giesbrechti</i>	□	○							□	□						
<i>armatus</i>																
<i>Ætideoopsis multiserrata</i>						+										
<i>Gaidius tenuispinus</i>								○	+							
<i>notacantha</i>																○
<i>Gaëtanus miles</i>		○			○											
<i>kruppi</i>			+													
<i>caudani</i>			+													
<i>latifrons</i>			+													
<i>minor</i>			+								○					
<i>armiger</i>					○											
<i>laticeps</i>												+				
<i>Haloptilus longicornis</i>	□	○	+		○		□									
<i>mucronatus</i>	□															
<i>acutifrons</i>			+								○					
<i>ornatus</i>		○			○											
<i>Augaptilus squamatus</i>			+			+										
<i>longicaudatus</i>			+		○											
<i>palumboi</i>			+		○											
<i>oblongus</i>			+													
<i>gibbus</i>			+													
<i>filigerus</i>					○											
<i>laticeps</i>																+
<i>sp. juv.</i>				□												
<i>Heterorhabdus norvegicus</i>			+		○	+			+	□	○	+				○
<i>brevicaudatus</i>			+													
<i>vipera</i>			+													
<i>papilliger</i>		○	+													
<i>longicornis</i>		○		□	○			○								
<i>spinifrons</i>											○					+
<i>Scolecithrix dane</i>	□															
<i>minor</i>		○		□												○
<i>Scolecithricella sp.</i>		○		□												
<i>minor</i>							□	○	+							
<i>Acartia dane</i>		○		□							□			□	○	
<i>clausi</i>											□					
<i>Centropages typicus</i>																
<i>Candace sp.</i>	□															
<i>Disseta palumboi</i>			+													
<i>Chiridius poppei</i>					○											
<i>armatus</i>								○	+							
<i>Phaenna spinifera</i>		○			○											
<i>Phyllopus bidentatus</i>			+			+										
<i>Bathypontia minor</i>						+										
OTHER COPEPODA																
<i>Oithona similis</i>							□			□				+		
<i>plumifera</i>														+		
<i>sp.</i>	□	○	+	□	○			○	+					+		
<i>Oncea conifera</i>	□	○	+	□	○											
<i>sp.</i>	□	○	+	□	○											
<i>Lubbockia squillimana</i>																
<i>Microsetella norvegica</i>										□						
<i>Ægisthus mucronatus</i>											○					
<i>Mormonilla minor</i>																
<i>Corycaeus sp.</i>	□	○		○												
<i>Copilia sp.</i>	□															
<i>Sapphirina sp.</i>	□															
OSTRACODA																
<i>Conchæcia elegans</i>								○							○	○
<i>sp.</i>	□	○	+	□	○	+		○	+	□	○					+
<i>maxima</i>																
<i>borealis</i>																
<i>obtusata</i>							□	○	+							
<i>Halocypris sp.</i>	□			□	○	+	□			□						
<i>globosa</i>																
<i>Conchæcilla sp.</i>		○	+			+										
<i>lacerta</i>																
<i>Conchæcissa sp.</i>			+													
<i>armata</i>																
Number of species	22	22	51	25	32	27	16	27	34	18	12	33	9	12	18	11

Our collections of minute crustaceans, especially Copepoda, are very extensive, but their examination will take a long time. In order to give some information about the distribution of these interesting forms, I asked G. O. Sars to determine the species contained in some of our closing-net hauls, and selected samples from certain stations (see Fig. 487), which I believed to be specially characteristic, viz. two stations in the Sargasso

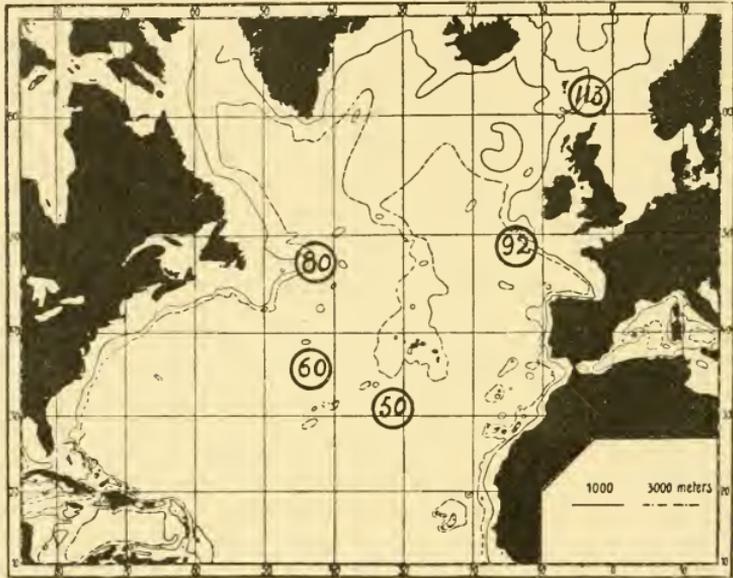


FIG. 487.—POSITIONS OF STATIONS FROM WHICH LISTS OF CRUSTACEA HAVE BEEN DRAWN UP. [Station 60 should be 63.]

Sea (50, 63), one station off the Newfoundland banks (80), one station off Ireland (92), and one station in the Norwegian Sea north of the Wyville Thomson Ridge (113). Before referring to Sars' determinations (see list, pp. 654-5) I may indicate the temperatures at the various depths where the nets were towed:—

Station 50.		Station 63.		Station 80.		Station 92.		Station 113.	
Depths.	Temp.	Depths.	Temp.	Depths.	Temp.	Depths.	Temp.	Depths.	Temp.
Metres.	° C.	Metres.	° C.	Metres.	° C.	Metres.	° C.	Metres.	° C.
200 to 0	17.7° to 20.3°	200 to 0	16.7° to 27.3°	200 to 0	7.6° to 11.8°	200 to 0	11° to 16.5°	100 to 0	8.3° to 11.6°
500 to 200	13.7° to 17.7°	500 to 200	13.8° to 16.7°	500 to 200	4.6° to 7.6°	500 to 200	10° to 11°	300 to 100	6.4° to 8.3°
1000 to 500	9.7° to 13.7°	1000 to 500	6° to 13.8°	1000 to 500	3.3° to 4.6°	1000 to 500	8.6° to 10.2°	500 to 300	1.1° to 6.4°
								1000 to 500	-0.5° to 1.1°

From a study of the list on pp. 654-5 we note the following points:—

(1) A certain number of genuine warm-water forms occur only in the upper hauls (200 to 0 metres) in the southern stations (50 and 63), such as: *Eucalanus attenuatus*, *Euchæta marina*, *Euchirella brevis*, *Haloptilus mucronatus*, *Scolecithrix danæ*, *Acartia danæ*, *Candace*, *Copilia*, *Sapphirina*.

(2) Some Atlantic deep-sea forms do not occur at the surface either in the Sargasso Sea or along our northern track; they do not enter the Norwegian Sea and are consequently distributed like the Atlantic bathypelagic fauna. Such are: *Amalophora affinis*, *Augaptilus squamatus*, *Phyllopus bidentatus*, *Bathypontia minor*.

(3) Some forms have a large vertical range in warm waters, like *Calanus gracilis* and *Pleuromma gracilis*.

(4) Other forms have a large vertical range in the southern as well as in the northern stations, like *Eucalanus elongatus* (see Stations 50, 63, 80, and 92).

(5) A peculiar group is composed of forms having at the boreal stations a large vertical range, but occurring at the warm southern stations only in deep water such as: *Calanus finmarchicus* (Stations 80 and 113 at all depths); *Euchæta norvegica* (Stations 80 and 113 at all depths, Station 92 only between 1000 and 500 metres, also, according to Nordgaard, Station 64, in 1250 metres, Station 62 in 1000 metres); *Metridia longa* (Stations 80 and 113 in all hauls); *Pseudocalanus elongatus* (Station 80 at all depths); *Scolecithricella minor* (Station 80 at all depths); *Heterorhabdus norvegicus* (Station 92 at all depths, and in deep water at Stations 50, 63, 80 and 113). All these forms occur in the Greenland Sea, where they also have a large vertical distribution (Damas and Koefoed).

(6) Certain forms recorded only from the deep hauls at Stations 80 and 113, where the temperature is lowest, such as *Euchæta barbata*, *E. glacialis*, *Calanus hyperboreus*, *Amalophora magna*. None of these occur in deep water at Stations 50 and 63, but, according to Nordgaard, *Calanus hyperboreus* and *Euchæta barbata* have both been taken at Station 62 in the Sargasso Sea in a horizontal haul at 1000 metres in great numbers, 65 specimens of *Calanus hyperboreus* being counted in a small part of the sample. These forms belong to the Arctic region in the Norwegian Sea, where according to Damas and Koefoed they are also deep-sea forms, except the surface species *Calanus hyperboreus*.

The general results may be summarised as follows :—

Summary.

In the northern North Atlantic we find Atlantic, boreal, and Arctic forms. On our track from Newfoundland to Ireland we met chiefly Atlantic species at the surface (see Station 92, 0–200 metres). In deeper water we find certain Atlantic deep-sea species which nowhere in the ocean reach the surface, mingled with boreal species. At Station 80, situated in an area where the cold waters of the Labrador current communicate directly with the deep bottom layers, the boreal forms occur at all depths (Group 5), as they do in the Norwegian Sea; but to the east of Station 80, where the warm layers are thicker, we meet only the boreal forms in the deeper water, and in the

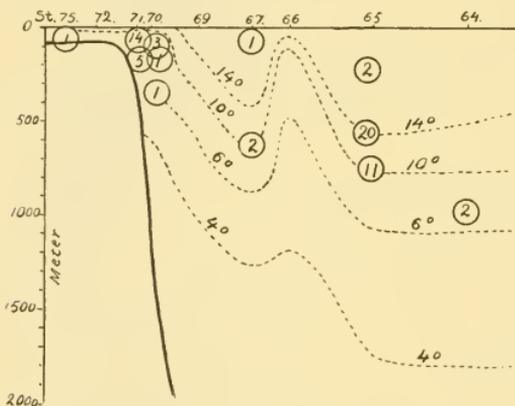


FIG. 488.—VERTICAL DISTRIBUTION OF *CLIONE LIMACINA* BETWEEN NEWFOUNDLAND AND THE SARGASSO SEA.

The encircled figures denote the number of individuals captured.

Sargasso Sea at depths of 1000 metres. Thus *Euchaeta norvegica* was taken at all depths at Stations 80 and 113; at Station 92 only from 1000 to 500 metres, and at Station 62 only at 1000 metres.

The genuine Arctic forms (Group 6) occur in waters with temperatures below 5° or 6° C., thus *Calanus hyperboreus* was taken on the Newfoundland banks at the surface,

at Station 80 only below 200 metres, and at Station 62 at 1000 metres.

As shown in Chapter III., this conformity appeared even during the cruise, and was obvious not only in regard to these small crustaceans, but for quite a number of other boreal and Arctic animals as well (see pp. 106-108 and 117-118). The most important boreal and Arctic forms encountered between Newfoundland and Ireland, besides the Copepoda previously mentioned, were: the medusa *Aglantha*, the Ctenophores *Beroë*, *Pleurobrachia*, and *Mertensia*, the worms *Sagitta arctica* and *Krohnia hamata*, and the pteropods *Limacina helicina* and *Clione limacina*.

During our voyage from the Sargasso Sea to Newfoundland and thence to Ireland, *Clione limacina* was, according to

Bonnevie, taken at the depths indicated by circles in Figs. 488 and 489. At Newfoundland it lived at the surface, but all the way from Newfoundland to Ireland it was taken only below 750 metres. Its occurrence in only 50 metres on the coast banks off Ireland is remarkable and important, showing that this form occurs in shallow water, both on the eastern and western sides of the North Atlantic, in cold and in warm water.

This distribution seems to be shared by *Aglantha digitalis*,

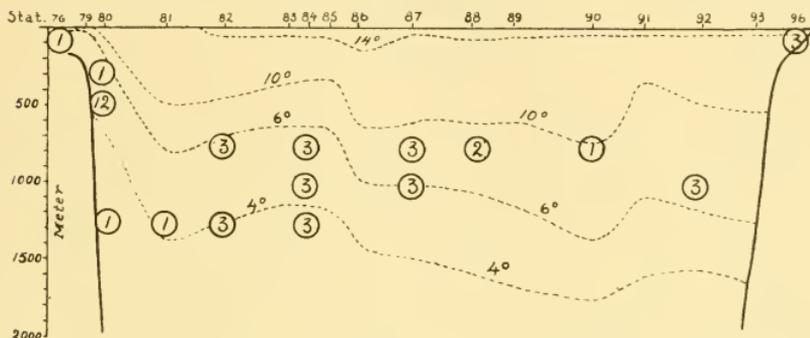


FIG. 489.—VERTICAL DISTRIBUTION OF *CLIONE LIMACINA* BETWEEN NEWFOUNDLAND AND IRELAND.

The encircled figures denote the number of individuals captured.

which was taken on the Newfoundland banks at the surface, at Station 80 in vertical hauls from 950 to 525 metres, at all the deep stations farther east (for instance Station 92) at 1000 metres, but close to the slope of the coast banks of Ireland it was taken only 100 metres beneath the surface.

In the deep water of our northern section our pelagic fishing appliances at, for instance, 1000 metres gave bathypelagic Atlantic forms like *Cyclothone microdon*, *Atolla bairdi*, *Gigantocypris*, *Pelagonemertes*, *Pyrosoma*, *Acanthephyra*, besides boreal forms like *Eucheta norvegica*, *Aglantha digitalis*, and *Clione limacina*.

J. H.

CHAPTER X

GENERAL BIOLOGY

ABOUT the beginning of the nineteenth century many distinguished men of science seem independently to have developed the idea that the structure of animals and their occurrence in various localities are determined by external conditions.

Lamarck in his *Philosophie zoologique* (1809) writes as follows: "The external conditions always and strongly exert their influence on all living beings. This influence is, however, difficult to ascertain, because its effects only appear, and may be recognised, after a very long time."

Goethe's zoological works all testify to his strong belief that "all living beings possess the faculty of adapting themselves to the manifold conditions presented by external influences, without, however, resigning a certain hard-earned and decided independence." In his *Skeletons of Rodents* he says that "the difference of forms is a consequence of their necessary dependence on the outer world." In his introduction to comparative anatomy he attempts to show the various influences exerted by certain climatic conditions, by water, and by air upon the shape of animals, which become altered on passing from one group of conditions to another. This again explains the fact that "no organism intended to live is conceivable without a perfect organisation." Goethe was full of such ideas, but felt the danger of following them up, and of "losing oneself in the infinite" (*Principles of Zoological Philosophy*).

Kant's view is still clearer as regards the idea of adaptations to surroundings. He endeavoured to show that all biological investigations had to take for granted that living beings are fitly organised in relation to their natural surroundings. But no definite human idea of the fitness of adaptations is of any value as knowledge. No more does any human idea necessarily correspond to the reality occurring in nature. The idea is only

valuable as stimulating the investigator to seek realities. And reality, in the scientific sense, means a definite positive mechanism, existing in the organism itself or in the surrounding medium. The object of investigation is to understand these mechanisms; the leading idea may often prove an empty fancy beyond the world of realities.

In the second half of last century the investigations on the history of the development of animals disclosed many organs (for instance, rudimentary organs), the function of which in the life of the organism could not be understood. According to the Darwinian idea the development of species consisted in innumerable minute changes. These changes were conceived as being due to "chance," which to a certain extent seemed to contradict the idea of "fit adaptations."

The historical way of explaining the structure or occurrence of organisms is, however, at present not considered contradictory to the ideas of adaptation. Even Lamarck, as mentioned above, thought that a species must exist for a very long time before the effects of the influence of surroundings appear or disappear.

As to the origin of variation it is now more and more recognised that a comprehension is only to be gained by studying the reaction of organisms against the influence of surroundings. One may endeavour to ascertain these reactions by experiment, by observing the changes taking place in the organisms when subjected to altered conditions. In nature we may also observe how the shape of individuals alters in various surroundings, and how similar shapes reappear in similar environments.

In recent times we note an increasing tendency to observe animals in their natural surroundings, and during frequent expeditions the influence of this tendency has been predominant. In recent literature we may find many investigations and many opinions, which remind us of the interest attached to these problems about a hundred years ago.

In the history of oceanic research nothing has possibly contributed so much to the awakening of this interest as the discovery of entirely different animal-communities living on either side of the Wyville Thomson Ridge (see Fig. 106, p. 124). Atlantic forms occur to the south and Arctic forms to the north of the ridge, corresponding to the very different thermal conditions on either side.¹

¹ See Murray and Tizard, "Exploration of the Faroe Channel, during the summer of 1880, in H.M.'s hired ship 'Knight Errant,'" *Proc. Roy. Soc. Edin.*, vol. x. p. 638, 1882; Tizard, "Remarks on the soundings and temperatures obtained in the Faroe Channel during the summer

Another series of investigations in this field were those of C. G. J. Petersen, regarding the distribution of mollusca in the Kattegat. In *The Cruises of the "Hauch,"* Petersen¹ has employed the only empirical method of investigating the distribution of animals, viz. to analyse the distribution of species in relation to various external conditions, as for instance, high or low salinity, high or low temperature, great changes in temperature or salinity, etc. It proved possible in the Kattegat to define areas of distribution of certain species, coinciding with areas where characteristic physical conditions prevailed.

Similar methods have been employed by Chun for the study of pelagic organisms. An important branch of this science has the object of studying the changes occurring in the physical conditions of the ocean, and the influence of these changes on the occurrence or abundance of organisms. By means of a continually increasing co-operation between hydrography and biology, both equally necessary in the study of such problems, oceanography has made great progress, especially during the international investigations in the study of the sea.

The additions which during the cruises of the "Michael Sars" it has been possible to make to these branches of science consist mainly of information regarding the vertical and horizontal distribution of animals, accompanied by physical observations of various kinds. These biological and physical investigations place us in a position to test certain ideas regarding the adaptations of animals, and thus acquire knowledge on certain important mechanisms of life.

The following review of some of our principal results can by no means claim to be complete. The literature referred to, the various fields of biology discussed, and even the selection made from the material collected by our recent expedition, have all been limited for the purpose of this review. Still I hope to indicate some new contributions to science, and at the same time to convey some idea of the general methods and aims of biological oceanic research.

COLOURS OF MARINE ANIMALS

From time immemorial seafaring men have possessed a certain amount of knowledge as to the colours of marine animals.

of 1882 (H.M.S. 'Triton')."
Proc. Roy. Soc. Lond., vol. xxxv. p. 202, 1883; Murray, "The physical and biological conditions of the seas and estuaries about North Britain," *Proc. Phil. Soc. Glasgow*, vol. xvii. p. 306, 1886.

¹ Petersen, *Det videnskabelige Udbytte af Kanonbaaden "Hauchs" togter*, Kjöbenhavn, 1893.

Sailors know well the sky-blue colours peculiar to the tropical surface forms. Herring-fishermen also know that the blackish-brown back of the herring is almost invisible from above, and only when occupying a slanting position or making a sudden turn does the herring become visible, its mirror-like sides emitting a silvery flash. The deep-sea fishermen are equally acquainted with the dark, black, brown, violet, or red colours peculiar to deep-sea animals. No scientist can claim the discovery of these phenomena, which are as well known as the colours of the ocean itself.

When considering the peculiar colours of marine animals, and their variation in different surroundings, many naturalists concluded that the colouring was due to their attempts to adapt themselves to the colours of their surroundings, in order to make themselves invisible or to protect themselves against enemies, just as is supposed to be the case with the land fauna.

This idea requires confirmation by acquiring more exact knowledge as to the conditions of light and the colours of animals from similar depths. Our knowledge regarding the penetration of light in the ocean has been as deficient as our knowledge of the vertical distribution of the animals, and the whole subject has thus been a matter of suppositions and ideas rather than of actual knowledge.

During the Atlantic cruise of the "Michael Sars" we investigated the intensity of light at different depths and also the colours of the animals. The results obtained by the photometer at a few stations in the Sargasso Sea are referred to on pp. 251-2. On a sunny day when the water was perfectly clear and transparent, light-rays of all colours, but very few red rays, were observed at a depth of 100 metres. At 500 metres the light acted strongly on the photographic plates, especially the blue rays, but the green rays were absent; even at 1000 metres the influence of the sunlight could be traced on the plates, but at 1700 metres no influence was noticeable.

Penetration
of light.

As we have seen in Chapter IX. the different water-layers in the Sargasso Sea contain animals of very different colouring, certain general features in the colouring being easily recognisable in certain regions. In the hauls from 500 to 750 metres and deeper we found only black fishes and red crustaceans (prawns). At 300 metres we found the laterally compressed *Sternopychidæ* with silvery sides and brownish backs. In the upper layers we met with transparent young fish, for instance *leptocephal*i, or silvery *Scopelidæ* and blue flying-fish.

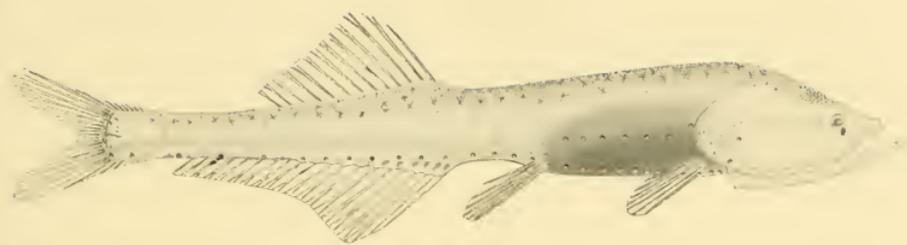
Animals of
the Sargasso
Sea.

Plates I.-VI. show certain forms found in the Sargasso Sea, representing a small selection from the numerous coloured drawings by Rasmussen. Plate I. shows the black *Cyclothone microdon* from deep water and the light coloured *C. signata*, which has its lower limit just at the upper limit of the black fish. Other black fish and some red prawns from depths beyond 500 metres are represented in Plates II. and III. The black and red colours are easily seen in strong sunlight. The theory of protective colours must therefore assume that these colours only appear in dark surroundings. In this connection it is very interesting to note that the upper limit to the occurrence of these black and red deep-water animals, which according to latitude varies between 500 and 750 metres, is also the limit within which most of the sun's rays are absorbed, and it is important also to note that the red rays belong to that part of the spectrum which is most rapidly absorbed by the water.

In connection with the question of the colouring of these bathypelagic forms we may refer to some observations made during the cruise regarding the vertical migrations of such dark-coloured forms, as shown in Fig. 490. Three species, *Gastrostomus bairdii*, *Cyema atrum*, and *Gonostoma grande* have been taken only at 750 metres or deeper, while two species, *Gonostoma rhodadenia*¹ and *Photostomias guernei*, have been taken also at lesser depths, even at 150 metres. I have already mentioned several instances (see p. 93) where forms like *Astronesthes* and *Idiacanthus* have been taken at the surface, but only at night. In the case of *Photostomias* and *Gonostoma rhodadenia* I have denoted the night-captures with a dark disc, while a ring denotes day-captures. These catches seem explicable only by supposing vertical migrations to take place, and as these occur in the darker part of the twenty-four hours they probably coincide so precisely with the disappearance and re-appearance of daylight that the dark colouring may be of no danger to the animals in their nightly migrations towards the surface of the sea.

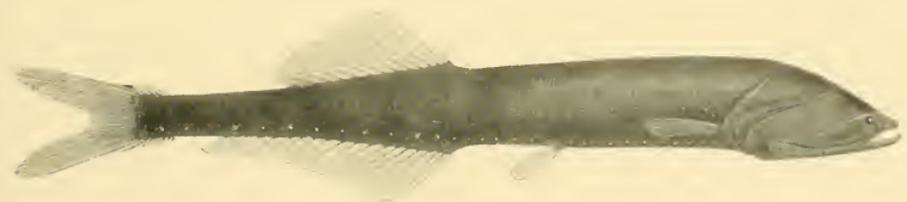
The occurrence of dark colours thus coincides with the region where the intensity of the sunlight is greatly diminished. Another circumstance seems to confirm this, viz. that in different waters the upper limit to the black fish and the red crustaceans seems to coincide with the same low intensity of light.

¹ The specimens which in Fig. 490 are referred to *Gonostoma elongatum* have, on closer investigation, proved to be the closely allied *Gonostoma rhodadenia*.



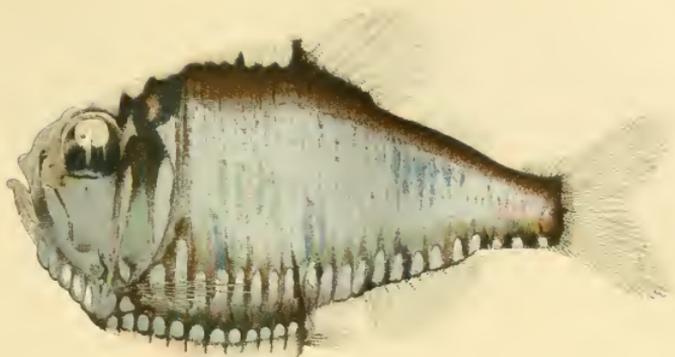
2.7 cm.

CYCLOTHONE SIGNATA.



5 cm.

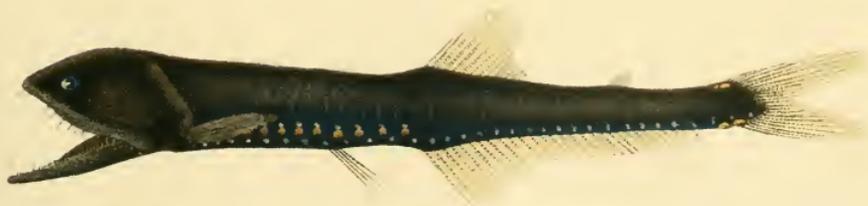
CYCLOTHONE MICRODON.



ARGYROPELECUS AFFINIS, GARM



GONOSTOMA GRANDE, COLLETT



GONOSTOMA ELONGATUM, GTHR



1. *Acanthephyra multispina* (Coutière), Sund
2. *Acanthephyra purpurea*, A. M.-Edwards
3. *Systellaspis debilis*, A. M.-Edwards

We have seen that the upper limit for *Cyclothone microdon* and the red crustaceans, in the northern section from Newfoundland to Ireland, or about lat. 50° N., was approximately 500 metres below the surface, and we have also noticed that the limit of depth for the same forms at the southernmost stations, or about lat. 33° N., was some 200-300 metres deeper. In the Norwegian Sea I have previously investigated the intermediate

Depths m.	Gastrostomus Bairdii.	Cyema atrum.	Gonostoma grande.	Gonostoma elongatum	Photostomias Guernei
150				• •	•••••••
300				••••••••	•••
500				••	○
750	○ ○ ○ ○		○ ○ ○ ○ ○	○	
1000	○ ○ ○		○ ○ ○		• ○
1250	○ ○ ○	○	○ ○ ○ ○ ○ ○	○	•
1500	○ ○ ○ ○ ○ ○	○ ○	○ ○ ○ ○ ○ ○ ○ ○ ○ ○ ○ ○	○ ○	○ ○ ○ ○ •
2000	○				•

FIG. 490.—VERTICAL DISTRIBUTION OF BLACK-COLOURED PELAGIC FISHES.

pelagic fauna, and found pelagic red prawns as well as the dark-red fish, *Sebastes norvegicus*, at depths of about 200 metres below the surface. *Sebastes* was taken, for instance, with floating long lines in considerable quantities on a course from Jan Mayen to Lofoten—that is to say, in about lat. 67° N.,—at a depth of 200 metres, and it was found, though in decreasing quantities, in even less depths. Along the Norwegian coast, in the fjords and sounds, we have a particularly rich fauna of red crustaceans (especially *Pandalus borealis*), occupying depths

whose upper limit in the north, at any rate, may be put at above 100 metres.¹ Now, if we calculate the depth to which the rays of the sun penetrate, after passing through the same distance in the water, assuming always that the rays are direct and that the rate of absorption is the same, we find that the rays will have passed through the same distance to reach a depth of 500 metres in lat. 50° N., that they will pass through to reach 650 metres in lat. 33° N., or 300 metres in lat. 67° N.

The transparency of the water, however, varies greatly in different regions. If we take the results of previous observations during different expeditions, we may set down the visible depth in the open sea as being roughly 50 metres in lat. 33° N., 40 metres in lat. 50° N., and 25 metres in the Norwegian Sea in lat. 67° N. Taking this into consideration, we find that there will be the same *intensity* from the rectilinear rays—

In lat. 33° N.	at about	800 metres.
” 50°	”	500 ”
” 67°	”	200 ”

The red and black animal forms, therefore, as has been found in the investigations I have just described, have an upper limit in the different waters which corresponds everywhere with the same intensity of light.

Very interesting also is the fact that certain dark bathypelagic forms appear as varieties differing in the intensity of their colours. Broch from his study of the “Michael Sars” collections thus recognises four varieties of the deep-sea medusa *Atolla bairdi*: (1) stomach alone containing pigment; (2) peripheral muscular belt also pigmented; (3) the brown pigment distributed also on the lower side of the bell, while gonads are

¹ Sir John Murray reports that in Upper Loch Fyne, in Loch Etive, and in some other sea-lochs of the west coast of Scotland, which are cut off from the ocean by submerged barriers, red prawns and other red crustaceans are very numerous in depths of 50 to 70 fathoms (about 270 to 310 metres); for example *Nyctiphanes* (*Meganetyphanes norvegica*), both adult and young, can always be captured in these lochs by dragging nets one or two fathoms above the bottom. This species possesses ten phosphorescent organs: one pair in the eye peduncle, two pairs on the under side of the thorax, and the remaining four in the median line of the abdominal segments. Sir John believes that these organs are used as a kind of “bull’s eye lantern,” and enable the *Nyctiphanes* to see and pick up the minute particles of organic matter which are settling on the bottom-deposits. Many specimens of this species were kept in aquaria for a considerable period, and were observed to light up and shut off their phosphorescent organs at will. The surface layers of water in these Scottish lochs are much less saline than the deeper layers, and contain much suspended matter, so that the penetration of light is much obstructed. Besides *Nyctiphanes* other red or red and transparent crustaceans are always to be captured in the deeper water-layers of the Scottish sea-lochs, such as *Calanus finmarchicus*, *Euchaeta norvegica*, *Conchoclea elegans*, *Boreophausia raschii*, *Pandalus annulicornis*, *Pasiphaea sivado*, *Crangon allmani*, *Hyppolyte securifrons*, etc. (see Murray, *Scot. Geogr. Mag.*, vol. iv. pp. 353-6, 1888; *Comptes rendus des Séances du 3me Congrès international de Zoologie*, Leyde, 1895, p. 107).

still visible; and (4) gonads also concealed by pigment when viewed from above.

For each of these varieties Broch has recorded the vertical distribution observed, as represented in the following table, the figures denoting the number of specimens found in each layer:—

Depth.	No. 1.	No. 2.	No. 3.	No. 4.
Surface
100 metres
250 " . . .	1
500 " . . .	17	4
750 " . . .	1	17	14	7
1000 " . . .	5	33	19	3
1250 "	1	2	4
1500 " . . .	1	9	6	4
2000 "	1

Even if the difference between Nos. 2, 3, and 4 is not strongly marked, the increase in dark pigment following the increase in depth is still very perceptible.

Another instance of this is afforded by the following table, showing the vertical distribution of eleven species of pelagic decapod crustacea, according to the results of Sund's examination of the "Michael Sars" decapoda:—

VERTICAL DISTRIBUTION OF THE ELEVEN MOST IMPORTANT SPECIES OF PELAGIC DECAPODA IN THE NORTH ATLANTIC
(the family Sergestidae excepted)

Serial Number	1		2		3		4		5		6		7		8		9		10		11	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Species . . .	<i>Franchalia woodwardi</i>		<i>Plesionika nana</i>		<i>Systellaspis debilis</i>		<i>Acanthephyra purpurca</i>		<i>Amalopenus tinneyi</i>		<i>Amalopenus vulcanus</i>		<i>Amalopenus elegans</i>		<i>Acanthephyra multispina</i>		<i>Acanthephyra Paraphaspisphaea sulcatifrons</i>		<i>Hymenodora gracilis</i>		<i>Amalopenus alicei</i>	
Colour of body	Transparent with pinkish tint		Transparent and red		Red, with blue luminous patches		Red, Eggs orange		Coralline, bright-blue patches		Coralline, bright-blue patches		Coralline, blue patches		Red, Eggs red		Red, Eggs red		Orange		Scarlet and orange, no blue	
Colour of eyes .	Black		Black		Black		Black		Dark brown		Brown		Brown		Black		Dark brown		Brown		Light brown	
Ratio of Carapace to eyes .	5.5		About 7		About 6.5		About 8		7.7		7.8		10.9		About 9.5		About 13		About 20		13.6	
Time of Catch .	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Surface
50 metres . . .	2	16	..	1	5	7	1	..	1
100 " . . .	2	17	..	10	2	57	1	19	..	7	..	42
150 "	12	..	22	16	74	2	102	..	12	..	7
300 "	1	..	1	20	3	3	31	..	5	..	1
500 " . . .	2	1	..	2	20	7	135	13	6	..	4	2	27	14	12	4	13	8
750 "	4	..	1	..	11	..	88	4	6	..	26	5	8	2
1000 " . . .	1	3	..	1	8	3	40	21	..	1	4	11	57	16	72	6	44	..	60	14	10	9
1250 "	1	2	3	1	20	1	5	..	12	30	10	17	..	17	5	22	16	1	33
1500 "	5	..	1	2	13	9	37	1	1	2	1	17	5	102	13	25	6	69	25	2	14
Over 1500 metres	3	..	8	1	1	1	1	4	1	1

The close correspondence between the development of pigment and the vertical distribution is very striking. Nos. 1 and 2 live above 150 metres, and are nearly transparent. Nos. 3 to 7 are distinguished by deep red colours with blue patches, and were taken above 500 metres during the night, but in the daytime have their maximum distribution at 500 metres or deeper. Nos. 8 to 11 have no blue pigment, but only red and yellow colours, and live deeper than 500 metres, not having been taken in less depths even at night.

As indicated in Chapter IX. the deep layers contain a great variety of animals, and in all these groups we repeatedly find the same dark colours. In the medusæ *Atolla*, *Periphylla*, *Crossota* we find dark-brown colours or, as in *Aglicera* and others, red colouring. Among the Sagittidæ we meet red colours (*Sagitta macrocephala*, *Eukrohnia fowleri*). All the crustaceans are red (*Euchæta*, *Cyclocaris*, *Gigantocypris*, Schizopoda, Decapoda); in the Pteropoda the colours are dark violet (*Peraclis diversa*, *Limacina helicoides*, *Clio falcata*). The squids are red, the fishes black or blackish violet.

Dark-coloured animals in the deeper layers.

In the Atlantic gray, mirror-like, and silvery colours are characteristic of the fishes between 150 and 500 metres. The silvery sheen is very often iridescent with dark green, violet, and blue tinges (see *Argyropelecus affinis* in Plate II.). The backs of these animals are brown or black. These colours correspond to those of the herring in boreal waters, and as previously mentioned they have been well known and recognized as protective colours. From above the fish are not easily seen because from this point of view the ocean looks dark or black. On the other hand, the light rays from above are reflected by the mirror-like sides of the body. From a position below the fish an eye would have great difficulty in distinguishing the outlines of the fish because of the rays coming directly from the source of light. This can only be understood when examining the fish in a living condition, for preserved fishes lose their silvery sheen very soon, generally turning black, and losing their original appearance. Most Scopelidæ have generally been represented as black, but many of them are really quite silvery (see Fig. 491, which, however, is not very good, because the silvery sheen does not come out well in this kind of reproduction).

Silvery and light-coloured animals in the shallower layers.

These remarks apply not only to the animals of this intermediate layer, but to many surface forms having a similar arrangement of colour. During our Atlantic cruise this was

especially conspicuous in the case of the minute young of *Scombresox* living at the very surface, the sides of which are mirror-like, while the back is not black, but intensely blue. This seems to correspond well to the fact that the uppermost layers of the ocean, viewed from above, appear blue. A similar arrangement of colour is met with in boreal waters, for instance in the colouring of the surface fish, the mackerel. The colours seem so intimately adapted to certain conditions, and the advantages they offer for the purpose of eluding observation are so obvious, that we can hardly avoid the conclusion that these colours must be considered as the result of adaptation to surroundings.

In the surface layers most animals are colourless. The eel larvæ (*leptocephali*) are specially interesting, being indeed so

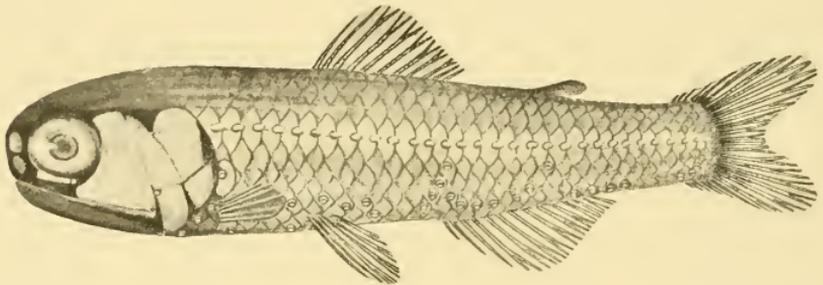
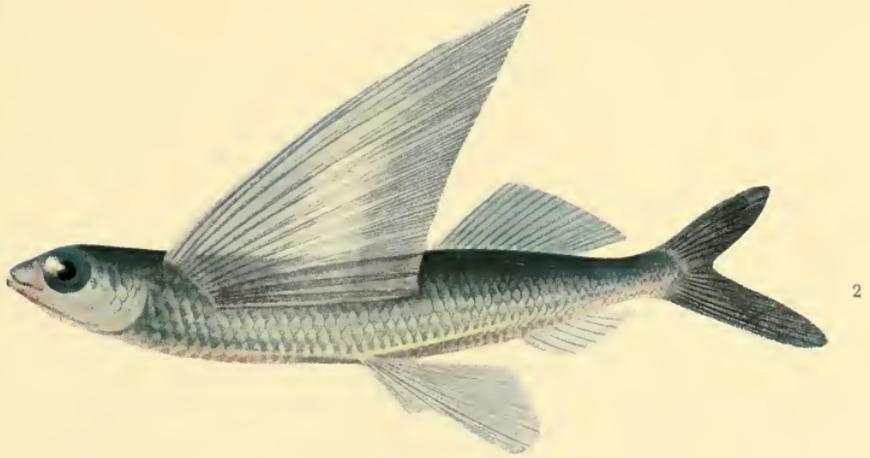
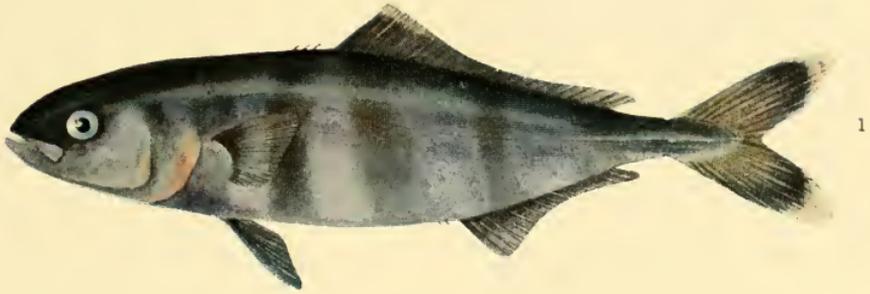


FIG. 491.

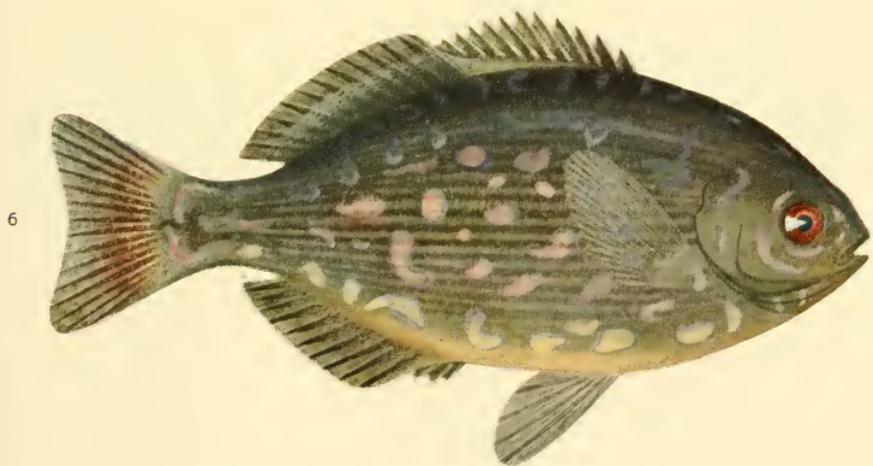
Myctophum (Diaphus) rafinesquei, Cocco. Nat. size, 7 cm.

transparent that when sorting them out of the living material captured, one can only see their small black eyes; even their blood is transparent and perfectly devoid of hæmoglobin.

The surface fishes are so well known that I may merely refer the reader to Plates IV. and V. One group containing sea-blue forms is represented by the flying-fish. The pilot-fish are also blue, but with some darker transverse bars. Is this because biologically it approaches another group of surface-forms, which live in the immediate vicinity of drifting or floating objects? To this group belong the wreck-fish (*Lirus, Polyprion*). We captured such fishes swimming around a log covered with barnacles, and the similarity between the colours of the fish and those of the log and its inhabitants was marvellous. The most intimate adaptations to life among drifting objects are met with among the animals of the Sargasso Sea (see Plates



1. *Naucrates ductor*, L.
2. *Exocoetus spilopus*, Val.



1. *Antennarius marmoratus*, Günth.
2. " "
3. *Monacanthus*, juv.

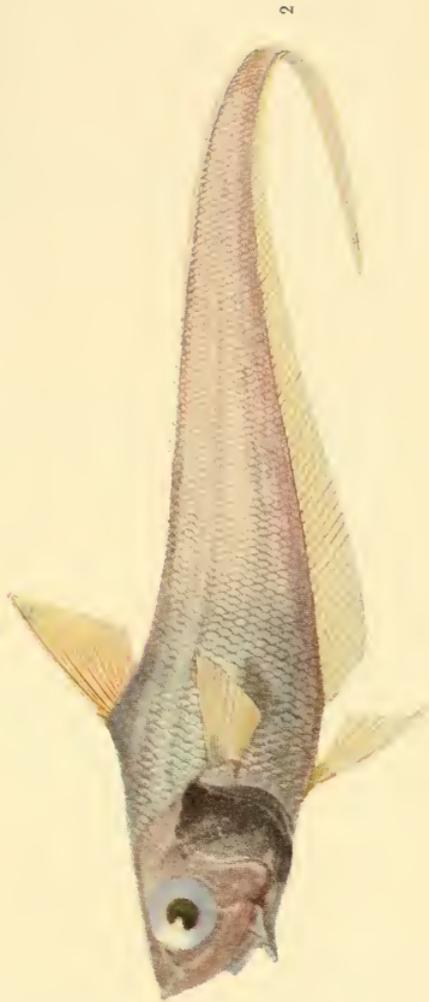
4. *Seriola*, juv.
5. *Syngnathus pelagicus*, Osbeck.
6. *Cyphosus boscii*, Lacep.



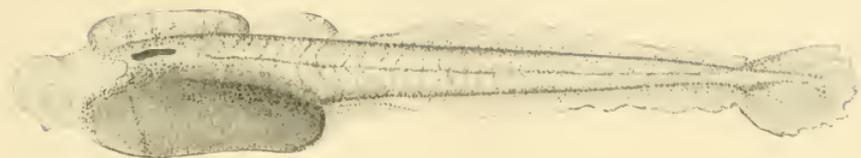
Planes minutus (L.)



1. *Dentex maroccanus*, Cuv. & Val.
2. *Pagrus vulgaris*, Cuv. & Val.
3. *Mullus surmuletus*, L.



1. *Chimæra mirabilis*, Coll.
2. *Macrurus æqualis*, Günth.



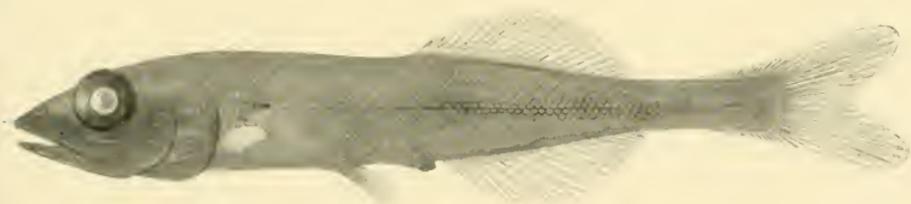
0.9 cm.



1.2 cm.



1.6 cm.



5.2 cm.

BATHYTROCTES ROSTRATUS

V. and VI.). The small fishes (*Antennarius marmoratus*, *Monacanthus*, *Seriola*, *Syngnathus pelagicus*), the crabs (*Planes minutus*), the prawns (*Latreutes ensiferus* and *Palæmon natator*), and also the naked snails, in fact all the animals of the Sargasso Sea, seem in regard to colours, shape (see for instance the remarkable prehensile organs of the pectoral fins of *Antennarius*), and size, to be intimately adapted to life among the drifting tufts of the Sargasso weed. The idea of the utility of these adaptations is here unavoidable. The occurrence of blue fins appeals to me as most striking, and this feature is specially noticeable in *Hippocampus* (the sea-horse). The specimen captured by us (see Fig. 71, p. 89) was reddish-brown, only the fins, which have to be freely moved in the blue water, being deep blue. Plate VI. shows five different specimens of the crab *Planes minutus*, exhibiting all the varieties of colouring presented by the Sargasso weed. This species ought to be a splendid object for experiments in order to test the possible effects of variation in the colour of the surroundings; *Antennarius* might possibly also be employed for this purpose, but on an expedition like ours the idea of performing such experiments had to be abandoned.

What I have said here refers mainly to the Sargasso Sea, which was examined by us in regard to the light-conditions at different depths, as well as the vertical distribution and the colouring of the animals. As to the animals of the coastal waters and those of the bottom of the ocean I have much less to say. In coastal waters the light-conditions are undoubtedly very different from those in the open ocean. The large amounts of suspended substances reduce the transparency of the water and prevent the light rays penetrating so far as they do in the clear tropical or subtropical ocean. Hermann Fol's interesting experiments at Nice have already been referred to (see p. 252); he went down in a diving dress as far as 30 metres, at which depth red animals appeared black.

Are the red, yellow, and blue colours of the coast-fish (as shown on Plate VII.) to be explained as protective colours? Are they adaptations to the red of certain algæ and other colours of the sea-bottom, like the gaudy paintings of the coral-reef fishes? Or are they to be considered like those adaptations which Darwin has ascribed to sexual selection?

Still more difficult is it to frame any idea as to the laws of colour in the abyssal region. Plate VIII. shows two bottom fishes from deep water, just on the limit where the traces of

sunlight disappear, viz. *Chimæra mirabilis* and *Macrurus æqualis*. Brown, blue, and violet are the principal colours of the abyssal fishes; very often the pupil of the eye is yellow, as in *Chimæra*. But has any eye at all the power of perceiving colours in the abyssal region? Is any other light present there than the light produced by the animals themselves?

In what has been said above I have compared the conditions of light and the colours of animals at various depths, and in every case we have had to acknowledge that there is some connection between the colours of the fauna and the light-intensity in the surrounding water. On the other hand it is in many cases difficult to show that the colours are actually protective colours, and many scientists have relinquished the idea that the colours are protective. The indisputable connection between light-intensity and peculiarities of colouring has been explained as resulting from a purely physiological process of assimilation. An interesting attempt in this direction has been made by Doflein,¹ who says: "In normal life certain gland-shaped organs in the higher decapod crustacea form pigments. The formation of these pigments is influenced by light. Feeble light is sufficient for the formation of red pigment. Under the influence of light and of still unknown processes of assimilation, the red pigment may be transformed into yellow or even into white pigment. Very little is known of the nature of the yellow and white colour substances, which may perhaps arise from a union of the pigment and other constituents of the body of the crustacean, for instance, the lime salts. The blue pigment is derived from the red under the influence of light, and dissolving passes into the tissues where it becomes colourless and disappears, evidently through the chemical processes into which it enters. The destruction of blue pigment occurs also under the influence of light, this substance thus being of a temporary nature, visible only when produced in great quantities, but under other conditions destroyed as soon as formed. This would explain the presence of red pigment in crustaceans living in deep water, and the lack of pigment in many pelagic crustacea, as well as the blue colours of oceanic forms. In the surface layers of the ocean the formation and destruction of pigment, under the influence of light, are in equilibrium. Small quantities of pigment indeed prove to be present in nearly transparent forms, but in the

¹ F. Doflein, "Lebensgewohnheiten und Anpassungen bei Decapoden Krebsen," *Festschrift für Richard Hertwig*, Bd. iii., Jena, 1910.

blue oceanic species, living in the intense light of the surface, the formation of blue pigment is so vigorous that it exceeds the destruction. Light is thus a very important agent in all these processes, bearing on the formation and transformation of pigment in the bodies of crustaceans, but it is not the only one. Other powers may equally influence the conditions of pigmentation. Experiments thus prove that when subjected to low temperatures blue colour developed in the animals; this was in my opinion due to the prevention of the destruction of the blue pigment in the tissues, thus causing an accumulation of this pigment."

I have quoted Doflein's theory because it opens up very interesting questions for future experimental research, though it hardly explains all the colour adaptations presented by the oceanic animals, for instance the mirror-like forms with dark backs and silvery sides, from intermediate layers, nor does it explain the profuse variation in the Sargasso animals and their peculiar conformity with the various colour-shades of the ocean and of the Sargasso weed. I fail to see any necessity for controversy over the two theories, one claiming the colours as due to adaptation serving the purpose of protection, the other explaining them as being due to peculiar processes of assimilation. Perhaps the latter theory alone may in many cases be sufficient, but may it not possibly signify the very mechanism by the aid of which the organisms adapt themselves in order to obtain protection?

A more perfect understanding can only be obtained from an increased knowledge as to the habitats of animals, as to the physical conditions there, and as to their life-history generally. The influence of various physical factors on the animals may be studied by experiment, and several interesting experiments have already been made. Gamble and Keeble, for instance, have proved the variations in colour of *Hippolyte varians* to correspond to variations in the colours of the surroundings. But the significance of such influences in the life of the animals can in my opinion only be understood by studying the life of the animals in nature.

LIGHT-ORGANS

That many organisms possess the power of emitting light has been known from earliest times. The Norwegian fishermen distinguish two kinds of phosphorescence: "dead phosphorescence" and "fish phosphorescence." The "dead

Phosphorescent light.

phosphorescence" resembles the stars in a clear sky, myriads of minute nearly invisible points emitting a scintillating light, now increasing, now decreasing, in intensity. The "fish-phosphorescence" appears like great dull bubbles of light which suddenly flare up, as if a dull electric lamp had been turned on and then extinguished, and is produced by large animals, fishes or squids, rushing through the water, sometimes, by the impetus of their movements, causing all the minute phosphorescent organisms to flare up intensely in response to the irritation produced. That the "dead phosphorescence" is also caused by living organisms has been recognised since time immemorial by fishermen and others who haul ropes or nets through the water at night. Very often small phosphorescent creatures, especially minute crustaceans, are captured and furnish proof that the light is not emitted by the water itself. But scientific men have not always recognised this, for Franklin believed that the phosphorescence of the sea was due to electric sparks caused by friction among the salts of sea-water. According to Steuer, the abbot Dicquemare is supposed to have filtered the sea-water and in this way proved that the water emitted no light. Later on microscopic examination of the minute organisms of the sea has finally proved that the emission of light is inseparable from living substance, and that it is restricted to certain organs built for the sole purpose of this peculiar function of life.

The power of emitting light is found in most groups of marine animals and plants, beginning with the bacteria. Among plants the peridineans and the remarkable ball-shaped flagellates, *Noctiluca miliaris* and *Pyrocystis noctiluca*, are noted for their power of emitting light. In animals this power is always attributed to certain structures, which may be said to represent all conceivable forms of glandular development, from simple epithelial membranes to more or less complicated tubular or lobular glands. These organs secrete a slimy luminous substance. As a rule a layer of black pigment is arranged around the gland, acting as a reflector. Very often the light is projected through a transparent lens-shaped organ. The light-organs thus very often resemble minute eyes, and were previously supposed to perform the function of perceiving instead of emitting light. As we reach the more highly organised groups in the animal kingdom the structure of light-organs exhibits an increasing complexity. In minute crustaceans (see Fig. 492) we very often find only a

single row of luminous cells in the usual epithelium, and a lens formed by the cuticula or chitinous layer of the epidermis. In squids and fishes the organs are very complicated, as we shall presently see.

The object of the "Michael Sars" Expedition being mainly the investigation of the distribution of animals, the examination of the collections has necessarily been limited to the determination of the species, and my contributions to this fascinating section of the science of marine life will largely consist in discussing the distribution of animals possessing light-organs, which occur in salt water only, for no luminous animals are known from fresh water and no phosphorescence occurs there.

Glandular, clearly defined, and localised light-organs are found mainly in pelagic animals. Among bottom animals from the coast banks luminosity is exceedingly rare, but on the other hand, many bottom animals have been brought up from the abyssal region in a luminous condition, and have continued to emit light when placed in dark surroundings on board (see Fig. 70, p. 88, representing a luminous umbellularian). No special luminous structure has been found in these cases, the luminosity being attached to the surface epithelium. As regards fishes, Günther has drawn attention to the fact that many deep-sea forms secrete a large amount of slime. The heads of

many deep-sea Macruridæ exhibit certain pits and channels, which produce great quantities of slime. This slime is supposed to be luminous, and to perform the function of ordinary glandular light-organs, which last are found only in a few fishes supposed to live along the bottom, for instance, sharks (Spinacidæ, *Spinax niger*), and even in these they occur only as isolated organs, not in such numbers as in the genuine luminous fishes.

Among the pelagic fishes of the coast banks no species is known to possess light-organs; neither the herrings nor the mackerels have any representatives with light-organs. As shown in Chapter IX. there is not a single independent pelagic fish-species in the northern boreal waters, and as a consequence no boreal pelagic fish-species possesses light-organs.¹ A minute examination of the lower forms has never been made, and at

Light-organs found principally in pelagic animals.

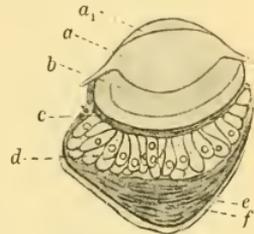


FIG. 492.

Light-organ of *Sergestes chalcengeri*, H. *a*, lens of the chitinous cuticle; *b*, inner lens; *d*, glandular cells; *e*, reflector; *f*, cover. (After Hansen, from Steurer.)

¹ I regard the Scopelidæ in the Norwegian Sea as visitors, and not as true boreal forms.

present it is probably impossible to lay down any rules relating to them.

If we take into account the exceptions here mentioned, we arrive at the result that in the higher groups, viz. squids and fishes, special light-organs are known mainly in oceanic forms belonging to warm areas.

Among the fishes the luminous forms are mostly found in the families Stomiatiidæ, Sternoptychidæ, Scopelidæ, and Ceratiidæ.

Luminous fishes.

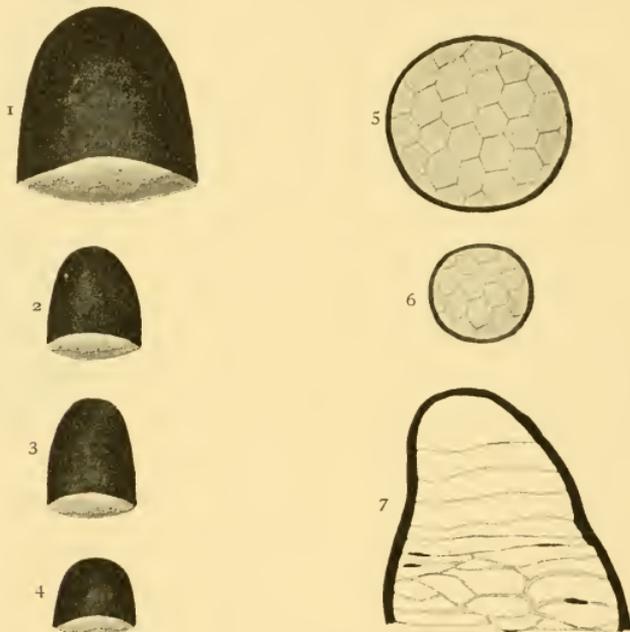


FIG. 493.

1. The largest photophore from the ventral series between the pectoral and the ventral of *Cyclothone signata*, Garm., and *C. signata alba*, A. Br.
2. The largest photophore from the ventral series between the pectoral and the ventral of *Cyclothone microdon*, Günth., and *C. microdon pallida*, A. Br.
3. The largest photophore from the ventral series between the pectoral and the ventral of *Cyclothone livida*, A. Br.
4. The largest photophore from the ventral series between the pectoral and the ventral of *Cyclothone acclinidens*, Garm.
5. The largest photophore from the ventral series between the isthmus and the ventral of *Cyclothone signata*, Garm.
6. The smallest photophore from the ventral series between the isthmus and the ventral of *Cyclothone signata*, Garm.
7. Reflector cells of a photophore from the ventral series of *Cyclothone microdon pallida*, A. Br.

(After Brauer.)

After carefully examining the specimens belonging to these groups captured by the "Valdivia," Brauer pointed out that a certain regularity in the arrangement of the light-organs seems

to correspond with different depths, and that the light-organs are not peculiar to the deepest and darkest water-layers. Previously this belief was generally adopted because the light-organs were looked upon as a means of illuminating the dark abyssal region. Brauer indicates that of the six species of *Cyclothone* five are black and live in deep water, while one species (*C. signata*) is grey, lives in much shallower water, and has by far the largest light-organs (see Fig. 493, showing the small light-organs of the dark forms and the large ones of *C. signata*). Of the Scopelidæ, the surface forms of the genus *Myctophum* (s.s.) possess the largest light-organs, while the sub-genus *Lampanyctus*, taken in closing-net hauls by the "Valdivia" between 800 and 600 metres, has very small light-organs.

If now we consider the captures of the "Michael Sars," and the vertical distribution of the fishes previously described, we see that our experience confirms Brauer's views. *Cyclothone microdon* with small light-organs was found much deeper than *C. signata* (see Plate I., showing these two forms, the difference between their light-organs being easily observed). Of special interest is Fig. 490, showing the vertical distribution of five black fish-species, two of which (*Gastrostomus bairdii*¹ and *Cyema atrum*) have no light-organs;

Gonostoma grande has very small light-organs, while those of *Gonostoma rhodadenia* and *Photostomias guernei* are large (see Plate II., showing the two species of *Gonostoma*, Fig. 67, a, p. 86, representing *Photostomias guernei*, and Fig. 494, showing a light-organ of *Gonostoma rhodadenia* magnified). Besides these we found in our deepest hauls many forms without light-organs, for instance, species belonging to the genera *Aceratias*, *Melamphaës*, *Cetomimus*.

Light-organs are, therefore, specially characteristic of fishes belonging to the upper 500 metres in warm oceanic waters.

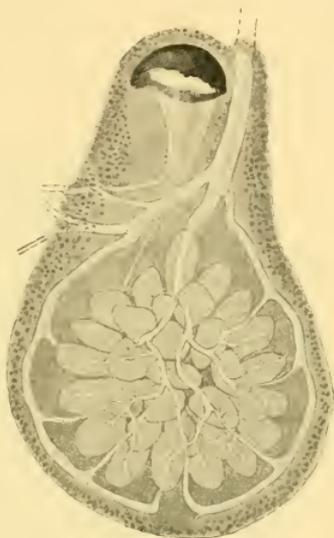


FIG. 494.
Gonostoma rhodadenia, Gilb. Photophore
from upper lateral series (♂♂).

¹ On the tip of the tail this species is provided with an organ, the function of which is unknown; it has been regarded as a light-organ, but this does not alter our view.

Our contribution to the knowledge of this subject consists mainly in determining the vertical distribution of the silvery

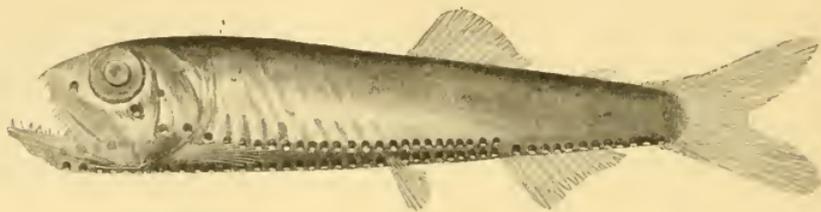


FIG. 495.
Vinciguerria lucetia, Garm. Nat. size, 4 cm.

luminous Sternoptychidæ and Stomiatiidæ more exactly than had previously been done (see Fig. 478, p. 629, showing the vertical

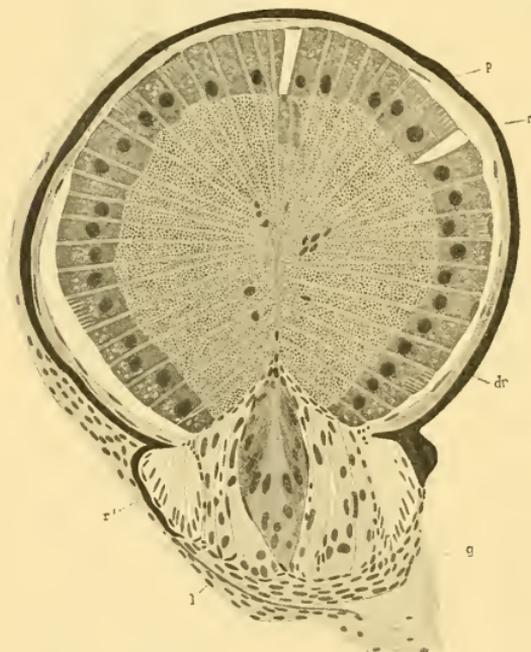


FIG. 496.

Light-organ of *Vinciguerria lucetia*, Garm., from ventral series of body (about $\frac{3}{4}$). *dr*, glandular cells; *L*, lens; *r*, reflector; *p*, black pigment. (From Brauer.)

distribution of some of the most peculiar luminous fishes). Fig. 495 represents one of these, *Vinciguerria lucetia* with its numerous powerful light-organs, the structure of which, according to Brauer, is shown in Fig. 496, where we see the black pigment behind the reflector, the gland, and the lens (see also Fig. 493, 7, which shows a section through the light-organ in *Cyclothone*).

Splendid light-organs have also been discovered in squids, and Chun has described them in many species (see

Fig. 434, p. 590). These forms are entirely pelagic. The Octopoda, being bottom animals, possess no light-organs. In the large group of squids light-organs have also been found in

species which live in intermediate depths, and are now and again, like the Scopelidæ, captured at the surface (see p. 649).

The function and importance of the light-organs in the life of animals have been subjects of controversy in the world of science. The production of light has been explained as a simple consequence of metabolism, and it has been supposed that the light itself serves no purpose. Comparisons have been drawn between the accumulation of mucous substance and the mucous secretion of the light-organs, and it has been pointed out that these organs occur particularly in pelagic animals, which in order to float in the water are supposed to need the mucus for the purpose of reducing their specific gravity. Brandt, who has studied the adaptations of animals to pelagic life, is perhaps right in supposing that metabolic factors have played a part in the history of the development of light-organs, but a closer scrutiny of the structure of these organs, and particularly the discovery of reflectors and lenses, seem to place it beyond doubt that the light-organs serve the function of projecting light in definite directions. This is the function for which the higher animals use their light-organs, but for what purpose do they project light? Is it in order to illuminate the surrounding water, to avoid foes, or to recognise their own kind? These questions are not easy to answer with any certainty. At all events the answers would probably tend to show that the many different kinds of light-organs serve different purposes. For instance, the large light-organs carried on the tentacles of the Ceratiidæ are probably used for other purposes than the smaller organs found in *Vinciguerria* on the side of the body.

Function of
light-organs.

Brauer has examined the position of light-organs in relation to body segments in different species, and has found them to be arranged in exactly the same manner in all individuals belonging to the same species, and consequently the number and position of the light-organs are specific characters. He advocates the idea that in the ocean the light-organs replace the specific colour-markings of terrestrial animals.

Light-organs
as specific
characters.

Is it possible to explain the peculiar geographical distribution of luminous animals, for instance, fishes? The fact that light-organs are found only in marine animals has been explained by supposing the salt to be necessary for the production of light. Experiments have shown that luminous bacteria develop and emit light only when sodium chloride or calcium chloride is present. As regards those organisms which secrete a slime

that only becomes luminous on the surface of the animal, the phosphorescence seems to present an analogy or likeness to certain chemical reactions, for instance, the slow oxidising of organic compounds (grape sugar, etheric oils), which are accompanied by a feeble emission of light. In higher specialized organs chemical processes of a more complex nature probably take place. From the structure of the organs we may be induced to believe that the development of the organ must have depended on the fact that its function was intended to be seen by an eye. The light emission must evidently be of vital importance to the life of the animal and to the maintenance of the species. The discussion of these questions must therefore be postponed until we have mentioned the eyes of the different animals.

EYES

Nothing has appeared more hopeless in biological oceanography than the attempt to explain the connection between the development of the eyes and the intensity of light at different depths in the ocean. In a trawling from abyssal depths in the ocean we may find fishes with large eyes along with others with very small eyes or totally blind. Nowhere would a more perfect uniformity be expected than in the dark and quiet depths of the ocean. Brauer, who has given a valuable contribution to our knowledge of the eyes of deep-sea fishes, remarks in his treatise on the fish collections of the "Valdivia" Expedition: "If the surroundings really acted directly on the organisms, and were the only agents which could produce alterations, their influence would be much more uniform and general. Instead of this we find the greatest variation. Thus we find the eyes now altered or permuted, now highly differentiated even in closely related forms."

The conditions, however, where these different forms live, are not so uniform as was supposed, or rather, these forms do not really live under the same conditions. First of all it made a great difference when we learnt that certain fishes were bottom dwellers and others pelagic in their habits.

Most, if not all, bottom dwellers from abyssal depths have large eyes, very often larger than those of bottom fish living in the strong light of the coast banks. Perhaps there is a maximum in the development of eyes in bottom fish at a certain depth followed by a decrease in size as we proceed still deeper. But even the deepest living forms, which must be supposed to

Variation in
the size of
the eyes.

migrate all over the abyssal plain of the oceans, have very large eyes, the diameter of the eyes in *Macrurus armatus*, for instance (see p. 417, and Fig. 272, p. 398), being equal to one-fifth of the length of its large head.

As regards pelagic fishes we must remember that light penetrates to far greater depths than was previously supposed, for, as already stated, in the Sargasso Sea photographic plates were strongly acted upon by light at 500 metres, and at 1000 metres traces of light were clearly perceptible, so that at least certain components of the sunlight penetrate to that depth.

If we now review the size of the eyes of the fishes in relation to their vertical distribution, we notice a strange change just about the bathypelagic limit often referred to in this book, viz. 500 to 750 metres, varying according to latitude.

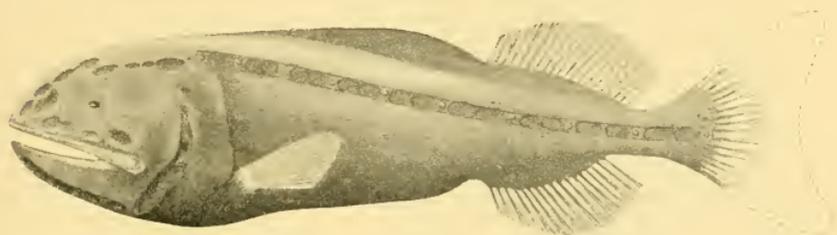


FIG. 497.
Cetomimus storeri, G. and B. Nat. size, 12 cm.

In the fish taken between 150 and 500 metres the diameter of the eye compared to the length of the head is, according to Brauer, as follows:—

<i>Stomias</i>	about 1 : 4	<i>Argyropelecus</i>	about 1 : 2
<i>Chauliodus</i>	„ 1 : 4	<i>Sternoptyx</i>	„ 1 : 2
<i>Ichthyococcus</i>	„ 1 : 2.6	<i>Opisthoproctus</i>	„ 1 : 4
<i>Vinciguerra</i>	„ 1 : 3		

If we consider *Cyclothone* and other fish which live deeper than 500 metres we find the following relations:—

<i>Cyclothone signata</i>	1 : 12 (see Plate I.)
„ <i>microdon</i>	1 : 12 (see Plate I.)
„ <i>obscura</i>	1 : 15 or 20,

and if we inspect the figures representing *Gastrostomus bairdii* (Fig. 83, a, p. 97), *Cyema atrum* (Fig. 69, p. 87), and *Gonostoma* (Plate II.), we obtain a still stronger impression of the small size of the eyes. Finally our deepest pelagic hauls contained blind forms which have never been taken in the upper layers; I reproduce two of these blind fishes (Figs. 497 and 498), of

which *Cetomimus storeri* has been taken before, while the other form will probably have to be referred to a new genus. It is



FIG. 498.

New blind fish, resembling *Cetomimus*, from Station 64. Nat. size, 6 cm.

also interesting in this connection to note that the only blind squid known was taken during our cruise at Station 82 in 1500 metres. Chun has called it *Cirrothauma murrayi* and has shown that its eyes are entirely concealed below the skin (see Fig. 499).

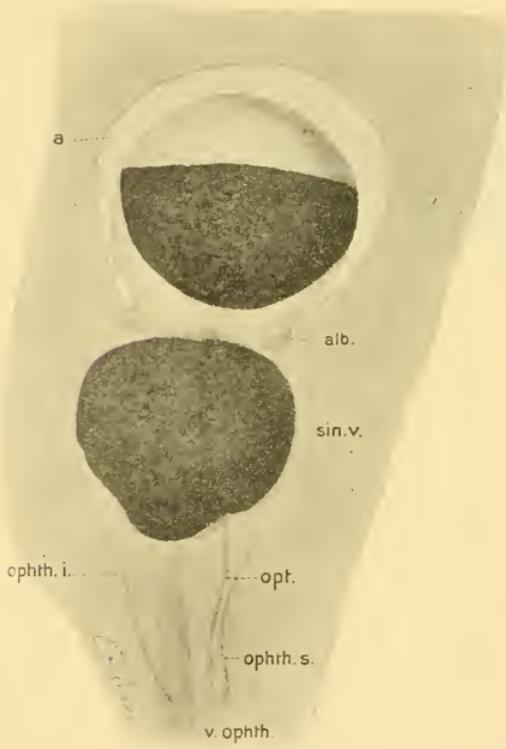


FIG. 499.

Rudimentary eye of *Cirrothauma murrayi*. (From Chun.)

There is consequently no doubt that as far as fishes are concerned, there is in the ocean a limit between an upper region down to 500 metres, where the pelagic fishes have large and well-developed eyes, and a lower region where imperfect organs of vision are typical. The only exception to this rule I can think of is that a few fishes, mainly belonging to the genus *Melamphaës* and having large eyes, were taken

in our deepest hauls beyond 1000 metres. Brauer remarks that in *M. mizolepis* he has found great variation in the relation of the diameter of the eye to the length of the head (from

1:5.2 to 1:7), and he imagines this to be due to differences in age. In the other species of this genus at all events the relation is usually 1:7 or 8. Further investigations are necessary to explain these relations.

Malacosteus also has a relatively large eye, but in this genus as well as in other Stomiatiidæ we must suppose that important vertical migrations occur. Thus we see from the table (Fig. 490) that *Photostomias guernei* has been captured at night in comparatively shallow water, and its eyes are considerably larger than those of the fishes which constantly live at great depths (see Fig. 67, a, p. 86).

The pelagic decapod crustacea show a similar correspondence between the development of eyes and vertical distribution (see table, p. 668). In the two species living above 150 metres the ratio of carapace to eye is 5-7, and in the five species with a maximum distribution about 500 metres the ratio is 6-11, while in the four species living below 500 and mostly beyond 1000 metres the ratio is 9-20.

Although in fact many cases as yet seem inexplicable, there seems to be reason for supposing that the efficiency of the eyes decreases with the decreasing intensity of light as we descend into deep water. That we cannot fully explain all cases seems to be a natural consequence of the fact that our knowledge of the vertical distribution of pelagic fishes is still imperfect, being based mainly on the closing-net hauls of the "Valdivia" and the long horizontal hauls of the "Michael Sars," and both these expeditions were of very short duration. Further investigations will probably furnish many interesting details as to differences within the regions recognised by us, for we are aware that various kinds of eyes occur in the region above 500 metres, such as stalked eyes, telescopic eyes, as well as eyes built on the principles of the common type of fish eye.

Stalked eyes seem to be peculiar to larval stages, and in certain cases are known to develop into normal eyes even during the larval stage (Lo Bianco). They seem to occur only in the uppermost layers, where all transparent fish larvæ live. Considering the insufficiency of our knowledge of the development of pelagic fishes, I do not venture to guess to what species our stalk-eyed larvæ belong.

Telescopic eyes are found only in fishes from depths less than 500 metres. We have observed them in *Argyropelecus*, in a new genus closely related to *Dysommia* (see Fig. 540, p. 746), in *Opisthoproctus*, and also in leptocephali. Fig. 500 represents

an *Argyropelecus* seen from above, and we see that the eyes point upwards, which is probably the case in most fishes possessing telescopic eyes, even if exceptions occur.

Two interesting facts go to explain this peculiar adaptation. Firstly, these telescopic eyes occur only in fishes which are very bad swimmers, fishes which practically only float in the water-layers. Secondly, the light-measurements in the Sargasso Sea showed that the light-rays acted more strongly on the top plate than on the side plates; for fishes possessing small swimming capacity the telescopic eyes seem to be most perfectly adapted to receive the faint rays of light which penetrate to these dusky depths.

Among eyes built on the general principle the difference in size first commands attention when the vertical penetration of light and the vertical distribution of each species come to be investigated. As regards the upper layers, an interesting subject will also be found in the detailed study of the anatomy of different eyes. In the retina of the human eye two special kinds of sensory cells are known to occur, viz. "rods" and "cones." These cells occur also in the eyes of fish from the surface layers. From Brauer's investigations we know that in all deep-sea fishes, as well as in silvery fishes from about 300 metres, only the "rods" are found in the retina of the eye. According to an old maxim of Max Schultze, nocturnal animals possess only "rods" while diurnal animals have both "rods" and "cones." It has therefore been generally believed that the "rods" alone possess the faculty of observing light-intensity, light and shade, while only the "cones" perceive colours, quality of light.

Further, an interesting difference has been found in the colour-substance or pigment of the retina by day and by night. Brauer has also found that these conditions in the eyes of deep-sea fishes signify that their eyes are constantly adapted to nocturnal conditions. The deep-sea fishes are "nocturnal animals" and "day-blind." But the gradual development of these peculiarities from the surface to the bottom, from the



FIG. 500.
Argyropelecus hemigymnus,
Cocco. Head seen from
above, enlarged.

larval stages living at the surface to the adult fishes of the deep sea, presents a vast field for future research and opens up a vista of possibilities, which may explain the adaptation to special surroundings peculiar to each species.

Investigations in the deep regions below 500 metres should evidently, first of all, attack the questions whether a regular decrease in the size of the eye occurs with increasing depth, and whether the number of blind species and blind individuals is not far greater than is generally supposed. Our pelagic hauls only exceptionally went below 1500 metres, but nevertheless we found in the deepest hauls no less than three species of blind fishes, of which two were new to science, besides one blind squid. In the deep oceans, where the depth exceeds 5000 or 6000 metres, we might perhaps expect interesting discoveries if large and efficient appliances were towed after the vessel with 5000 or 6000 metres of wire out.

But if it be the case that the size of the eyes in pelagic fishes decreases vertically with the decreasing intensity of light, how can we explain the fact that the bottom-fishes, like *Macrurus armatus*, living in abyssal depths possess large and apparently well-developed eyes? In order to explain this, the possible existence of a source of light other than sunlight has been sought for, but nothing has so far been discovered beyond the light produced by the organisms themselves. We shall therefore have to consider at the same time the power of emitting and the power of perceiving light possessed by the animals, so that we must take their light-organs as well as their eyes into account.

From what has been said we see that a remarkable coincidence exists between the development of light-organs and eyes in pelagic fishes. The Scopelidæ, Sternoptychidæ, and Stomiatidæ, which live above 500 metres, possess well-developed light-organs and eyes, while from 500 metres downwards light-organs and eyes both decrease in size.

Along the sea-bottom, however, the fishes possess only eyes and no special light-organs. We have previously seen that the invertebrates are luminous even in abyssal depths, and at present the large eyes of the bottom fishes cannot be explained otherwise than by supposing that the light emitted by the invertebrate bottom animals is so strong that objects on the bottom may be seen by the eyes of fishes. As regards most of the bathypelagic fishes we may, on the other hand, suppose that they have little use for eyes, because pelagic life in great depths is scanty, and not so definitely localized as on the sea-bottom.

Large eyes in
abyssal fishes
from the sea-
bottom.

Abyssal
bottom fishes
have eyes but
no light-
organs.

These are the explanations offered at present, but they open up new questions. How is it possible, for instance, for the bathypelagic fishes to find their food in the dark, sparsely populated, water-layers? Clearly we can advance no farther in this field without more knowledge gathered from new and extensive investigations. Even with our present knowledge, and accepting the explanations given as perfectly correct, many questions arise in regard to details. I will mention one very interesting instance.

During the "Challenger" Expedition some specimens were captured of a certain blind fish (*Ipnops murrayi*), which was taken in the trawl only at great depths, between 3000 and 4000 metres. As already mentioned, the "Michael Sars" also captured a small blind fish, apparently a near ally of *Ipnops*, which we have called *Bathymicrops regis* (see Fig. 305, p. 416). *Ipnops* and *Bathymicrops* both belong to the family Scopelidæ, and among allied forms we find a remarkable series in respect to the development of the eyes. This series has been represented in Fig. 501, *a* to *e* :—

a represents the head of *Chlorophthalmus productus*, Gthr., taken at Fiji in 575 metres.

b represents the head of *Bathypterois dubius*, Vaill., taken by the "Talisman" at the Canaries, and by the "Michael Sars" at Station 41 between 843 and 1635 metres.

c shows the head of *Benthosaurus grallator*, G. and B., taken off America, and by the "Michael Sars" at Station 53 in about 3000 metres.

d shows the head of *Bathymicrops regis*, n.g., n.sp., taken by the "Michael Sars" in about 5000 metres.

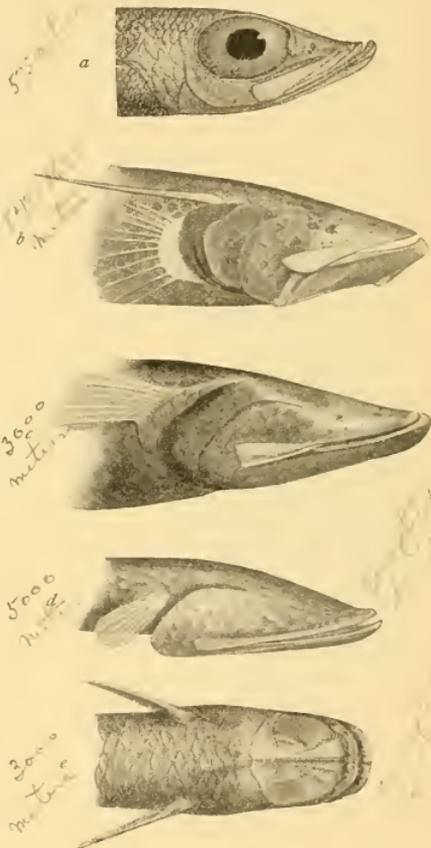


FIG. 501.

DEVELOPMENT OF EYES IN SCOPELIDS.

Pelagic fishes
living near
the bottom.

e represents the head of *Ipnops murrayi*, Gthr., taken by the "Challenger" in about 3000 metres.

a shows a "normal" eye like the eyes of bottom-fishes on the slopes of the coast banks; *b* and *c* exhibit very small eyes; finally, *d* and *e* are perfectly blind. In *Bathymicrops* the whole head is covered with scales, including the eyes, which are only faintly visible through the covering as minute black dots. In *Ipnops* the head is covered with filmy bony plates, and eyes are entirely absent. A peculiar organ, which has been regarded as a light-organ, is situated below the plates, and supposing this interpretation to be correct it is the only light-organ known in these forms.¹

How is this series of remarkable forms to be arranged conformably to the biological classification of the fishes according to their light-organs attempted above? They have all been taken only in the trawl, but are they really bottom fish? Why then (if we may be allowed the expression) do they not all possess large eyes, like other bottom fish living at similar depths? On the other hand, we must admit that they all differ from pelagic fishes in appearance. Most bathypelagic fishes are black, and their scale covering is but poorly developed.

As a "working hypothesis" I would suggest that these fishes belong to the deepest water-layers near the ocean-floor, and for this reason they unite qualities characteristic of both bottom fishes and pelagic fishes. The fact that they belong to the family Scopelidæ seems to strengthen this view, as this family comprises such a wealth of pelagic forms. Several of these fishes, as for instance *Benthosaurus grallator* (Fig. 502), are also provided with long filaments or whip-like appendages indicating pelagic habits; to the south of the Azores we took some splendid specimens, in which these appendages, really transformed fin-rays, were intact, as seen in the figure.

Another problem attaches to the remarkable fact, previously mentioned, that light-organs are lacking in all pelagic fishes of the coast waters and also of the boreal area. Neither are they found in the fishes of tropical coast waters, where the temperature cannot be supposed to prevent their development, nor do they occur in those of the Norwegian Sea, where the depth is sufficient

Pelagic fishes
of coast
waters and
of the
boreal area.

¹ Sir John Murray and Professor Moseley at first described these organs as modified eyes, — without lens or vitreous humour, and with only rods arranged in hexagonal bundles in the retina. Later Moseley stated they were certainly not eyes, but phosphorescent organs (see Manchester Science Lectures, Dec. 18, 1877, p. 132; Narr. Chall. Exp., vol. i. p. 239, 1885; Zool. Chall. Exp., Part LVII. Appendix A, 1887).



to enable us to find all degrees of light-intensity, at all events during summer. *Paraliparis bathybi*, the large black bathypelagic fish found by us in the Norwegian Sea (see Fig. 107, p. 127), possesses well-developed eyes, although it lives in deep water and undoubtedly in surroundings just as devoid of daylight as does *Cyclothone microdon*. The same remark applies to *Rhodichthys regina*.

Is it the rich phosphorescent pelagic fauna peculiar to the coast waters and the boreal area which renders light-organs useless and eyes useful to the fishes of these regions? Is it the case that the peculiar light-organs and the wonderful eyes can develop only in warm oceanic waters of low specific gravity? Are all these features only special adaptations to special and definite conditions, like the splendid colours of animals in tropical lands? Are the small light-organs and the minute organs of vision peculiar to the deep, dark, and cold oceanic waters only rudimentary organs, which are no longer of vital importance to the fishes? Are they to be considered as evidence that these fishes are descended from ancestors living under entirely different conditions in lesser depths?

FLOATING AND ORGANS OF FLOATING

If organisms did not possess the power of floating; thus preventing them from sinking into deep water, the ocean would become a lifeless desert, because in the surface layers of the ocean live the minute plants which form the source of nourishment for all animals in the various depths of the ocean.

In order to understand the faculty of floating possessed by

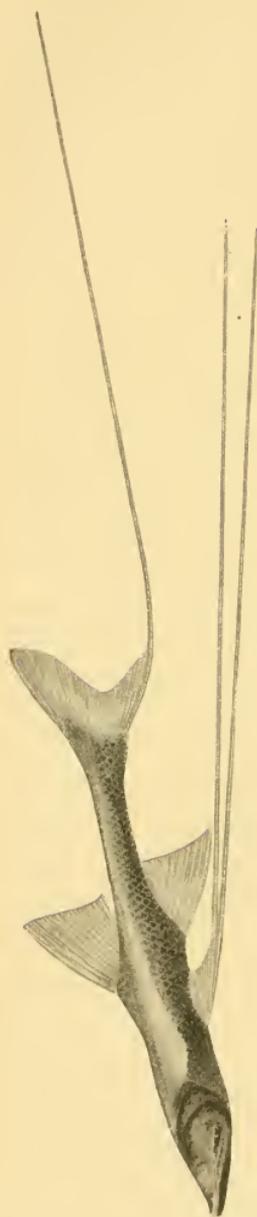


FIG. 502.
Benthosaurus gallator, G. and B. Nat. size of fish without the prolonged fin-rays, 32 cm. Station 53.

various organisms, we must first of all become acquainted with the external conditions governing floating and sinking; mainly owing to the investigations of Chun and Ostwald our knowledge on this point has increased greatly in recent years.¹

First and foremost among these conditions is the specific gravity of ocean water. If an organism has the same specific gravity as the sea-water it floats, because, according to the law of Archimedes, it displaces a volume of water equal to its own weight. When the specific gravity of the organism is greater than that of the water it has a surplus gravity and may possibly sink. If nothing counteracts its sinking, the velocity will be proportionate to the value of the surplus gravity (equal to the specific gravity of the organism minus the specific gravity of the water).

Specific gravity of the water.

Experience shows, however, that all objects of the same specific gravity do not sink with equal velocity. Fine sand particles float much longer in water than large pebbles, although they have the same specific gravity. This is due to a property more or less peculiar to all liquids, called the viscosity or the internal friction of the liquid, but in a liquid with a definite viscosity objects sink with varying velocity, which depends on what has been termed the surface resistance of bodies.

Viscosity of the water.

An object has a great surface resistance, and sinks slowly, when its surface is large compared with its volume, and when its surface presents a large area at right angles to the direction of the sinking.

Surface resistance of bodies.

Surplus gravity and surface resistance are the two properties in sinking bodies which determine the velocity of their sinking. The greater their surplus gravity and the smaller their surface resistance the greater is the velocity of their sinking. High specific gravity and great viscosity of the water counteract the sinking and require lower specific gravity and less surface resistance on the part of the organisms in order to keep them floating.

We will first consider the two "external conditions," the specific gravity and the viscosity of the water, and then discuss the faculty of regulating the surplus gravity and surface resistance possessed by the organisms, enabling them to adapt themselves to their surroundings. The importance of the two elements, specific gravity and viscosity, anywhere in the ocean

¹ See, for instance, Chun's *Reisebericht* (*loc. cit.*); W. Ostwald, "Theoretische Planktonstudien," *Zoologische Jahrbücher*, Abtg. Systematik, etc., Bd. 18, Jena 1903; "Zur Lehre vom Plankton," *Naturwissenschaftliche Wochenschrift*, N.F., Bd. 2, Jena, 1903.

depends first of all on the salinity and temperature, but the influence of salinity and temperature is essentially different in regard to specific gravity and to viscosity. This fact is easily seen from the following table, compiled from Knudsen's tables for specific gravity and from Ostwald's measurements for viscosity :—

Temperature C.	Viscosity.		Specific Gravity.	
	30 ‰ Salinity.	35 ‰ Salinity.	30 ‰ Salinity.	35 ‰ Salinity.
0°	102	103	24.11	28.13
5°	87	88	23.75	27.70
10°	75	76	23.09	26.98
15°	66	66	22.16	26.00
20°	58	59	20.99	24.79
25°	52	53	19.61	23.37
30°	47	47	18.02	21.76

We see from this table that within the common limits of salinity, 30 to 35 per thousand, the salinity influences viscosity very little; in other words, viscosity is almost entirely dependent on temperature. If the viscosity of pure water at 0° C. is placed at 100, ordinary sea-water at 0° C. has a viscosity of 102-103; at 10° C. it has decreased by one-fourth, and at 25° C. by one-half. Sea-water at 25° C. is only half as viscous as the same water at 0° C., that is, the same body sinks twice as rapidly at 25° as at 0° C. Variations in salinity alone, it will be observed, influence the specific gravity as well as variations of temperature. In the ocean specific gravity and viscosity therefore do not run parallel, but they run in the same direction. Thus a body, which can maintain its specific gravity independent of changes in temperature and salinity, will have its velocity of sinking increased with falling specific gravity and viscosity of the sea-water, and its floating faculty will be augmented when viscosity as well as specific gravity increase.

Osmotic
pressure.

Temperature, and especially salinity, influence the floating faculty of living bodies, through changes in osmotic pressure. If the salinity of a cell is higher than that of the surrounding water, the cell will, if not surrounded by an impermeable membrane, give off salt and absorb water. The volume of the cell will then increase, but although the cell actually increases in weight, its specific gravity will decrease. In

salter water, on the other hand, such a cell will give off water ; its volume will decrease, and it will attain a higher specific gravity. These alterations will, however, react on the surface resistance of the cell and influence its relations to the viscosity of the water, as we shall subsequently see.

These three elements—specific gravity, viscosity, and osmotic pressure—constitute the external conditions governing the faculty of floating at different depths. Ostwald has in various ways attempted to explain many of the peculiar features of pelagic organisms. He cites instances from interesting experiments made by Chun, Verworn, and Brandt, showing how organisms decrease in size and volume with increasing salinity, when sea-water evaporates in open vessels. The animals sink when the sea-water is diluted with fresh water, and rise towards the surface when the salinity increases. After some time the difference in osmotic pressure becomes adjusted, so long as the difference between the cell and its surroundings has not been too great. These ideas due mainly to Chun and Ostwald have, during recent years, largely stimulated the scientific world to study the influence upon organisms of variations in the external conditions.

All groups of pelagic plants and animals are now known to have a wonderful power of adaptability pertaining to their faculty of floating in surroundings of varying specific gravity, viscosity, and osmotic pressure. As regards the pelagic plants, Gran has in Chapter VI. mentioned some important and characteristic instances of the alterations in shape to which certain plants are subject in various waters. When dealing with the various groups of pelagic animals I mentioned a few instances of the differences in the general characters of the animals as to shape, size, and appearance in warm and cold waters.

The various means adopted by different organisms in order to increase their faculty of floating may perhaps be classified as follows :—

(1) Certain organisms seek to diminish their specific gravity by secreting and depositing specifically light substances in their cells. A very important part is here played by the fats and oils, which are also of enormous importance as a reserve food for the animals in question. From the radiolarians to the whales, the fats are of great significance to pelagic life. In the crustaceans, for instance the northern *Calanus finmarchicus*, in fish eggs, which frequently possess oil-globules, in fishes and in pelagic mammalia, the fats are specially important.

Floating devices.

Secretion of fat.

Absorption
of water.

Numerous forms absorb water to such an extent that their water-contents may amount to 90 per cent of the whole organism, as in the medusæ, ctenophores, and many fish eggs. In fish eggs chemical analysis shows how the amount of water decreases during development, and how this decrease continues as the larvæ seek deeper water and finally settle on the bottom. Salpæ and Pyrosomidæ with large soft integuments also contain a high percentage of water.

Air-bladders.

All the forms living in the surface waters of the sea, which have developed special floating devices in the shape of air-bladders or bells, may also—at all events in order to avoid a too formal classification—be ranged into this group. These remarkable devices are specially noticeable in the wonderful group of the siphonophores. The air-filled lungs of whales and seals and the air-bladders found in most fishes are also instrumental in diminishing the specific gravity of these animals.

(2) A reduction of the specific gravity of the kind mentioned above must necessarily reduce or abolish the surplus gravity, which tends to make the animals sink. But even if a surplus gravity is present they will float, if they can offer a sufficient amount of surface resistance, which may be effected either actively by swimming, or passively as a consequence of the shape of the body.

In order to understand the various and complicated adaptations within this field, we should have to compare the various types of shape found in pelagic animals. I will at present limit myself to pointing out the main laws as laid down by Ostwald and Chun. In considering surface resistance two points are essential: (1) the size of the organism, and (2) the shape of the organism.

If we take two bodies, for instance two balls, consisting of the same substance but with different diameters, and let them sink in the same fluid, the larger one, that is, the ball in which the relation between surface and volume is smallest, will sink the faster; thus the smaller the body the slower will it sink. Ostwald terms the relation between surface and volume the "specific surface," and gives the above-mentioned fact in the following words: "small bodies sink slower than similar large bodies which have the same surplus gravity, because their specific surface is greater."

Next it is important to take into account the diameter of organisms transverse to the direction in which they sink. A thin plate sinks much faster in a vertical than in a horizontal

Specific
surface.

position. Ostwald terms this relation the "size of projection," and has asserted that the velocity of sinking decreases in proportion to the increase in the size of projection.¹ Size of projection.

These two principles of "specific surface" and "size of projection" have in a most wonderful manner been employed by organisms for the purpose of developing their faculty of floating. First of all, in organisms which cannot lower their specific gravity by depositing fats or absorbing water, we find a dominant tendency to develop minute forms in specifically light waters. In this connection we may note that small radiolarians are found in shallow water, and large ones much deeper, as

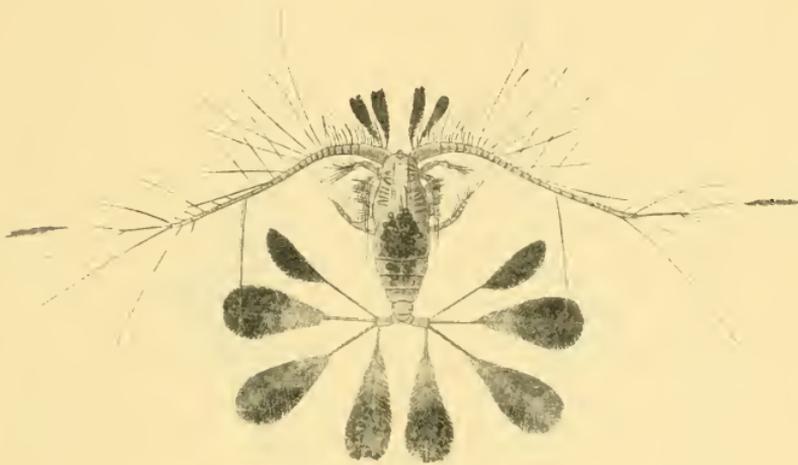


FIG. 503.

Calocalanus pavo, Dana. ♀ (about $\frac{2}{8}$). (From Giesbrecht.)

mentioned in Chapter IX., and in Chapter VI. Gran refers to the minute coccolithophoridæ of the light oceanic surface-layers. A large "size of projection" is found in countless numbers of crustaceans, especially in warm oceanic waters. The copepoda, for instance, show magnificent devices for enlarging their surface, developing feather, plate, or rod-shaped appendages (see Fig. 503). The surface resistance of these appendages depends on their position in the vertical line, and thus they serve the purpose of vertical locomotion as well.

Ostwald next points out the necessity of studying in nature

¹ Since this was written Sandström has published a paper, "Hydrometrische Versuche," *Meddelanden från hydrografiska byrån*, Stockholm, 1912, showing that the velocity of sinking is not exactly proportional to the size of projection, other circumstances, which are not yet clearly understood, also influencing the process.

the specific gravity and viscosity of different waters, and comparing them with the distribution and structure of the animals. In this way I shall presently attempt to compare various areas of the waters investigated by the "Michael Sars." For this purpose Mr. Einar Lea has, on the basis of the observations made by Dr. Helland-Hansen on our cruise, worked out the three sections representing temperature, specific

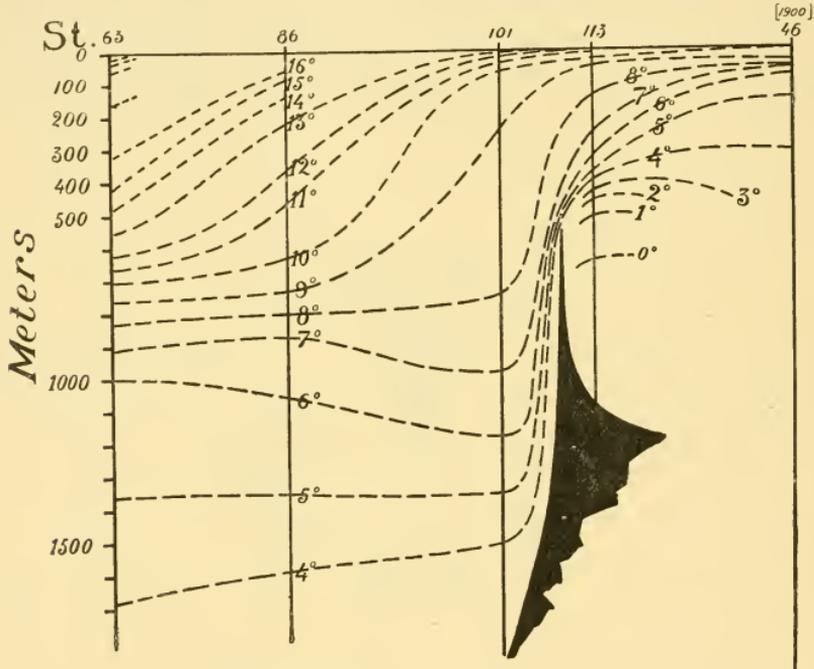


FIG. 504.—DISTRIBUTION OF TEMPERATURE FROM THE SARGASSO SEA (STATION 63) TO LOFOTEN (NORWEGIAN SEA).

Depth in metres ; temperature Centigrade.

gravity, and viscosity from the Norwegian Sea, west of Lofoten, to the Sargasso Sea (see Figs. 504, 505, and 506).

As to these sections, I wish to remark that they must not be considered as representing the direct continuity of the water-masses from the Sargasso Sea to the Norwegian Sea. The currents do not run directly between the two terminal stations, and perhaps it would be more correct to represent each of the stations separately without connecting the curves. With this reservation in mind, however, it should prove very instructive to compare the conditions as shown in the sections.

We see from the little chart (Fig. 62, p. 83) that Station 63

Temperature,
specific
gravity, and
viscosity along
section from
the Sargasso
Sea to the
Norwegian
Sea.

is situated in the Sargasso Sea, Station 86 on our northern track, Station 101 to the south of, and Station 113 to the north of, the Wyville Thomson Ridge, while Station 46 from the year 1900 is west of the Lofotens.

Figs. 504 and 505 show that just on the verge between the two seas, between Stations 101 and 113, a marked drop occurs in the temperature and specific gravity. In the Norwegian Sea (Station 46 of 1900) a specific gravity of 1.0278 is

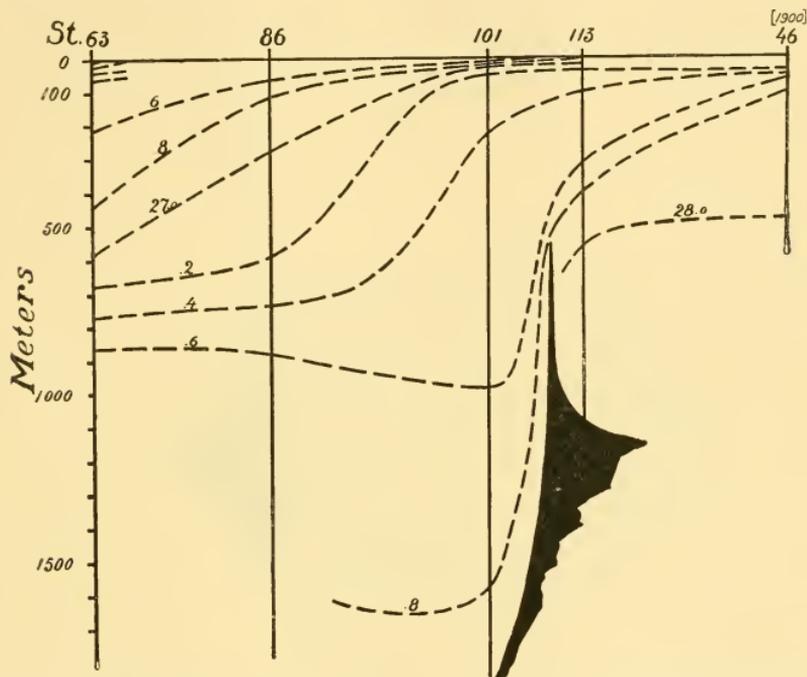


FIG. 505.—DISTRIBUTION OF SPECIFIC GRAVITY FROM THE SARGASSO SEA (STATION 63) TO LOFOTEN (NORWEGIAN SEA).
28 = 1.028.

found only at 100 metres, and towards the Wyville Thomson Ridge even at 1500 metres. A specific gravity of 1.028 does not occur in the Atlantic at all at the depths here treated of, while the entire deep layer in the Norwegian Sea is of a specific gravity even higher than 1.028. In the Atlantic the curves all fall away towards deep water and as we approach the tropics. In the Sargasso Sea we find the same specific gravity at 600 or 800 metres as occurs in the Norwegian Sea at 50 metres. The densely gathered curves at the surface denote water of low specific gravity.

The viscosity exhibits, as shown in Fig. 506, a similar course. We find a much greater viscosity in the waters of the Norwegian Sea than in those of the Atlantic. The conditions of viscosity at a depth of 50 metres in the Norwegian Sea correspond to the conditions at about 800 metres in the Atlantic, where at the surface we meet water-layers of small viscosity: "thin water."

If now we compare the distribution of animal life, as

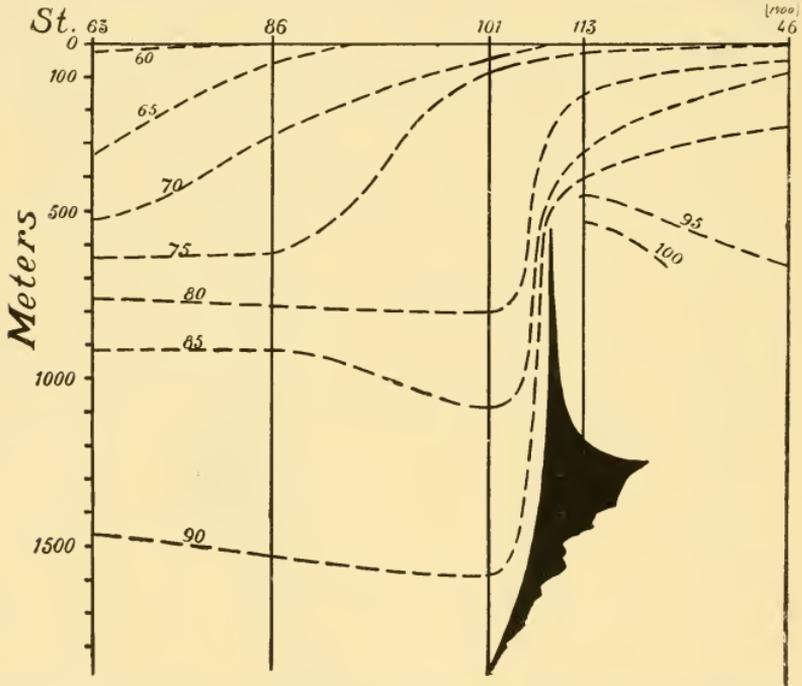


FIG. 506.—DISTRIBUTION OF VISCOSITY (see text) FROM THE SARGASSO SEA (STATION 63) TO LOFOTEN (NORWEGIAN SEA).
100 = the viscosity of distilled water at 0° C.

described in Chapter IX., with these facts, we may clearly understand many of the peculiarities of distribution.

Warm-water
oceanic life.

From the distribution of specific gravity and viscosity it follows that in light, thin, and warm oceanic waters only those animals are found which have lowered their specific gravity by the aid of light substances (fats, water), or have increased their surface resistance by reducing their size or by developing special organs for floating. To the first type belong the Siphonophores (*Physalia*, *Physophora*, *Agalmopsis*, and many others), besides *Medusæ*, *Salpæ*, *Doliolum*, *Pyrosoma*, and

large fishes which, like the sunfish, have a layer of blubber round their body, and may be seen floating at the surface, the dorsal fin above the water (see Fig. 507).

The organs of floating have previously been described and

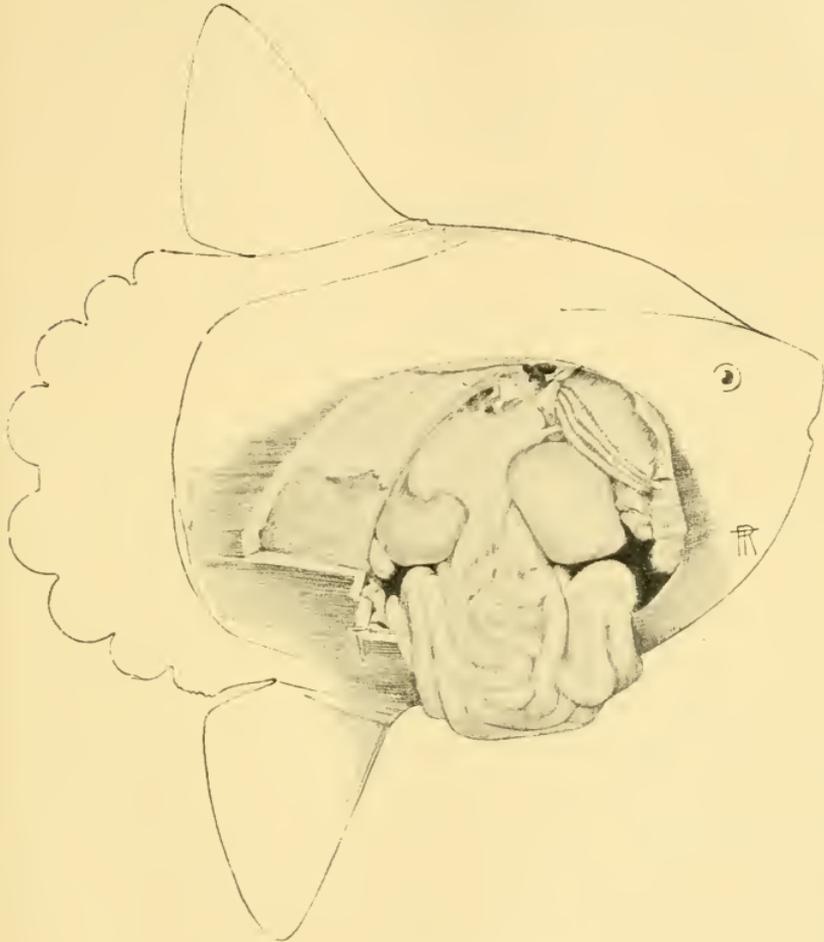


FIG. 507.

Mola rotunda, to show the thick fat covering under the skin.

figured (see the Copepoda in Figs. 416-418, and the radiolaria and foraminifera with siliceous and calcareous spines and filiform pseudopodia, pp. 146-153).

Of special interest to us, however, is the oceanic fauna, the members of which are remarkable for their small size, and in this fauna the fishes especially appeal to us. The whole fauna

of typical surface fish (Scopelidæ, young fish), besides the silvery fishes of the intermediate layer, the Sternoptychidæ and the Stomiatiidæ found mainly between 150 and 500 metres, live just in the specifically light and thin water-layers (see Fig. 526, representing an adult *Argyropelecus hemigymnus*, only 34 millimetres long, but with almost ripe ovaries). Excepting the long ribbon-like Trachypteridæ, *Regalecus glesne*, etc., these minute fishes are, as far as we know, the principal if not the only ones peculiar to these light water-layers. In the surface-layers it is possible to recognise three distinct types: (1) the minute Scopelidæ; (2) the larger oily fish like the sunfish; and (3) the species which live near solid floating objects, such as the Sargasso fish.

One meets exceedingly few large fish in the ocean belonging to the good swimmers, for instance, mackerels, pilot fish, swordfish, and sharks. Little is really known about the distribution of all these, but several of them spend at least some part of their lives in coast waters.

Boreal
pelagic life.

A comparison of the fauna of the Norwegian Sea and that of the Atlantic is very interesting. We have seen in Chapter IX. that numerous fishes which live mainly in the Atlantic have been found in the Norwegian Sea as very rare visitors. From the notes of Professor Collett, covering many decades, I have given a list (see p. 643) recording the frequency of the occurrence of these Atlantic forms. The most remarkable feature is the fact that most of them have been found at the very surface, or have drifted ashore and have been found stranded on the beach. Among these fishes there are several species, for instance those belonging to the genus *Argyropelecus*, which live at 300 metres in the Atlantic and have not been captured at these depths in the Norwegian Sea. Figs. 504-506 show that the lines of temperature, specific gravity, and viscosity situated in 300 to 500 metres in the Sargasso Sea rise up to the very surface as we approach the Norwegian Sea. In this direction the Gulf Stream runs, at all events in the northern part of the section.

The facts pertaining to the occurrence of boreal species in the Atlantic are just the reverse. In Chapter IX. we have learnt that on our track from Newfoundland to Ireland we found boreal species, *Clione limacina*, *Aglantha*, *Calanus*, *Euchaeta*, and several others, at depths between 750 and 1000 metres, while in the Sargasso Sea we took *Calanus hyperboreus* and *Euchaeta* at 1000 metres. At these depths we find the same specific

gravity and viscosity as in the Norwegian Sea, and also the same temperatures. These boreal species are essentially larger than the warm-water forms belonging to the Atlantic surface-layers, and have far smaller organs of floating. This applies equally to the genuine deep-sea forms of the Atlantic in whose company the boreal forms are found (see, for instance, what I have previously said about the radiolarians, the trachymedusæ, and the crustaceans). A parallel is also found in fishes and squids, of which some larger forms commence to appear in the deeper layers, their size apparently increasing as we descend towards the bottom (compare the measurements of *Cyclothone signata* and *C. microdon*, Fig. 473, p. 620, and the two figures representing ripe *Cyclothone*, Figs. 527 and 528). The bathypelagic *Gastrostomus bairdii*, one of our deepest-living pelagic fishes, was found to attain a length, including its long tail, of 75 cm. In these regions we also find large prawns, which appear to increase in size with increase of depth (*Acantheephyra*, *Notostomus*). The squids seem to be arranged in two groups, a number of small forms living in the upper layers and the larger species living in deeper water. Although our captures from a systematic point of view may be characterised as exceedingly rich, they are not satisfactory for a study of the vertical size-distribution of squids.

The peculiar agreement between size, form, and distribution of species and the occurrence of a certain specific gravity and viscosity of the water seems entirely absent in coast waters, where the specific gravity of the water is lower than in the ocean, because the inflow of fresh water from continental rivers lowers the salinity. The viscosity, mainly dependent on temperature, should, as a rule, be similar to that of the open ocean outside. One would therefore expect to find, for instance on the coast banks of Africa, similar oceanic forms, or the same faunistic characters on the whole, as in the Atlantic Ocean. On the contrary, we find that the fauna as well as the flora have entirely different features. For unicellular plants as well as for animals, the rule holds good that all forms are much larger than those in the open ocean. Among plants the minute coccolithophoridæ are replaced by peridineæ; instead of the minute oceanic scopelidæ we meet with pelagic herrings and mackerels, animals of quite another size and character.

As to the northern part of the Atlantic we perceive that several boreal forms (among others *Clione limacina*), which in

the open ocean are found from 750 to 1000 metres, ascend not only to the coast banks of Ireland, where the water is warm and the specific gravity low, but also to the coast banks of Newfoundland (see Fig. 489, p. 659, showing the vertical distribution of *Clione* on our northern track).

How is this remarkable distribution to be explained? First of all it shows that our conclusions as to the distribution of animals must be drawn with great caution. Except the single occurrence of *Clione* to the west of Ireland, all the captures agree as to temperature, specific gravity, and viscosity, both in deep water as well as on the Newfoundland banks. We require further information regarding the physical and biological conditions in order to understand the difference between the coast banks and the ocean. The biological conditions, especially the great difference between the food supply on the coast banks and in the ocean, will be discussed after touching upon certain physical conditions.

As previously mentioned, Ostwald has pointed out the influence exercised by salinity on the size of organisms; in surroundings of low salinity certain organisms absorb water and increase in volume, while in high salinities they diminish in volume. To what degree this fact may entail a difference between the size of organisms belonging to the salt oceanic waters and the size of organisms in the fresher coast waters, can only be decided by future investigations. Possibly the richer nourishment offered by coast waters affords the organisms a better chance to store up fatty substances (*Clione* as well as *Noctiluca* store up fat), which increase the power of floating. Finally, we may raise a question which seems to be worthy of future investigation. Is the viscosity of the water influenced by the number of organisms suspended in it? That this may be so is conceivable when we think of china ink, for instance, which is more or less viscous according to the amount of substance dissolved in the water. Investigations as to the actual facts occurring in nature have not yet been made. Those who have observed the extent to which coast water may be filled with suspended substances, detritus as well as living organisms, may perhaps find this question worth consideration.

MIGRATIONS

We have considered how far and in what manner the appearance, shape, size, and also the several organs of different

organisms may be supposed to have been adapted to certain external conditions prevailing in the water-layers which surround them. But these water-layers are not stationary, and the conditions in a certain water-layer may change in many different ways from time to time. These changes alter the habitat of the animals and cause active or passive migrations. The study of these migrations is specially interesting as showing the influence of physical conditions acting upon the animals.

From time immemorial it has been known that many animals ascend at night to the surface of the ocean. Fishermen have during ages turned this knowledge to advantage in setting their drift-nets at night at the surface of the sea to capture the herring. Recently it has proved possible to trawl successfully for herring along the sea-bottom, but only during the daytime. All sailors can tell us that at night great numbers of animals gather in the surface waters, which are never seen there in the daytime. An interesting instance of this was mentioned in Chapter IX. While fishing with long-lines on the Faroe banks our lines were set for cod along the bottom in about 200 fathoms; the lines were hauled at night, and the stomachs of the cod contained squids, which had been eaten during the day, while at night numerous squids were seen at the surface darting into the glare of our electric lamp hanging over the side. Most fishermen have had similar experiences.

Daily vertical migrations.

A certain amount of information has also been gathered as to the vertical migrations of minute pelagic organisms moving towards the surface at night. Chun especially has investigated the extent of these migrations, and found that the majority of small pelagic organisms migrate generally within a vertical range of 30 to 50 metres. Steuer draws attention to the fact that vertical migrations very rarely involve all the pelagic forms of a locality; at all events they do not migrate in the same manner, for there are many transitions between forms which only retreat vertically during a few hours in the daytime, and forms which rise only during the darkest nocturnal hours. If the forms were large enough to be seen in the water, we should "by day as well as by night be able to observe a continuous rise and fall of organisms. Only during the day we should see a larger congregation in deeper water, and at night at the surface."¹

Some instances of the difference plainly observable in our catches by day and by night have already been mentioned

¹ Steuer, *op. cit.*

(see p. 95). Specially striking were the fishes *Astronesthes* and *Idiacanthus* occurring at the surface only at night. It was also very interesting to note the remarkable coincidence between the vertical migrations of the fishes and the development of their light-organs. Fig. 490 shows the vertical occurrence of five black fishes, each mark denoting the capture of one individual; in the case of *Gonostoma rhodadenia* and *Photostomias guernei*, a black dot denotes a specimen captured at night, while a ring-shaped dot denotes a specimen taken during the day. In *Gastrostomus*, *Cyema*, and *Gonostoma grande* only slightly developed light-organs, if any, are met with. In *Gonostoma rhodadenia* and *Photostomias guernei* particularly large light-organs are present (see Fig. 494 and Plate II.). Specially interesting is a comparison of the two species of *Gonostoma*, the light-organs along the side of the body in *G. rhodadenia* having a length of 2.5 mm., while in *G. grande* they are only 0.5 mm. long. Evidently we have here a type of deep-sea fishes, living in deep water, but with the power of migrating towards the surface. These forms have retained their well-developed light-organs, which in other black fishes of the deep sea must be considered as extremely reduced, perhaps even quite rudimentary, organs. A perfect analogy is found in the decapod crustacea. The deepest living species (see table on p. 668, Nos. 8-11) have no light-organs and make no vertical migrations. Light-organs, or organs which are believed to produce light, are found only in species living between 150 and 500 metres with a maximum distribution at about 500 metres. These species have been found much higher up in the water during the night than during the day, as is brought out quite clearly by the table.

During our southern cruise we might have had a good opportunity of making an exact study of vertical migrations by the aid of precise closing-net hauls, but time did not permit, though our isolated observations are very interesting, for instance those made at Station 48. While towing our big trawl all day at this station, we were continually taking hauls with surface tow-nets, the catches during the day consisting only of the common surface forms: *Ianthina*, *Pterotrachea*, fish eggs, pteropoda, radiolaria, etc.; but between 6 and 7 P.M. the nets suddenly captured a mass of small red copepoda, which during the day had been taken at about 70 metres. At Station 53, during the day, we captured only radiolarians at the surface; at 30 metres there were a few copepoda, no young

fish or scopolidæ, while at 60 metres there were several copepoda, and no scopolidæ. In the same place, during the night, we obtained at the surface a rich collection of copepoda, numerous scopolidæ, and thirteen black fishes (*Astronesthes niger*). These instances furnish conclusive proof of vertical migrations of considerable extent.

Ostwald, after studying the variations in the viscosity of the water from time to time, has made an attempt to explain the vertical migrations as due entirely to physical laws. During the twenty-four hours certain changes occur in the temperature of the ocean surface, and the viscosity of the water is, as we have seen, largely dependent on temperature. According to Buchan, the mean diurnal fluctuation of the surface temperature, as shown by the "Challenger" observations, was in mid North Atlantic 0.8° Fahr., in mid South Atlantic also 0.8° F., in mid North Pacific 1.0° F., and in mid South Pacific 0.9° F.; near the equator both in the Atlantic and Pacific the diurnal range is only 0.7° F. The mean daily range deduced from the whole of the "Challenger" observations during the three years and a half is 0.8° F.¹

According to Krümmel² the daily range of temperature occurring in the surface waters of the open ocean amounts to about 0.5° C.; in the North Atlantic 0.59° C. Although several investigators, like Aimé and Hensen, tackled the problem we have very little knowledge regarding the daily changes at different depths. From Krümmel I give the following differences found by Aimé between evening and morning at different depths in the Mediterranean:—

Depth. Metres.	Temperature.		Difference.
	Evening.	Morning.	
0	15.1° C.	14.6° C.	0.5
2	15.1° C.	14.6° C.	0.5
4	15.0° C.	14.5° C.	0.5
6	14.8° C.	14.5° C.	0.3
10	14.6° C.	14.4° C.	0.2
14	14.4° C.	14.3° C.	0.1
18	14.3° C.	14.3° C.	0.0
22	14.3° C.	14.2° C.	0.1

¹ Phys. Chem. Chall. Exp., Part v. p. 6, 1889.

² Otto Krümmel, *Handbuch der Ozeanographie*, Bd. 1, Leipzig, 1907.

From this it does not seem that such migrations as those mentioned above are due to changes in temperature and viscosity alone. We must, for the present, suppose that the animals have the power of actively altering their level in the water-layers. Ostwald's observations on the viscosity of sea-water, and on the floating capacity of organisms, should render these questions easier of solution, and their further investigation should form a very interesting object for future expeditions.

Effect of
currents
on the
distribution
of animals.

The currents of the ocean exert a very strong influence on the distribution of many animals. All seafaring men and the inhabitants of all shores have known for ages that drifting objects are carried very far by the currents of the sea, and that "rare" and strange animals are stranded on the coasts. Along the entire coast of Norway, even up to the Barentz Sea, drifting objects and stranded fish are found, which really belong to the distant warm Atlantic. Numerous accounts of the passive migrations of animals through currents are to be found in literature, many of them valuable notwithstanding the fact that these conditions have only exceptionally been made the subject of systematic investigation.

Looking at the current-chart (Fig. 508), we see that the central part of the North Atlantic, south of a line drawn from the Bay of Biscay to the northern United States, forms a separate current-system. The branch of the Gulf Stream flowing north-east towards the coasts of northern Europe receives an admixture of cold water from the Labrador current, and also large volumes of water, as well as numerous organisms, from the main body of the Gulf Stream. Entering the Norwegian Sea this branch of the Gulf Stream runs through the Faroe-Shetland Channel, sending off one branch to the North Sea and another branch along the coast of Norway right up to the Barentz Sea. This current system enables us to understand many of the laws governing the distribution of pelagic forms as referred to in Chapter IX. Thus the warm-water fauna of the North Atlantic belongs mainly to the central current system; isolated specimens belonging to this fauna not only occur in the north European Gulf Stream, but are found in the Norwegian Sea, and on the northernmost coasts of Norway (see the discussion of the distribution of pelagic fishes in depths between 150 and 500 metres in the Atlantic, and the occurrence of Atlantic fishes in the Norwegian Sea, p. 644). The distribution of the animals of the coast banks

is peculiar in so far that southern species of molluscs, for instance, occur as isolated specimens even far north in the Norwegian Sea, while northern species have a sharp southern limit (see Chapter VII.). Vast numbers of small pelagic organisms are introduced into the Norwegian Sea from the Atlantic.

As the water-masses of a current are carried along, the

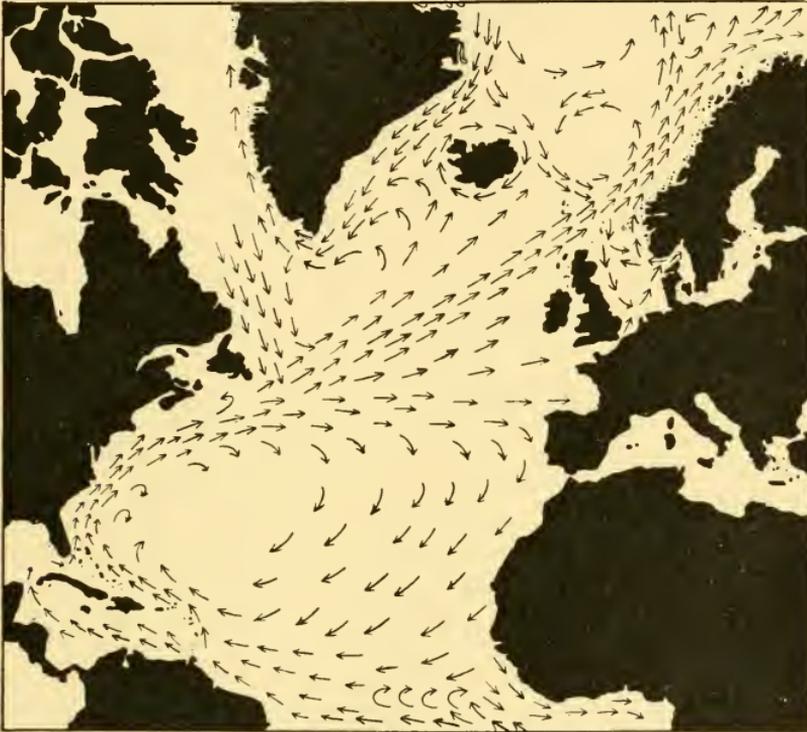


FIG. 508.—CURRENTS OF THE NORTH ATLANTIC. (From Schott's "Valdivia" Report and Helland-Hansen and Nansen's memoir on *The Norwegian Sea*.)

conditions of existence for certain animals change, and as a consequence the fauna gradually changes in character. This change of fauna from place to place in the same expanse of water has always presented interesting problems in oceanic research. Sir John Murray writes upon this point as follows: "Where cold and warm currents meet at the surface of the ocean, there is a rise of temperature for the animals of the cold current, and a fall of temperature for the animals of the warm current, which results in a plentiful destruction of organisms.

Effect of large range of temperature in the surface waters.

The tow-net collections during the 'Challenger' expedition gave frequent illustrations of this fact by the dead animals collected in such positions off the coast of North America, off the Cape of Good Hope, in the North Pacific, and elsewhere. Dr. O. Fischer records a remarkably large number of bacteria on the borders of such meeting currents. This destruction of life is not limited to minute pelagic organisms, but occasionally affects animals which live at the bottom of the sea. Some remarkable instances of this kind have been observed between depths of 50 and 100 fathoms off the eastern coast of the United States.

"Lieutenant-Commander Tanner, commanding the United States Fish Commission steamer 'Albatross,' reports that 'on the morning of July 20, 1884, in lat. $37^{\circ} 47' N.$, long. $74^{\circ} 15' W.$, near the 100-fathom line, we passed numerous dead octopods floating on the surface. This unusual sight attracted immediate notice and no little surprise among those who knew their habits, as it was not suspected at first that they were dead. We lowered a boat and picked up three or four specimens, which we were unable to identify, but in general appearance they resembled *Alloposus mollis* (Verrill) of unusually large size. These dead cephalopods were seen frequently on the 100-fathom line and outside of it, from the position given above to the meridian of Montauk Point, a distance of 180 miles. They were less numerous, however, as we went to the northward and eastward. Several dead squid were seen also, and two specimens were picked up with a scoop-net.'

"A still more remarkable instance of this kind is furnished in the well-known case of the destruction of the tile-fish (*Lopholatilus chamaeleonticeps*) in the same locality in the spring of 1882. In the months of March and April 1882, vessels arriving at Philadelphia, New York, and Boston reported having passed large numbers of dead or dying fish scattered over an area of many miles, and from descriptions and the occasional specimens brought in, it was evident that the great majority of these were tile-fish. Naturally, these fish were not evenly distributed over all the area in which they were seen, some observers reporting them as scattering, and others as at times so numerous that there would be as many as fifty on the space of a rod square. As one account after another came in, it became apparent that a vast destruction of fish had taken place, for vessels reported having sailed for forty, fifty, and sixty miles through floating fish; and in one case, the schooner

'Navarino' sailed for about 150 miles through waters dotted as far as the eye could reach with dying fishes. Computations made by Captain J. W. Collins seem to indicate that an area of from 5000 to 7500 square statute miles was so thickly covered with dead or dying fish that their numbers must have exceeded the enormous number of one billion. Since there were no signs of any disease, and no parasites found on the fish brought in for examination, their death could not have been brought about by either of these causes; and many conjectures were made as to the reason of this wholesale destruction of deep-water fishes, such as would ordinarily be unaffected by conditions prevailing at the surface, submarine volcanoes, heat, cold, and poisonous gases being variously brought forward to account for the loss of life. Professor Verrill has noted the occurrence of a strip of water having a temperature of 48° to 50° Fahr., lying on the border of the Gulf Stream slope, sandwiched between the Arctic current on the one hand and the cold depths of the sea on the other. During 1880 and 1881 Professor Verrill dredged along the Gulf Stream slope, obtaining in this warm belt, as he terms it, many species of invertebrates characteristic of more southern localities. In 1882 the same species were scarce or totally absent from places where they had previously been abundant; and this, taken in connection with the occurrence of heavy northerly gales and the presence of much inshore ice at the north, leaves little doubt that some unusual lowering of temperature in the warm belt brought immediate death to many of its inhabitants. This is the more probable, as it is a well-known fact that sudden increase of cold will bring many fish to the surface in a benumbed or dying condition."¹

Destructive effect of large range of temperature.

From the Barents Sea we know many instances of a similar destruction of animals on a large scale. The case of the boreo-arctic fish, the capelan (*Mallotus villosus*), is specially striking, millions of this fish having occasionally been found drifting dead at the surface. In the Barents Sea very sudden changes of temperature occur, and it is natural to conclude that the death of the fish is caused thereby. The greatest destruction of this kind probably occurs among the young stages, eggs and larvæ of fishes. As we shall see later, these young stages may be removed by currents very far from the places where they are capable of developing, and in all probability they are also liable to

¹ Sir John Murray, "On the Annual Range of Temperature in the Surface Waters of the Ocean," *Geogr. Journ.*, vol. xii. pp. 128-130; 1898.

encounter catastrophes which sweep them off in enormous numbers. I come to this conclusion because our investigations on the age-composition of various fish-species have proved the frequency of the different year classes to be so variable (see section on age and growth).

As the Gulf Stream flows northwards its waters are gradually cooled, partly because they give off heat to the cold air, and partly because of the admixture of cold water. With the cooling the southern forms disappear, and their place is taken by entirely different boreal species; very little is known about the actual stages of this change.

During the cruise of the "Michael Sars" from the west coast of Scotland to Rockall, and north to beyond the Wyville Thomson Ridge we found vast numbers of *Salpæ* (*S. fusiformis*), the great majority of which were wholly degenerated. Bjerkan, who is examining our collection of *Salpæ*, informs me that the mantle and the muscular system of the specimens were generally in a very ragged condition, in many cases only the intestine being distinctly recognisable. Here then, on the border between the Atlantic and the Norwegian Sea, it appears that certain forms die in large numbers, while others degenerate. Gran refers to the degeneration of certain coast diatoms found drifting far out at sea (see p. 342).

When organisms cannot within a certain time regain conditions necessary for them, or to which they can adapt themselves, they invariably die sooner or later. The isolated specimens of such fishes as *Argyropelecus* found in the northernmost parts of the Atlantic undoubtedly represent a few survivors of the change.

The boreal fauna which in northern waters replaces the genuine Atlantic forms also belongs to a great current-cycle. If we look at the current charts (Fig. 193, p. 284 and Fig. 508), we observe that the Gulf Stream receives admixtures from boreal and boreo-arctic currents, which consequently carry boreal organisms. As we have previously seen, we meet with a wealth of boreal forms in deep water even in the Sargasso Sea, and probably much farther south, living below the warm-water fauna of the surface.

The velocity of ocean currents is subject to many varieties of periodical and non-periodical changes (see pp. 284-5). The annual changes are of peculiar interest, and are very noticeable in northern waters, though also important in the Atlantic. If we compare the two charts (Figs. 159, p. 227, and 160, p. 228)

Mixing of
Gulf Stream
and boreal
waters.

Annual
changes in
velocity of
currents.

we see that the surface temperatures of the North Atlantic change very considerably from February to August. In February the isotherm of 15° C. follows approximately the 40th degree of latitude, while in August it reaches the north-western corner of Iceland, north of the 50th degree. The isotherm of 10° C. has in February a course approximating to that of the 15° isotherm in August, when the isotherm of 10° runs far north in the Norwegian Sea, where the seasonal difference is

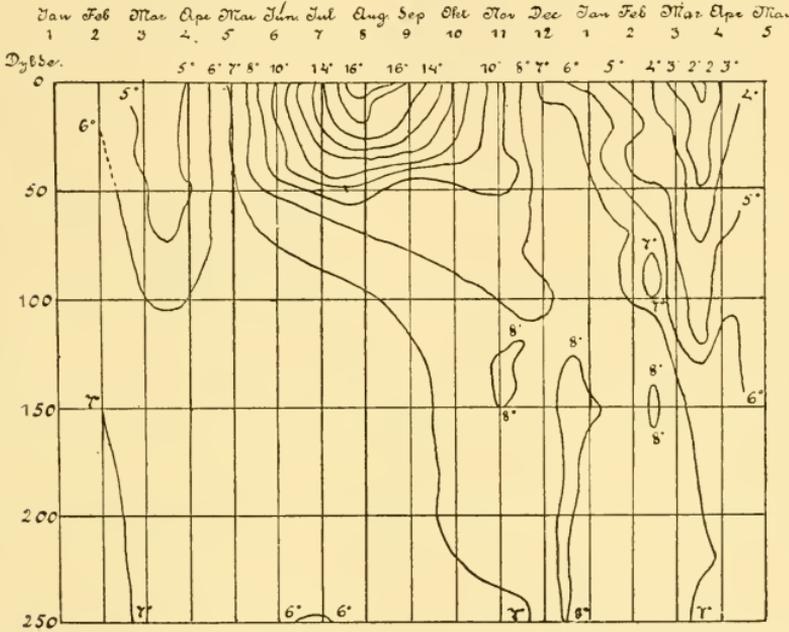


FIG. 509.—VARIATION OF TEMPERATURE ACCORDING TO DEPTH DURING DIFFERENT SEASONS, OFF THE NORWEGIAN WEST COAST.

still more pronounced. Fig. 509 shows the vertical distribution of temperature during approximately fifteen months, as observed by me in the 'nineties of last century while making repeated investigations in one locality off the west coast of Norway. We perceive that during the summer months warm temperatures occur in the upper 50 metres, temperatures which during winter we can find in the Atlantic only south of the 40th degree of latitude (see Fig. 159, p. 227). During autumn high temperatures (8° C.) pass down through the water column, so that towards the close of the year the warmest water is found at 250 metres. At the same time the surface-layers cool

rapidly and the lower temperatures gradually descend towards deep water during early spring and summer. Great changes in specific gravity, viscosity, and light-intensity accompany these changes in temperature; in the very magnitude of these changes we must look for the essential difference between the tropical and subtropical conditions on the one hand, and the arctic-boreal conditions on the other.

The greatest interest attaches to the fact that the immigration of Atlantic forms into the Norwegian Sea occurs at the season when the conditions in the latter are most similar to those of the Atlantic. The international investigations have contributed to our knowledge on this immigration. Schmidt,¹ for instance, in the Danish investigation-steamers "Thor," had the opportunity of studying the immigration of *Salpæ* from the Atlantic into the Norwegian Sea, and writes as follows:—

"The organisms concerned were the distinctly Atlantic *Salpæ* (especially *Salpæ fusiformis*), which are so characteristic and which were taken often in hundredweights in each haul of our pelagic apparatus in the Atlantic beyond the 1000-metres line. The year 1905, during which we several times crossed the North Sea, made two cruises to and from Iceland and the Faroes, following approximately the 1000-metres line, then sailed southwards west of the British Isles to the Bay of Biscay, was thus specially well suited to give light on these conditions, as I have endeavoured to delineate on the accompanying Chart [reproduced in Fig. 510]. The shaded lines

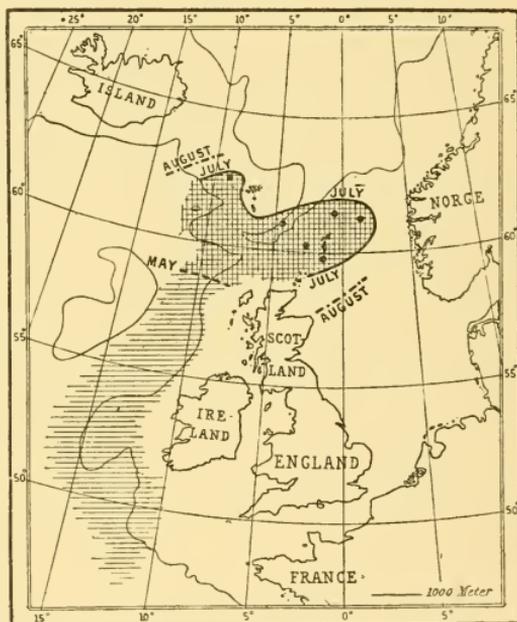


FIG. 510.—DRIFT OF SALPÆ (*SALPÆ FUSIFORMIS*) IN 1905. (From Schmidt.)

¹ Johs. Schmidt, "The Distribution of the Pelagic Fry and the Spawning Regions of the Gadoids," etc., *Rapports et procès verbaux du Conseil International*, vol. x., Copenhagen, 1909.

(single or double) on this Chart represent the regions where the Salpæ occurred. As will be seen, up to the end of May the Salpæ were limited to the Atlantic, where the northern boundary was found on the voyage of the 'Thor' southwards to lie to the west of the Hebrides, and absolutely none were found in the Norwegian Sea or North Sea. Towards the end of July the conditions had quite changed, a fact of which I was able to convince myself on a cruise from Scotland to Bergen and from Bergen to the Shetlands, the Faroes, and Iceland. From the chart, on which the places where we found the Salpæ are marked by black spots, we see how the northern boundary has moved to the east and north. Thus a large tongue of the Salpæ had pushed its way north of the British Isles in a north-easterly direction, far towards the Norwegian coast, and in a northerly direction we see now that the Salpæ reached as far as north-west of the Faroes. And it was not a matter of small quantities. Thus at our station (Station 121, 1905) north of the Shetlands we took many hundred litres per half-hour haul; and in the quiet, calm weather we could see under the clear surface how the water was quite thick with the Salpæ which occurred here and, it is to be remarked, over small depths (less than 200 metres), along with other distinctly Atlantic oceanic forms, in almost as large quantities as we had found them anywhere, even in the Atlantic over deep water where they really belong. At the end of August, when the 'Thor' was coming southwards from Iceland, the northern boundary had moved somewhat, yet not very much. We see also that the south-eastern boundary in the North Sea had spread out farther, corresponding to a greater development of the large tongue in July."

Similar experience has also been gained during the Norwegian investigations. Thus in the survey of the "Michael Sars" investigations on pelagic organisms in the years 1900-1908, Damas writes as follows:—

"In the middle of the summer the invasion of oceanic forms from the Atlantic commences in the Faroe-Shetland channel. There we find an imposing array of species that are entirely absent from the Norwegian Sea, and that certainly do not belong to the fauna appropriate to that sea-basin. Among the most characteristic we may name: *Lepas fascicularis*, *Physophora borealis*, *Cupulita sarsi*, *Solmaris corona*, *Salpa fusiformis*, *S. runcinata*, and *S. irregularis*, *Arachnactis albida*, *Clio pyramidata* and *C. uncinata*. These forms do not enter *en bloc*, and the water-masses which convey them do not seem to have

a homogeneous composition. Their approach is heralded by an immense swarm of *Lepas fascicularis*, which at the beginning of May and June float passively on the surface of the northern portion of the North Sea. *Arachnactis albida* follows soon afterwards, as does also *Physophora borealis*. The salpæ and doliolids, which with *Cupulita sarsi*, constitute the bulk, generally make themselves visible in July, August, and September."

We know that these warm surface forms approach the coast of western Norway, and as far north, for instance, as the Trondhjem fjord.¹ Even within the Norwegian Sea such seasonal migrations occur, the warm water layers from the eastern part spreading out over the deeper areas during summer.

Active
migrations.

The foregoing remarks refer only to the passive migrations or drift of pelagic forms with the currents of the sea. Fishermen have, however, long recognised the vast active migrations of the powerful swimmers, especially fishes, generally supposed to be undertaken in order to reach definite localities. The first to submit these migrations to scientific investigation was probably G. O. Sars. As to the herring fisheries on the coasts of Norway he was struck with the fact that while herrings of all sizes are captured along the entire coast from the Skagerrack to the Barents Sea, spawning herrings are only caught in large quantities on a definite restricted portion of the coast, viz., from Stavanger to Romsdal (the Norwegian North-Sea coast), and he concluded that the herrings must necessarily migrate to these places to spawn, enormous spawning-migrations entering as a necessary link in the life-history of the herring.

Numerous instances of such migrations are known from the fishing industries, on the coast of Norway principally in the case of herring and cod, and in Iceland of cod and plaice. I refer the reader to my description of the migrations of the capelan (*Mallotus villosus*) in the Finmark Sea² (Barents Sea). This small boreo-arctic fish spawns in spring on the coast banks of Finmark, and during summer it migrates far north into the Barents Sea towards the ice-limit. In March 1901, when many miles off the Finmark coast and over deep water, I could observe and fish the capelan, the shoals being followed by millions of auks, fulmars, kittiwakes, and gulls, the stomachs of which contained capelan.

¹ See Nordgaard, *loc. cit.*

² Hjort, *Fiskeri og Hvalfangst i det nordlige Norge*, Bergen, 1902.

The exact experimental proofs as to migrations obtained during recent years from the marking of fish are also of great value. Marking experiments on marine fishes were started in the 'nineties of last century by C. G. J. Petersen, during his studies of the life-history of the plaice. During the international investigations they have been carried out on a large scale, especially by Heincke, Garstang, Trybom, and Schmidt, the investigations by the last named on the migrations of cod and plaice at Iceland having perhaps yielded the clearest results. The Iceland plaice



FIG. 511.—SCHMIDT'S MARKING EXPERIMENTS SHOWING THE MIGRATIONS OF PLAICE IN ICELANDIC WATERS. (From Schmidt.)

spawn during spring south and west of the island, but at other times they migrate to the north and east coasts. Schmidt marked a number of plaice in Skjalafandi Bay on the north coast, and a number in Vápnafjörður on the east coast (see chart, Fig. 511). He got a great many of these back from the west and south coasts, where they were taken in the spawning season. From the North Sea interesting results from marking experiments are also available, but the fishes do not appear to migrate to such an extent as in Icelandic waters.

While investigating the fisheries and the whaling in northern Norway, I was successful in obtaining similar conclusive

evidence as to the migration of whales. With the aid of Captain Sørensen I obtained the two harpoons or bomb-lances which in the years 1888 and 1898 were found in the bodies of blue whales (*Balaenoptera musculus*) killed in the Barents Sea (see Fig. 512). Such harpoons were never used there, being employed only by the whalers of the Atlantic, for instance, off the coast of North America, and they bear the stamp of the American patent-holder, testifying to their American origin. They must, therefore, be considered as proving enormous migrations on the part of the whales in which they were found.

G. O. Sars attempted to show that some migrations were undertaken in order to obtain food, and others for the purpose of reproduction, and he thus distinguishes between feeding-migrations and spawning-migrations. When the capelan gather in millions on the coast banks of Finmark, when countless numbers of cod approach the banks of Lofoten, and when the herrings flock to western Norway, they migrate to spawn. The fat-herring collecting off the coast of Nordland, and the cod gathering around the shoals of capelan in the Barents Sea, are examples of feeding-migrations. Such were the ideas of Sars. A more detailed discussion could only be given by reviewing the whole natural history of each species.

An attempt at explaining a vast migration of fishes by means of mechanical laws has recently been made by Otto Pettersson.¹ Each year during late autumn large numbers of herrings gather off the island belt at Bohuslän

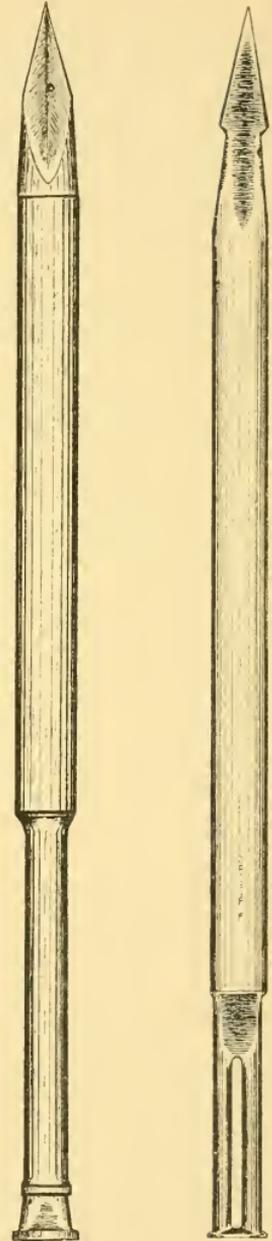


FIG. 512.—AMERICAN "BOMB-LANCES" TAKEN IN BLUE WHALES IN NORTHERN NORWAY, FINMARK, 1888 AND 1898.

¹ Otto Pettersson, *Studien über die Bewegungen des Tiefenwassers und ihren Einfluss auf die Wanderungen der Heringe*, Fischerbote, 1911.

(on the west coast of Sweden), and are captured in the deep channel of the Kattegat, or in the fjords of Bohuslän. Pettersson discovered that the regular occurrence of these herrings in several cases coincided with certain large submarine waves which he could register in the Gullmar fjord, and he sets up the hypothesis that there is a certain connection between these two phenomena. Fig. 513 shows curves denoting different salinities in the Gullmar fjord in November and December 1910, and it is seen that the deep salt layers rose several times during November, like huge waves, up towards the surface. Extensive investigations off the coast in the Kattegat proved the occurrence of similar deep-sea waves

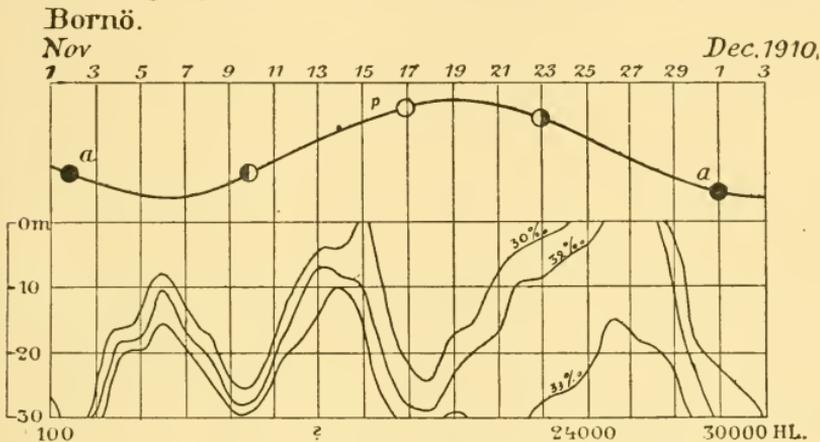


FIG. 513.—SUBMARINE WAVES IN THE GULLMAR FJORD IN NOVEMBER AND DECEMBER 1910. (From Pettersson.)

in the latter locality. These waves, according to Pettersson, carried the water of the Jutland coast banks (bank-water with a salinity of 32 to 34 per thousand) like a torrent into the Kattegat and its fjords, forcing the fresh surface water out. The herring shoals dwelling on the Jutland coast banks were literally, Pettersson says, sucked into the fjords of the Swedish west coast as by an enormous vacuum pump. This inflow, Pettersson points out, takes place periodically and coincides with the phases of the moon (see Fig. 513). One wave, on the 15th of November, occurred at full moon, when the moon was nearest to the earth (perigee), another wave on the 28th of November occurred at new moon, when the moon was farthest from the earth (apogee). Coinciding with the last wave the herring shoals appeared, and between the 23rd and 24th of November 24,000 barrels of herring were taken.

Pettersson's observations made by the aid of his ingenious self-registering appliances are of very great interest, but it must be pointed out that the relations between the phases of the moon and the waves are not very well marked. Further, it is well known that similar oscillations in the water-layers of the Scottish lochs are produced by the varying winds that blow over the surface.¹

Nordgaard has compiled an account recording the months of the year when southern Atlantic fish-species are stranded on the coasts of Norway, and has found that such strandings generally occur from January to May. On this subject he remarks: "It is hardly accidental that so many specimens of these pelagic deep-sea fishes arrive on the coast during the first months of the year, during the time of the cod fisheries (when the shoals of cod appear in order to spawn). It is obvious that during this season especially the deeper layers move towards the land, probably as a compensation current in deep water caused by the off-shore winds forcing the surface layers out to sea." If we look at Fig. 509, showing the annual changes of temperature in the sea off western Norway, we shall see that towards the new year and during spring a marked drop in temperature occurs in the surface layers. We must take it for granted that the organisms consequently tend to move towards the surface, the specific gravity and viscosity of the water increasing enormously compared with the conditions in warmer seasons.

These conditions and their influence upon animal life are to a great extent mere guess-work, but they open up a vast field for future oceanic research.

NUTRITION

Sir John Murray divides marine deposits (see p. 161) into two main groups: (1) *Terrigenous deposits* formed in deep and shallow water close to the land masses; and (2) *Pelagic deposits* formed in deep water remote from land.

Corresponding to this division we may define the nourishment of marine animal life as derived from two main sources: (1) *Organic detritus* carried into the sea from land or formed by disintegration of the plants of the coast belt and the animals living upon them; and (2) *Pelagic plants*.

As a third source, Pütter has suggested the organic com-

¹ See Murray, *Scott. Geogr. Mag.*, vol. iv. p. 345, 1888, and vol. xiii. p. 1, 1897.

pounds dissolved in sea-water, which must be formed, however, when all is told, either by dissolution of the detritus or as excreta from living organisms.

It has long been recognised that the dust-like detritus plays an important part in the nourishment of certain bottom-animals (see Chapter VII. and the reference to Murray's "mud-line"). Investigations on the food of the oyster by Redeke and American investigators have proved that detritus forms the main contents of its stomach and intestines. Zoologists know that great numbers of bottom forms (holothurians, worms, and many others) are "mud-eaters," which live by passing the soft mud of the sea-bottom through their digestive tract. Lohmann and Rauschenplatt have lately shown that detritus also plays an important part in the nourishment of pelagic forms. Our ideas on this subject have recently been advanced by the systematic investigations of C. G. J. Petersen.¹

Organic
detritus.

In the Limfjord Petersen studied how detritus was formed by the disintegration of the dead plants along the coast, how it was found suspended in the water, and finally settled on the bottom as a soft layer 2 or 3 millimetres in thickness. In every respect this fine mud was similar to that found in the digestive tract of mussels and other animals. Petersen has proved this phenomenon to be of general importance in all the waters examined by him, and it will be necessary to examine the conditions in various areas of the sea in a very extensive way before we can arrive at a more perfect knowledge as to the nutrition of animals. In the open ocean conditions are still practically unexplored, and I will here only draw attention to some points worthy of examination in the future.

How far out to sea is the organic detritus carried? During our Atlantic cruise Gran was continually looking for detritus, centrifuging water-samples for this purpose, but as he tells us in Chapter VI. only insignificant quantities were found in the open ocean. If we may draw conclusions from bottom-deposits like Blue mud, there are vast differences in various areas of the ocean. In Chapters IV. and VII. we have seen that the terrigenous deposits on the eastern side of the Atlantic are limited to the African and European coast banks, while on the western side they extend far into the ocean beyond the coast banks of America (see Map IV.). These facts may obviously be explained as being due to currents (see current-chart, Fig. 508), which on the western side

¹ *Report of the Danish Biol. Station*, No. XX, Copenhagen, 1911.

run off-shore and on the eastern side run towards the land. The distribution of the Sargasso weed also furnishes evidence, for, wherever found it has actually been derived from the shore, and, as we know, the Sargasso weed covers a vast area of the western part of the Atlantic. Even the Sargasso weed must become detritus. Hensen has shown that the tufts of this weed gradually become overgrown with heavy bryozoa, which causes them to sink, and then they are gradually disintegrated, being transformed into detritus while sinking, and furnishing nourishment for the animals in deep water. During the cruise of the "Michael Sars" the deep waters of the western part of the ocean proved to contain a far more abundant animal life than the corresponding depths in the eastern part. We have seen from Chapter IX. that by far the greater number of the Pteropoda collected, about 3500 or 4000 specimens, were taken in the south-western portion of our track, that is in the Sargasso Sea, and the same remark applies to the pelagic fishes, for instance *Cyclothone microdon*. In giving some figures in support of this, I wish to point out that these figures must only be looked upon as relative values, and are therefore only suited for a comparison between different localities.

I choose for comparison two stations east of the Sargasso Sea, between the Canaries and the Azores (Stations 42 and 49), and two stations in the Sargasso Sea (Stations 62 and 64), and indicate the number of specimens taken at corresponding depths with the same fishing gear :—

	East of the Sargasso Sea.		In the Sargasso Sea.	
	Station 42.	Station 49.	Station 62.	Station 64.
Young - fish trawl, 1000 metres .	6	8	90	448
Large tow-net, 1500 metres	9	14	76	332

In northern boreal waters, like the Norwegian Sea, the water-layers of the coast banks cover nearly the whole of the deep area; we know this because many of the animals which are born on the coast banks are found to have drifted out into the waters above the deep area. Are also the detritus and dissolved substances carried so far from the shore? How far is the abundant life peculiar to boreal waters due to supplies

of nutriment derived from the shore? These questions must be left to future research.

In Chapter VI. Gran has described the vertical distribution of pelagic plants. In the open Atlantic he found that the great majority of the plants occur in depths between 10 and 50 metres; at 75 metres the numbers decrease to about one-half, and at 100 metres to one-tenth, of the numbers found in the upper layers. The whole of the animal life in the oceans, 5000 or 6000 metres deep, thus mainly depends on the pelagic plants suspended in the uppermost 100 metres of water. The animals frequenting this upper layer feed partly on plants, partly on other animals, while in deeper water only animal food is available, besides the dead plants and animals sinking from the surface. Nutrition in the upper "plant"-region must therefore be different from that in the deeper layers.

Many animals of the plant-region are typical plant-eaters, and their bodies are organised for this purpose. This is especially the case as regards appendicularians and salpæ, the foremost part of their digestive tract, the so-called branchial sac, being provided with a grating of the finest and most delicate structure, retaining even the most minute plants (the coccolithophoridæ). Many of these minute plant-forms were indeed first discovered by examining the stomach-contents of salpæ (Stein, Sir John Murray, Lohmann), and during the Atlantic cruise of the "Michael Sars" Gran also collected salpæ in order to secure material for comparison with our tow-net captures of minute plants. The coelenterates (medusæ, ctenophores, siphonophores) are well adapted to capture minute plants by the aid of their tentacles, and so are the unicellular animals (foraminifera and radiolaria) by the aid of their long thin plasma threads (pseudopodia). The most important of all plant-eaters are, however, the small crustaceans, particularly copepoda, which seem specially adapted for feeding on the microplankton of the ocean. Gran has examined the excrements of copepoda, which sink through the water in the shape of minute sausage-like lumps, and are very often taken in considerable quantities in the silk nets. All the soft parts have been digested, but the shells of the plants eaten, the calcareous shells of the coccolithophoridæ, the armour of peridineæ and the silicious shells of diatoms, can be identified. In the Norwegian Sea Gran observed that the copepoda were present in enormous numbers just below the layers containing a wealth of diatom plant-life, but nevertheless the excrements of these copepoda consisted of the frustules of the diatoms. The

food of copepoda in deep water has not yet, as far as I know, been made the subject of systematic investigation, although this point is essential to a more complete understanding of marine biology. Nordgaard, who is describing the copepoda from our Atlantic cruise, has at my request been kind enough to examine the stomachs of a large number of copepoda from our deepest hauls in the Sargasso Sea, but has not been able to find anything morphologically definable in their stomach-contents. Do these copepoda there feed on detritus formed by the dead and disintegrating organisms falling from the surface of the ocean?

Importance
of minute
crustacea as
food-animals.

Along with other small animals (foraminifera, radiolaria, sagittidæ), the copepoda and other crustacea form the main food-supply for the majority of the somewhat larger oceanic animals. Thus the stomach-contents of the pteropods *Clio falcata* and *Limacina helicoides* taken at depths between 500 and 1500 metres consisted of foraminifera and radiolaria. In the stomachs of large prawns, *Acantheephyra purpurea* and *A. multispina* taken below 500 metres, Sund found the remains of copepoda, sagittidæ, and fragments of minute fishes (*Cyclothone*). Koefoed has examined numerous stomachs of *Cyclothone* without finding any contents, but their guts contained organic remains, mainly the jaws of minute crustaceans. The stomach of the fish *Gonostoma grande* from deep water was found to contain a mysid (*Eucopia australis*), and in *Gonostoma rhodadenia* were found five euphausiidæ (*Nematoscelis*, *Stylocheiron*, *Euphausia*, *Thysanopoda*), seven sagittæ, five copepoda (*Euchæta*, *Eucalanus*), and some lumps consisting of radiolaria.

Many of the pelagic fishes are extremely voracious. Repeatedly other fishes have been found in their stomachs of a size nearly equal to that of the devourer. Thus a small *Astronesthes niger* had a scopelid in its stomach, and a *Chauliodus* had eaten a *Stomias boa*. The record for voracity is held by the remarkable *Chiasmodon niger* (of which we took three specimens in the Atlantic), which is known to swallow fishes several times its own size. Fig. 514 shows a specimen with only slightly extended abdomen; Fig. 515 shows a specimen that has swallowed a fish much larger than itself, and most strangely one of the same species.

Abundance
of minute
crustacea in
various areas
and depths.

Generally speaking, the very minute animals, especially the minute crustacea, play an exceedingly important part as nourishment for other and larger animals. These minute crustaceans are constantly taken in the fine silk tow-nets, and in nets with a somewhat larger mesh they constitute the bulk

of the catches. If we compare such catches at different depths and in different waters, we generally get a fair idea of the relative amount of nourishment present, and it may be of interest to examine some catches of this kind from the Atlantic and the

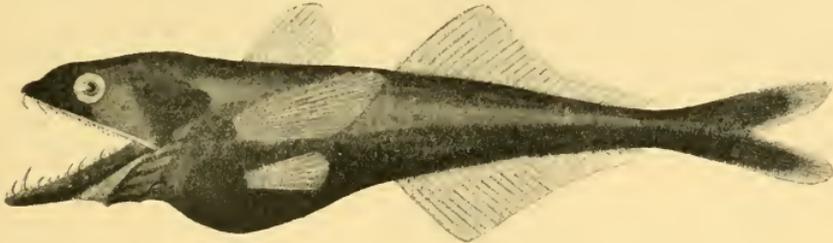


FIG. 514.
Chiasmodon niger, Johns. Nat. size, 9.5 cm. From Station 52.

Norwegian Sea, where the "Michael Sars" employed the same silk hoop-nets, 1 metre in diameter, with $\frac{1}{4}$ millimetre mesh. To commence with, we will consider the same hauls from the

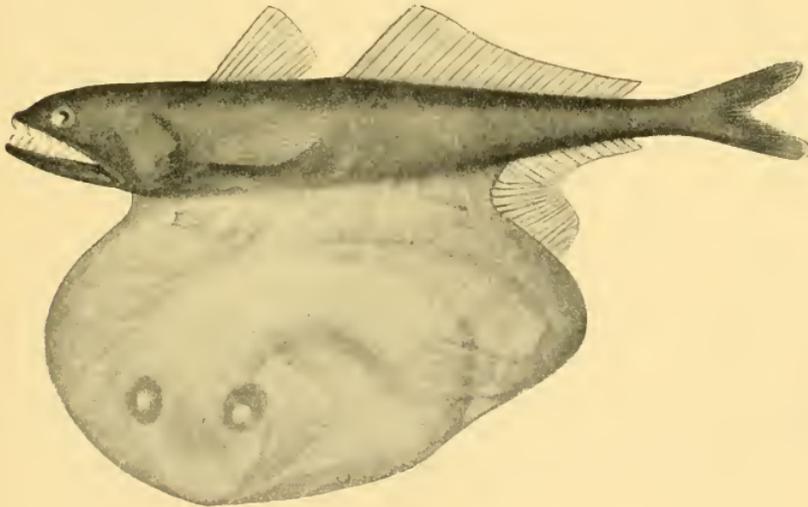


FIG. 515.
Chiasmodon niger, Johns. This specimen had swallowed a larger specimen of the same species.
Nat. size, 5.7 cm. From Station 56.

Atlantic which in Chapter IX. we have discussed from a systematic point of view, noting the volume of small pelagic animals captured, compared with the temperature, specific gravity, and viscosity of the water at corresponding depths.

During the first cruise of the "Michael Sars" in the Norwegian Sea in 1900 I was convinced that in deep water a great quantity of food would accumulate wherever a rise in the specific gravity occurs, and where, consequently, all sinking bodies either stop or have their sinking velocity reduced, forming as it were a "bottom" in mid-water. In my report on the cruise¹ I mentioned the matter, and the following observations appear to confirm this hypothesis.

In the Sargasso Sea series of hauls with closing-nets were taken at Stations 50 and 63, the net employed at Station 50

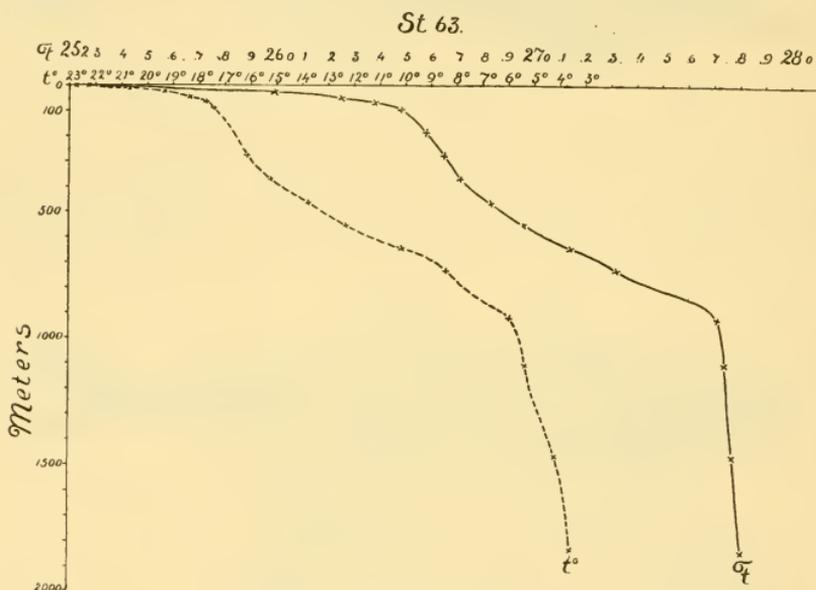


FIG. 516.—CURVES OF TEMPERATURE (t°) AND SPECIFIC GRAVITY (σ_t), STATION 63. (Sargasso Sea.)

being 1 metre in diameter, and at Station 63 half a metre in diameter, made of very fine silk. At Station 50 hauls from

200 to	0 metres	gave 3 c.c.,	containing 22 species of Crustaceans.
500 to	200	" 1.5	" 22
1000 to	500	" 6	" 51

At Station 63 hauls from

100 to	0 metres	gave 1.6 c.c.
200 to	100	" 0.5 "
500 to	200	" 1.6 "

¹ Hjort, *Die erste Nordmeerfahrt des norwegischen Fischereidampfers "Michael Sars,"* 1900, Petermann's Mitteilungen, Bd. 47, 1901.

These figures show a minimum below 100 metres, and a maximum between 500 and 1000 metres. Comparing this with the curves for specific gravity at these two stations (Figs. 516 and 517), we notice a pronounced rise in specific gravity in the upper 100 metres (the plant region), followed by a very slow rise and then a rapid rise towards 1000 metres, beyond which the specific gravity becomes very uniform. The temperature, which greatly influences the viscosity, falls gradually, corresponding to the rise in specific gravity, and in consequence the viscosity increases towards deep water.

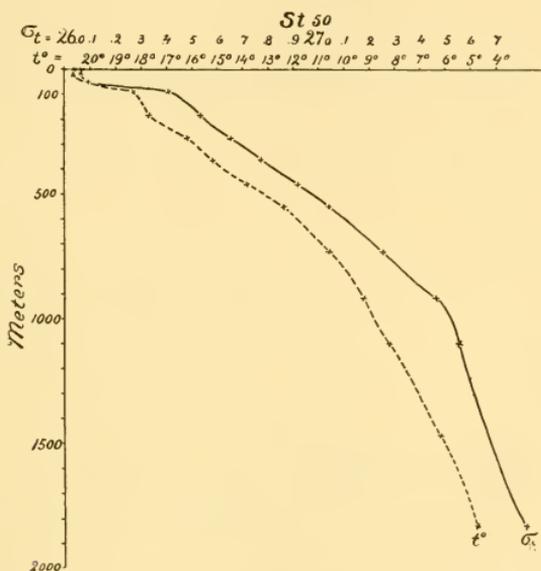


FIG. 517.—CURVES OF TEMPERATURE (t°) AND SPECIFIC GRAVITY (σ_t), STATION 50. (South of the Azores.)

Off the banks of Newfoundland we took the following series at Station 80:

235 to	0 metres gave	5 c.c. containing	16 species of Crustaceans.
525 to	235	45	27
950 to	525	28	34

The curve of specific gravity here (see Fig. 518) is essentially different from those in the Sargasso Sea, for a rapid rise occurs down to about 500 metres, beyond which the specific gravity becomes practically uniform, and at this station no minimum quantity of organisms is noticeable between 500 and 200 metres, but on the contrary a considerable rise.

The abundant plankton peculiar to boreal waters in summer (August) apparently accumulates in those layers where the highest specific gravity occurs, the volume thence decreasing in the deep uniform layers below 500 metres. A series of hauls taken close to the Wyville Thomson Ridge in the southern part of the Norwegian Sea at Station 113 gave the following results:—

100 to	0 metres gave	10 c.c. containing	...	species of Crustaceans.
300 to	100	5	"	21
500 to	300	12	"	18
1000 to	500	140	"	11

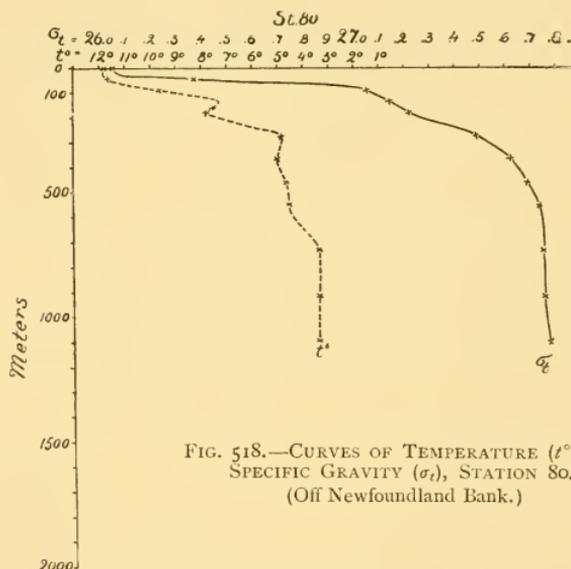


FIG. 518.—CURVES OF TEMPERATURE (t°) AND SPECIFIC GRAVITY (σ_t), STATION 80. (Off Newfoundland Bank.)

The curve for specific gravity shows here (see Fig. 519) a rapid rise down to 100 metres, then a slow rise down to about 300 metres, and finally a rapid rise down to about 600 or 700 metres. A pronounced minimum in the volume of crustacea occurs between 300 and 100 metres, and an enormous increase is found between 1000 and 500 metres, where the volume is fifty times larger than the volume in the surface layers of the Sargasso Sea.

In my opinion these facts prove the correctness of the hypothesis that minute pelagic crustacea (and consequently nourishment suitable for larger organisms) tend to accumulate at those depths where a pronounced rise in the specific gravity

and viscosity occurs. Especially convincing is the fact that although this rise occurs at very different depths in the three localities mentioned, the increase in the volume of small organisms captured in the nets in every case coincides with the rise in the specific gravity.

An important point for our conception of the animal life of the Atlantic is that the greatest volume of pelagic crustacea has never been found in the upper 100 or 200 metres, where the production of minute plants takes place; the great majority of small pelagic crustacea live everywhere in the deeper intermediate layers. The examples cited above show further that the volume of organisms captured differs greatly in corresponding depths at the different stations, being strikingly small in the Sargasso Sea compared with the boreal waters off Newfoundland and the southern part of the Norwegian Sea.

All these investigations indicate the quantity of organisms present only at the moment of examination. We cannot, from our results, conclude that similar conditions always prevail, nor that the aggregate quantities of food-animals which live and

die during the year are proportionate to the quantities found at a given moment in the different localities. The quantity of food-animals changes first according to seasons and second according to the intensity of production, but very little is known about these two important factors. Only in restricted areas of the coastal waters have attempts been made to investigate these questions systematically at different seasons, and at present we can only compare the conditions found in different localities. Such comparisons have led us to recognise a vast difference between boreal and subtropical conditions, which we may with advantage consider separately.

The boreal waters are mainly characterised by great seasonal changes. We have previously noted the great seasonal changes in temperature principally in the surface layers where pelagic plants are produced. A no less important part is played by the changes in light intensity from summer to winter

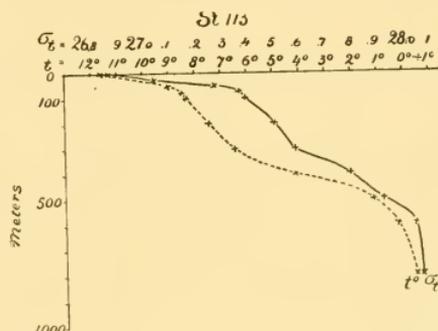


FIG. 519.—CURVES OF TEMPERATURE (t°) AND SPECIFIC GRAVITY (σ_t), STATION 113. (North of Wyville Thomson Ridge.)

Seasonal changes in the abundance of minute crustacea.

and from winter to summer. Any one who has examined the quantity of organisms obtainable in silk nets at different seasons in boreal waters will know the magnitude of these changes. I may cite some of my own results from the coast waters of Norway.

During my winter cruises in the sea between northern Norway and Spitzbergen and 240 miles west of Tromsø, the sea was everywhere found to be so poor in organisms from the surface down to 100 fathoms that we had to drag our nets for $1\frac{1}{2}$ or 2 hours before we perceived any organisms at all on the silk cloth of the nets. In February I made a haul in the Westfjord (Lofoten) with an 8-foot hoop-net from 200 metres to the surface, and caught only 380 specimens of *Calanus finmarchicus*, although perhaps 1000 tons of water were filtered by the net. On the 10th of April a haul was made on the bank off Tromsø (Svendsgrund), with the same net and from 100 metres to the surface, when 2356 specimens of *Calanus* were taken. Another haul yielded 16,420 specimens of *Calanus*, and a third about one litre of *Calanus*. This obvious increase in their numbers continued during spring, and on the 1st of June in the Altenfjord a 10-minutes' haul with a 1-metre net at the surface yielded so many individuals of *Calanus*, that their weight, after squeezing off the water, amounted to 0.8 kilogram,—a weight corresponding to at least two millions of individuals. In July some hauls with the 8-foot net were made in the Norwegian Sea, generally from 200 metres to the surface, and as a rule 200 or 250 c.c. of *Calanus* were taken, mainly consisting of *Calanus finmarchicus*. These hauls indicate the characteristic features of the occurrence of minute crustaceans in boreal waters: the poverty of winter, the abundance of summer.

Gran and Damas have continued these investigations during the cruises of the "Michael Sars," at the same time taking up the study of the life-history of *Calanus finmarchicus*. Gran arrived at the conclusion, now confirmed by more recent investigations, that the life-cycle of this species is annual. During winter only adult animals are met with. They breed in spring, and the young pass through five larval stages; in the sixth stage they assume the shape of the adults. From a detailed study of the material collected in the nets Damas attempted to draw a chart showing the spawning places, arriving at the conclusion that spawning does not take place to any important extent in the fjords, nor on the coast banks, but principally above the

continental slopes of the Norwegian Sea. From these localities the young stages spread over the whole sea, including the coast banks and the fjords of Norway. During summer only young individuals are met with, immediately recognizable by the presence of large oil-globules. These minute calani constitute the main nourishment upon which more or less directly the animal life of the Norwegian Sea depends. Even the enormous whalebone whales feed on calani. During the last months of the year the number of calani decreases enormously, and in winter only a few adult individuals remain.

In Chapter VI. Gran gives an account of Lohmann's attempts at calculating the relation between the increment in pelagic plants and the consumption of plants by animals in the fjords at Kiel during the course of a year. According to Lohmann's calculations the volume of plants increases daily by 30 per cent, which increase may be used up by animals without endangering the existence of the plant-stock. Copepoda and other multicellular animals are supposed to need a daily supply of food equivalent to about one-tenth of their own weight. Starting from these assumptions Lohmann attempts to calculate the relation between production and consumption in the course of the year, and arrives at the conclusion that there is generally a surplus of plants except in the winter. For details I refer to the table on p. 384, recording the daily increment of various food producers during the year, which varies greatly from summer to winter, the relation amounting sometimes to 35 : 1.

In tropical and subtropical waters no seasonal changes of this kind appear to take place. At least all the tow-nettings taken in the tropics by various expeditions have always yielded remarkably uniform catches in the upper layers, which are the ones most thoroughly examined, these catches being very small compared with similar catches during summer in boreal waters. As instances of this I may mention that the closing-nets of the "Michael Sars" when hauled from 200 metres to the surface in the Sargasso Sea yielded on the average 3 c.c. of plankton, while in the Norwegian Sea from 85 to 225 c.c. were obtained in numerous similar hauls.¹ Similar results were obtained during the German Plankton Expedition.

Conditions in
tropical
waters.

It is, however, at present impossible to form any idea whether the volumes thus obtained really tell us anything whatever about the annual production. First of all in boreal waters we have to deal with the enormous seasonal changes. Secondly,

¹ Damas and Koefoed, *loc. cit.*

we know nothing whatever about the "daily increment" in the producing organisms of the open ocean, and therefore the futility of every attempt at comparison is evident. The small volume of plants and animals peculiar to the upper strata of the warm regions of the ocean cannot, in consequence, justify the conclusion that the production is small. The abundance of animals found in the deeper layers of the open ocean seems to indicate rapid production associated with rapid consumption in the upper plant region of the sea.

Although it is as yet quite impossible to form an opinion on the absolute magnitude of the production in certain regions, it has been supposed that the relative amount of nutriment contained in various waters might be compared. As mentioned by Gran on pp. 367-381, botanists are of opinion that in the open ocean, far from land, certain of the nutritive substances essential to plant life, especially nitrogen, are present in very small quantities (the minimum of Liebig), and consequently the plants cannot develop as profusely as they otherwise would do. Pelagic plant life draws its principal supply of dissolved or undissolved nitrogen either from the coasts (see remarks on detritus), or from localities where cold and warm currents meet. In these latter localities the conditions may suddenly become favourable for the development of life, just as development in boreal waters begins in spring, when the rays of the sun raise the temperature of the surface water. The organic substances contained in the cold waters become transformed into inorganic salts through the action of bacteria, and these salts are used by the microscopic plants to build up new protoplasm. Murray and Irvine¹ first drew attention to the importance of this process in the ocean, which plays a great part wherever large sheets of cold and warm water are mixed.²

The boreal waters should, accordingly, present favourable conditions for developing an abundant animal life during the warm season, the coast waters carrying detritus spread out over the whole oceanic area, while arctic currents mix with the warm Atlantic Gulf Stream, for instance in the Barentz Sea, north and east of Iceland, and off the coast banks of Labrador and Newfoundland.

¹ "On Coral Reefs and other Carbonate of Lime Formations in Modern Seas," *Proc. Roy. Soc. Edin.*, vol. xvii., 1890.

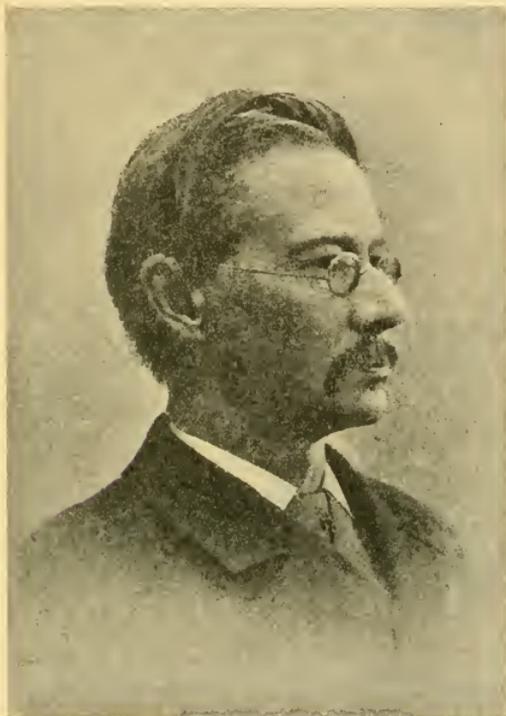
² Similar ideas have been expressed by Nansen, "The Oceanography of the North Polar Basin," *Norwegian North Polar Expedition*, Christiania, 1902.

PROPAGATION

During autumn and the last months of the year thermal conditions alter greatly in boreal waters, high temperatures retreating from the surface down to 200 or 300 metres (see Fig. 509). At the same time the sexual organs develop in most boreal food fishes: the cod family, the herrings, the flat-fishes and others, and during the three or four first months of the year they spawn. Most of these edible fishes possess large ovaries containing enormous numbers of eggs, the cod, for instance, having apparently on the average no less than five million eggs.

Late in the 'sixties of last century, G. O. Sars commenced his investigations on the famous cod fisheries in the Lofoten Islands. He found that the eggs of the cod were pelagic, floating in the surface layers of the sea, and he carefully studied the development of these eggs, making a number of excellent drawings, which I regret to say have never been published. These original

Develop-
mental stages
of the cod.



G. O. SARS.

drawings foreshadow much of the knowledge gained in recent years on the early development of the cod, and I consider it interesting to reproduce some of them illustrating certain stages. The characters distinguishing these stages are just as law-bound as those of the adult individuals. One stage (see Fig. 520) is characterised by dark transverse bars of black pigment, which subsequently dissolve into fine longitudinal bands, following the dorsal and ventral side of the body, a fine stripe running along the lateral line. Later on the

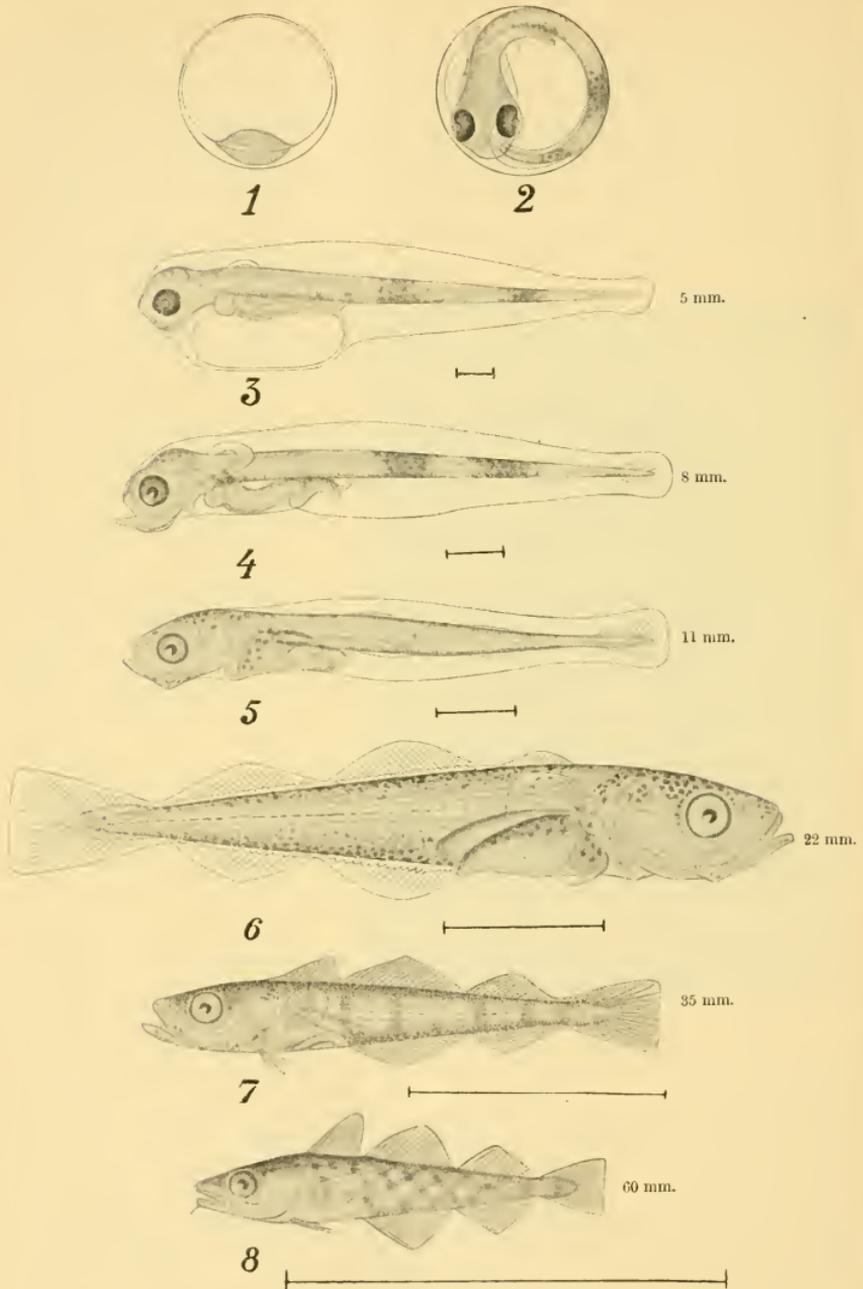


FIG. 520.

Development of the cod (*Gadus callarias*) from the egg to the young-fish stage.
(From drawings by G. O. Sars.)

pigment is arranged in a chequered colour pattern, resembling the squares of a chess-board. So regular and characteristic are these stages that, once knowing them, we can separate a young cod from every other young fish, and define its stage of development or even its age.

Since Sars discovered the eggs of the cod to be pelagic, a great many other species have been found to possess floating eggs and larvæ, for example all the cod-species and flat-fishes, the sprat, the mackerel, and many others. A voluminous literature recording the investigations has accumulated, Agassiz,

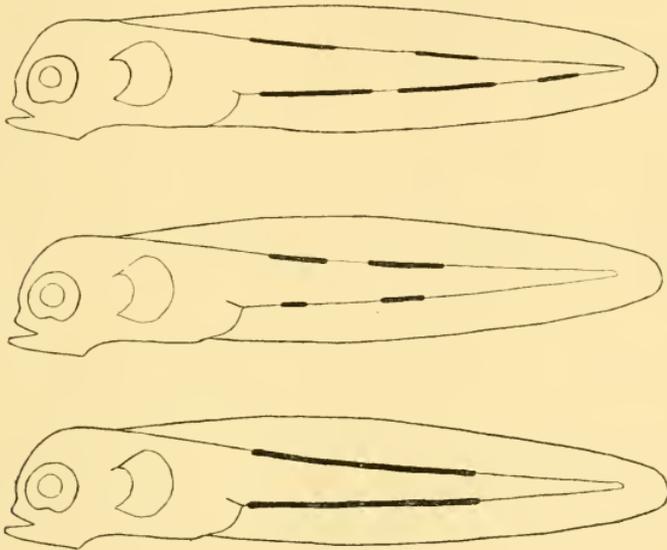


FIG. 521.

Diagrammatic figures to show the arrangement of the postanal pigment in the earliest stages of *Gadus callarias*, *G. virens*, *G. pollachius*. (After Schmidt.)

Ehrenbaum, Heincke, Hensen, Holt, M'Intosh, Masterman, Petersen, and Schmidt having made valuable contributions to our knowledge of the eggs and larvæ of various fishes.¹ From Schmidt² I reproduce some outline drawings (see Fig. 521) of the pigment arrangement in a corresponding larval stage of three closely related cod-species, viz. *Gadus callarias*, *G. virens*, and *G. pollachius* (the cod, saithe, and pollack). Although these larvæ closely resemble each other, the arrangement of the pigment is different.

¹ Ehrenbaum gives an excellent summary in "Eier und Larven von Fischen," *Nord. Plankton*, Lfg. 4, 1905, Lfg. 10, 1909.

² Schmidt, *loc. cit.*

Spawning
areas.

This power of distinguishing the different species in early stages has been of great advantage to oceanography. By securing the eggs and larvæ floating in the surface waters, we can decide what species spawn in a definite area. We capture in our silk nets a profusion of different eggs and larvæ, and can with certain limitations separate them as belonging to various species, just as we assort the catches of adult fishes from a haul with the trawl. The spawning area of a species can thus be determined by merely taking numerous tow-nettings, and ascertaining the presence or absence of the eggs belonging to the species in question.

To catch the adult spawners is very often difficult, and takes a long time. The floating eggs can, on the other hand, be taken with the greatest ease, and the simple appliance of the tow-net furnishes an excellent means of ascertaining where the fishes spawn, for most species remain some time underneath the recently spawned eggs. In April 1901 I followed up this reasoning on the coast banks off northern Norway, and succeeded in finding enormous shoals of cod on certain banks, where no fishing was carried on, and where, as a consequence of our discovery, millions of cod were afterwards taken.¹

Stimulated by this experience I advised the International Council for the Study of the Sea to effect a systematic survey of the spawning areas of the cod family. My proposals were adopted, and an enormous amount of material relating to the natural history of the cod family was accumulated, thanks to the exertions of those on board the Danish, Belgian, English, Scottish, Dutch, Norwegian, Swedish, and German investigation steamers.

The Danish steamer "Thor," under the leadership of Schmidt, investigated certain parts of the Atlantic and the waters round Iceland. The Norwegian steamer "Michael Sars" examined the Norwegian Sea and the northern portion of the North Sea, while the steamers of the other countries worked mainly in the North Sea. The results obtained through this organisation of the work proved that even closely related species presented certain peculiarities as regards the situation and extent of their spawning places,² as shown in the following table:—

¹ *Fiskeri og Hvalfangst i det nordlige Norge*, Bergen, 1902.

² "Rapport sur les travaux de la commission A dans la période 1902-1907," *Rapports et Procès verbaux du Conseil international*, vol. x. Copenhagen, 1909.

I. SPAWNING IN THE ATLANTIC, IN THE NORTH SEA, AND IN THE NORWEGIAN SEA.

A. On coast banks in depths less than 100 metres.

<i>Gadus merlangus</i> ,	Optimum 20 to 60 metres.
„ <i>callarias</i> , ¹	„ 40 to 80 „
„ <i>aglefinus</i> ,	„ beyond 60 „
„ <i>esmarki</i> ,	„ „ 80 „

B. On the slopes of the coast banks.

<i>Molva molva</i> ,	Optimum 60 to 200 metres.
<i>Gadus virens</i> ,	„ 100 to 200 „

C. On the edge of the coast banks.

Brosmius brosme, Optimum 100 to 500 metres.

II. SPAWNING ENTIRELY, OR ALMOST ENTIRELY, IN THE ATLANTIC.

A. On coast banks beyond 100 metres.

<i>Gadus luscus</i> ,
„ <i>minutus</i> ,
„ <i>pollachius</i> , ¹

B. On the slopes towards the edge.

Merluccius vulgaris, Opt. 100 to 200 metres.

C. On the edge of the coast banks.

<i>Gadiculus argenteus</i> , ¹	} Optimum from 200 to 1000 metres.
<i>Gadus poutassou</i> ,	
<i>Molva byrkelange</i> , ¹	
„ <i>elongata</i>	

From the point of view of general biology it is interesting to note from this table that species, which in shape and general anatomy are very similar, present such pronounced differences as to their habitat during this most important process of life (see the chart, Fig. 522, showing the spawning area of the three ling species).

C. G. J. Petersen² was one of the first to draw attention to the influence exerted by currents on pelagic eggs. After his investigations in the Lesser Belt (Faenoe Sund) he sums up as follows: "It is one of the facts that have astonished me most during these researches that the fry of pelagic eggs, which were sometimes found in such huge numbers in Faenoe Sund, was not hatched there, or at any rate was only to be found there quite exceptionally. This condition did not only apply to the cod, but indeed to all species which possess floating eggs, in contrast to the fishes which deposit their eggs on the bottom." It has proved very important to investigate the drift of pelagic eggs, and this study has yielded important results regarding the different species. The drift of the eggs depends on physical as well as biological conditions. The direction and velocity of the currents, the temperature, the duration of the hatching and development, the actual duration of the pelagic life which varies in different species, all these are important points. Finally, the specific gravity of the eggs and larvæ is of great importance in determining the depth at which they float. From my investigations on the distribution of cod eggs, larvæ, and pelagic fry in

Effect of
currents on
floating eggs.

¹ Also spawn in the Norwegian fjords.

² *Report of the Danish Biol. Station*, 1893.

northern Norway I reproduce Fig. 523, in which the different curves denote :—

- I. The outer limit of pelagic cod eggs during the spring of 1901.
- II. " minute larvæ and young, June-July, 1901.
- III. " large pelagic fry, August 1900.

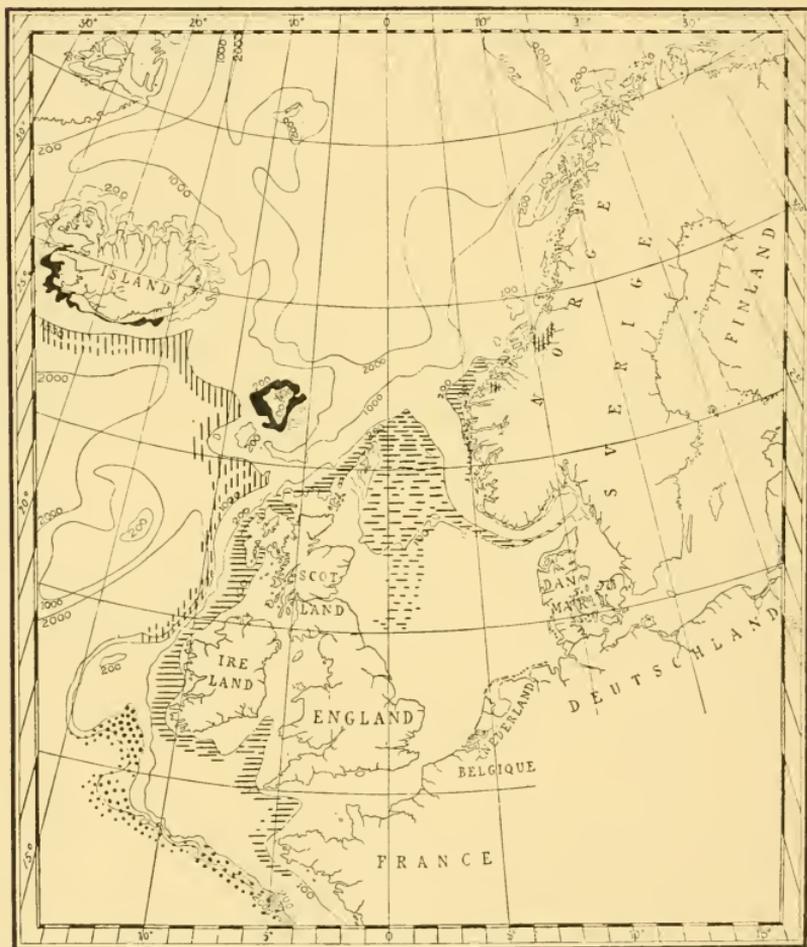


FIG. 522.—SPAWNING REGIONS OF THE THREE SPECIES OF THE GENUS *MOLVA*.
Vertical lines, *Molva byrkelange*; horizontal lines and black portions, *M. molva*; dots,
M. elongata.

(From *International Reports*, vol. x.)

In northern Norway there is plainly a movement along the coast and away from land. During development the minute fish are carried hundreds of miles away from the spawning places.

The direction of the movement will, of course, depend on the currents, and on other conditions peculiar to various localities. In the district of Romsdal Damas made some excellent investigations on board the "Michael Sars," and ascertained that spawning took place almost exclusively on the coast banks, that in the fjords being quite insignificant (see Fig. 524). The young fry, however, were later found in vast quantities in the fjords, having been carried in by currents. Schmidt has

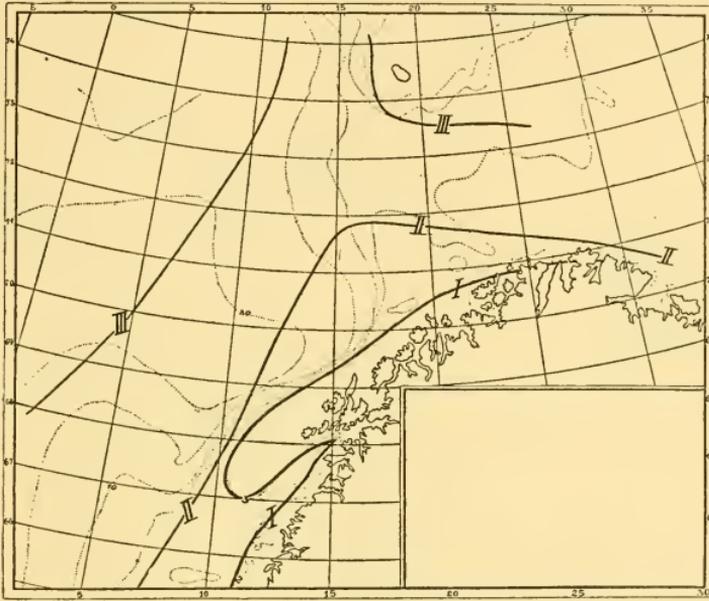


FIG. 523.—DISTRIBUTION OF PELAGIC EGGS AND YOUNG-FISH OF THE COD AT DIFFERENT SEASONS.

- I. Outer limit of pelagic eggs in the spawning time, January to April 1901.
- II. Outer limit of pelagic young-fish, June to July 1901.
- III. Outer limit of pelagic young-fish, August to September 1900.

given an account of the spawning of different cod-species off Iceland, the occurrence of pelagic eggs and their subsequent fate (see Fig. 525). Most cod species and flat-fishes spawn on the south and south-west coasts of Iceland, the northern and north-eastern sides of the island being encircled by cold waters during winter and spring. The freshly spawned eggs drift from the south to the west coast, and farther to the north and east coasts, the current running in this direction. The duration of the pelagic stage is, however, different in different species of the cod family; their spawning seasons also differ. As a con-

sequence the distribution of the first bottom-stages is different, for instance, in cod and saithe, as shown in Fig. 525. The young saithe, having a comparatively short pelagic life, occur mainly on the south and west coasts, and only to a small extent on the north and east coasts. The eggs and fry of the cod are pelagic for a longer period, and consequently the majority of them drift round to the north and east coasts.

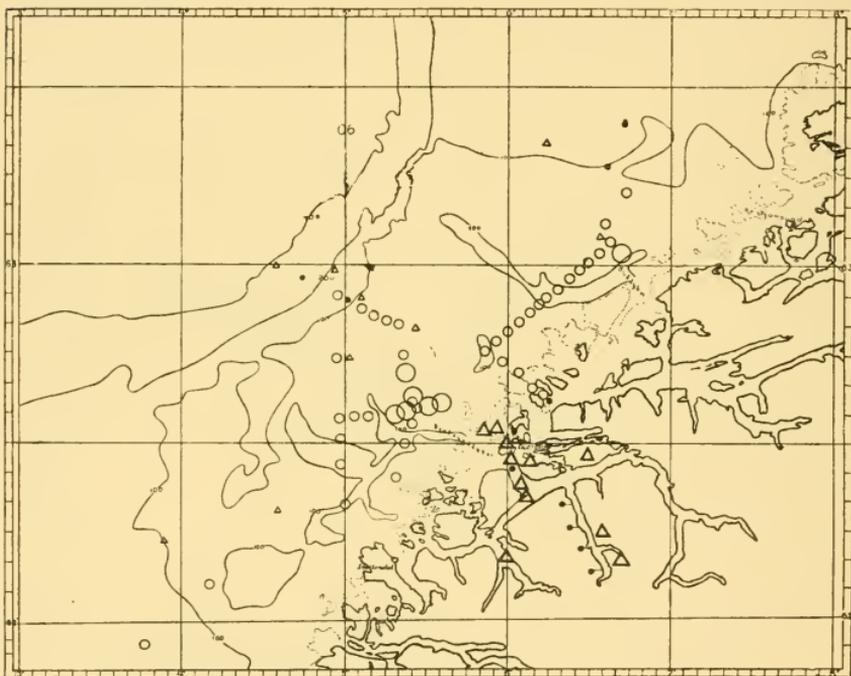


FIG. 524.—DISTRIBUTION OF EGGS AND LARVÆ OF GADOIDS IN THE ROMSDAL DISTRICT. Dots denote that less than 500 eggs were taken; small circles, that 500 to 10,000 eggs were taken; large circles, that 10,000 to 100,000 eggs were taken (March to April 1906)—all in hauls of five minutes' duration. Small triangles denote that less than 100 pelagic fry were taken, large triangles, that 100 to 10,000 pelagic fry were taken per hour in May to June 1906. (From Damas' investigations with the "Michael Sars.")

When currents run off-shore, the direction of the current and the extent of the influence of the coast-water in the open ocean can be ascertained by studying the distribution of organisms born on the coast banks. As we have seen, this study is also very important for our ideas as to the amount of nutriment carried from the land to the open ocean. Fish fry are actually such current indicators, and in the Norwegian Sea they are accompanied by stinging medusæ (*Cyanea capillata*),

which have also a bottom stage on the coast banks. In August 1900 their distribution was identical with that of the pelagic cod fry, and was limited by curve III. in chart, Fig. 523. Similar instances might be quoted in profusion, especially from recent Danish and Norwegian investigations. Of special interest is the great number of observations of larvæ and young fish drifting from the Atlantic coast banks off the west coast of Scotland into the North Sea and the Norwegian Sea (compare the drift of *Salpæ*).

We will now proceed to review our knowledge as to the

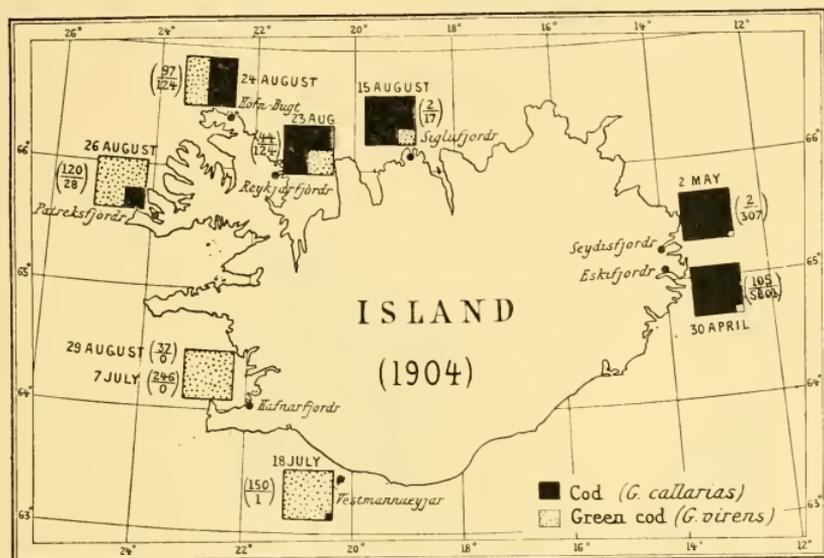


FIG. 525.—RELATIVE NUMBERS OF THE EARLIEST BOTTOM-STAGES OF *GADUS VIRENS* AND *G. CALLARIAS* AROUND ICELAND IN THE SUMMER OF 1904. (From Schmidt.)

conditions of the Atlantic, referring, for want of space, mainly to our own investigations.

It is not an easy matter to examine the reproduction of animals in the open ocean. Very few studies have, therefore, been made on the development of the oceanic fishes, and little is known as to their characters in early stages. Valuable information has been gathered and drawings have been made, especially by Günther and by Danish naturalists, Lütken and others, but complete series, showing the development of the species, are only available for a very limited number of species. Every expedition must, therefore, in the present state of our knowledge, make a laborious systematic study of the collections

brought home. As regards our own expedition we have as yet been able to accomplish only a small part of this work, and at present I am unable to pass a definite opinion on our material as a whole, nor to say what this material does not contain.

Spawning
seasons.

Do our collections of fish eggs and fry from the Atlantic indicate any definite spawning seasons in the Atlantic, as there are in the Norwegian Sea? It is generally known that in the tropics many animals propagate at all times of the year. Thus Carl Semper writes as follows: "During my stay in the Philippines nothing struck me as being more peculiar than the

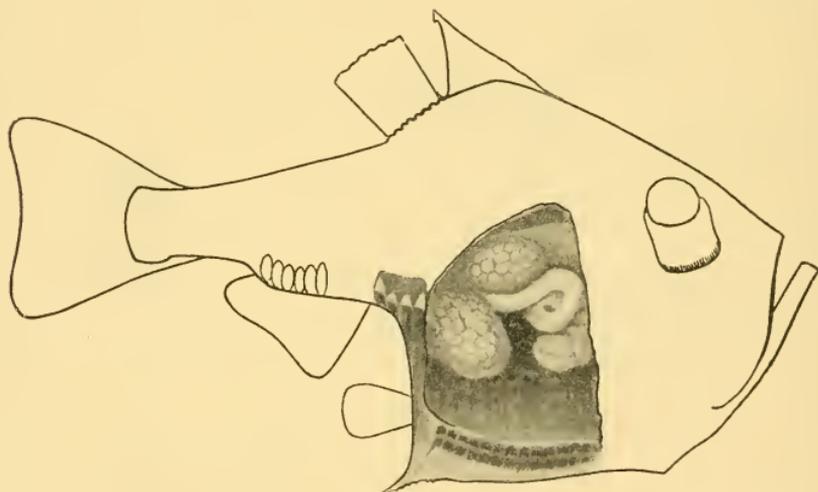


FIG. 526.

Argyropelecus hemigymnus, Cocco. Nat. size, 3.4 cm.

evident lack of periodicity in the life of the animals, peculiar even to insects, land mollusca, and other terrestrial animals. I could always find eggs, larvæ, and adult individuals of a species at the same time, during winter as well as in summer." It is quite evident that a short voyage in a steamer, passing over enormous stretches of ocean in the course of a few days, offers no opportunity of studying the conditions of propagation all the year round. I can only point out how desirable it is that the Atlantic should be examined at all seasons of the year, for only by this means can the conditions be fully understood.

Although we could effect no reliable quantitative analysis, it struck me on our cruise that the number of fish larvæ and fry

seemed far to exceed that of the pelagic fish eggs; this also appears to have been the case with the catches of the German Plankton Expedition, but these catches were very small. The scarcity of fish eggs and the abundance of pelagic fish fry might appear to indicate a continuous production of rapidly hatching eggs, the larval and post-larval stages being of much longer duration, but a study of the ovaries of the adult fishes does not favour this supposition. In *Cyclothone*, for instance, the eggs seem to be equally developed in every portion of the ovary, and to ripen throughout the entire length of the ovary at the same time. During our cruise the ovaries were found to be ripest at Stations 53 and 64 on the southern section.

Any observer previously acquainted only with the spawning of large boreal fishes must be strongly impressed by the appearance of the minute, sexually mature, oceanic fishes. Figs. 526 to 529 represent some ripe fish of genuine oceanic types and their ovaries. In the laterally compressed *Argyropelecus hemigymnus* (Fig. 526), the ovaries, containing only a few hundred eggs, lie wholly or partly above one another, and the full-grown individual, the ovaries of which approach ripeness, is only 3.4 cm. long. *Cyclothone signata* (Fig. 527) becomes sexually mature when 3 or 3.5 cm. in length, the aggregate number of eggs contained in both ovaries being about 1000. *Cyclothone microdon* (Fig. 528), on the whole a larger species, becomes mature when about 6 cm. in length, the ovaries containing a total of about 10,000 eggs. A specimen of *Photostomias guernei* 10.8 cm. in length had, according to Collett, about 400 eggs in each ovary. *Gonostoma grande* had, according to Collett, 2798 eggs. On the other hand, the larger pelagic fishes from deep water, like *Gastrostomus bairdii* (see Fig. 529), have many eggs, but they

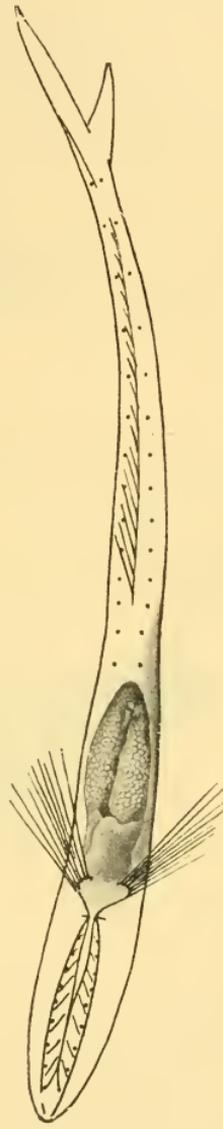


FIG. 527.
Cyclothone signata, Garm.
Nat. size, 3.5 cm.

are very small (according to Gill and Ryder 0.7 mm. in diameter).

An important question is: Where does the spawning take place? I do not believe in any general vertical spawning migration among deep-sea pelagic animals, even if the eggs develop in the upper strata of the ocean; the eggs themselves must rise to the surface. If this were not so, we

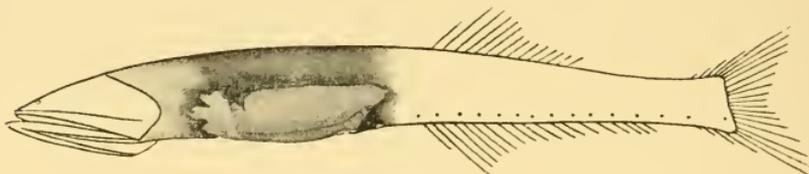


FIG. 528.

Cyclothone microdon, Günth. Nat. size, 6.3 cm.

should undoubtedly have taken, in the upper layers, many more of the pelagic fishes peculiar to deep water, whereas we took them with ripe eggs in deep water. The eggs captured and examined by us vary greatly in size and appearance; Fig. 530 shows the relative size of some of them. A is a small egg a little more than $\frac{1}{3}$ mm. in

Size of fish
eggs.

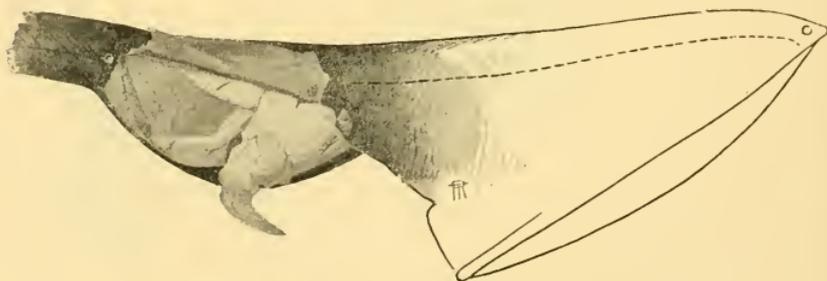


FIG. 529.

Gastrostomus bairdii, Gill and Ryder. Nat. size, 76 cm.

diameter, taken between the Canaries and the Azores; B and C are nearly ripe eggs from *Cyclothone signata* and *C. microdon* (0.46 and 0.56 mm. in diameter); D is the egg of *Gastrostomus bairdii*. It is interesting to compare these with the cod egg (E), especially when we consider the number of eggs produced by this fish. *Cyclothone signata*, the eggs of which are perhaps only one-tenth of the volume of the cod eggs, has only 1000 eggs compared with the five million eggs of the cod.

This great contrast in the conditions of propagation is obviously a very characteristic feature. At this point, however, we encounter the same difficulty met with in discussing the reproduction of the minute plants and food animals of the ocean, for we are ignorant as to how often these small fishes reproduce their kind during the year.

Figs. 531 and 532 represent the eggs of *Scombresox* and *Trachypterus*, and show that oceanic eggs are not all small. The large egg of *Trachypterus* (2.8 mm. in diameter) was captured at Station 52, south of the Azores, and plainly shows that the large and remarkable Trachypteridæ propagate in

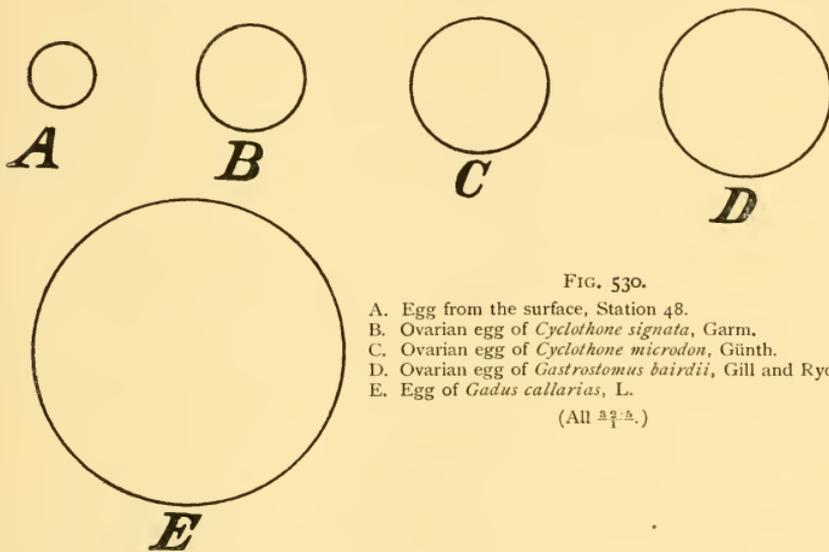


FIG. 530.

- A. Egg from the surface, Station 48.
- B. Ovarian egg of *Cyclothone signata*, Garm.
- C. Ovarian egg of *Cyclothone microdon*, Günth.
- D. Ovarian egg of *Gastrostomus bairdii*, Gill and Ryd.
- E. Egg of *Gadus callarias*, L.

(All $\frac{3}{4}$ in.)

entirely oceanic conditions. Judging from their appearance they probably live at similar depths as *Argyropelecus* and the Stomiatiidæ.

During the whole of our Atlantic cruise we constantly captured young fish, in fact many thousands in all. According to their vertical distribution these young fish may be divided into two groups. Fig. 533 shows that the majority of the 3604 young fishes examined were taken in the uppermost 150 metres of the sea. Most of the young fishes taken in appliances used in deeper water have, in all probability, been taken while hauling in the gear, and nearly all the peculiar large leptocephali have also been taken in the upper layer. But there is a certain group of young fishes which show a maximum frequency about

Vertical distribution of young fish.

300 metres, mainly those of the genus *Argyropelecus*, the adults

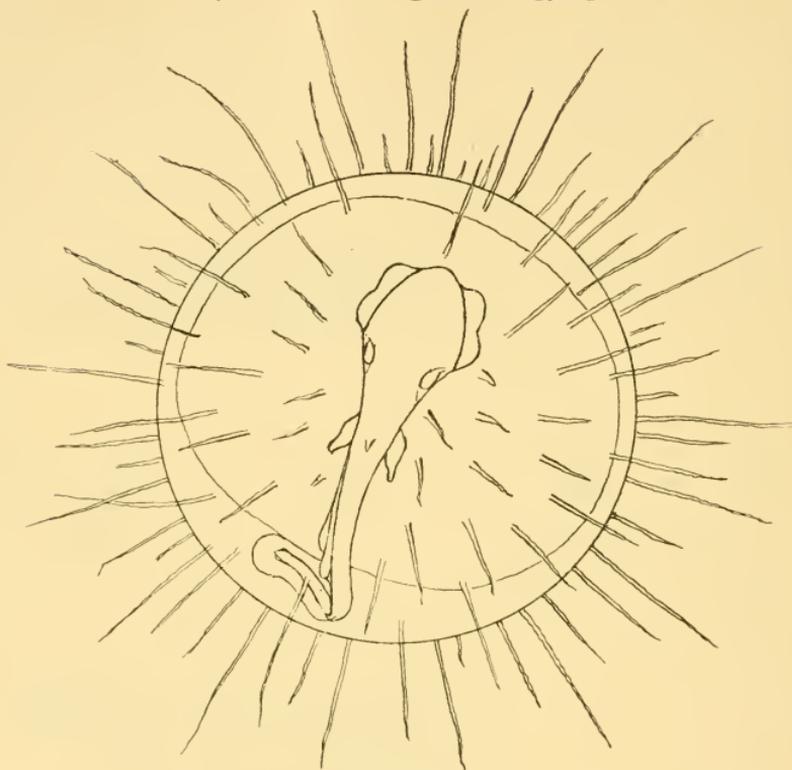


FIG. 531.

Egg of Scombresocid. Diameter, 2.2 mm. Station 64.

of which live at these depths. A third group containing larvæ and young of *Alepocephalidæ* has only been taken below 500 metres. We see from Fig. 474, p. 621, that even the small stages of *Cyclothone* are found at 300 and 500 metres.



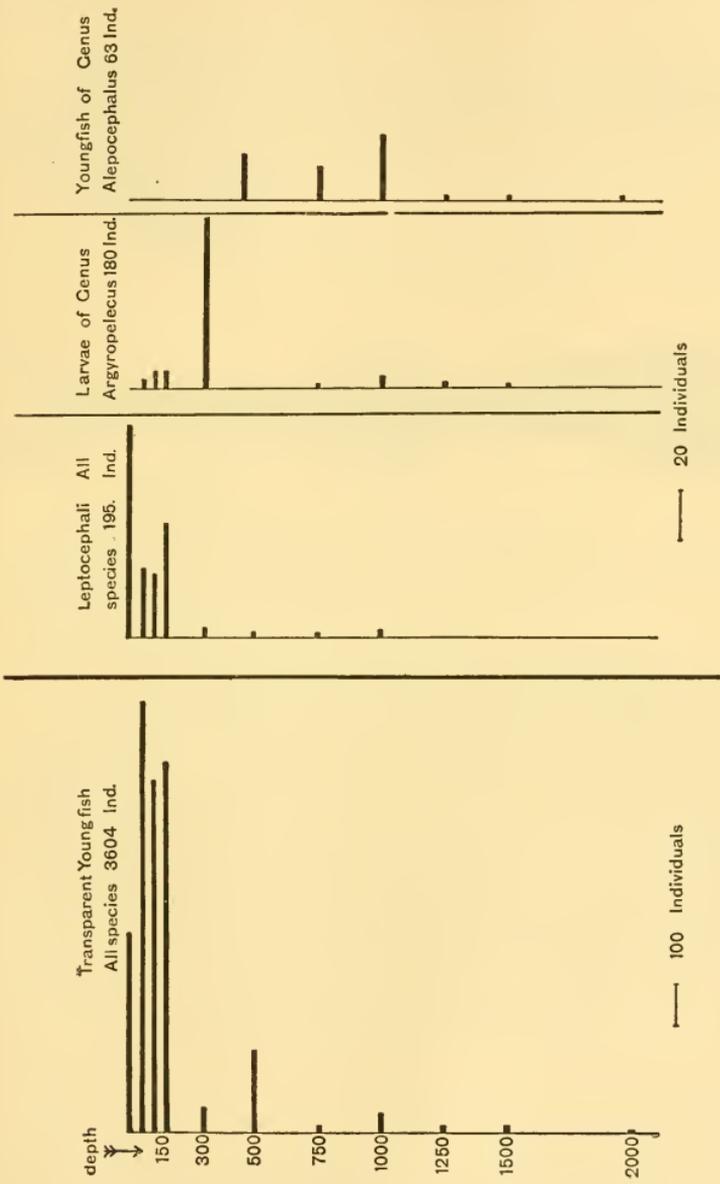
FIG. 532.

Egg of *Trachypterus*.
Diameter, 2.8 mm. Station 52.

It is interesting to note that the young stages of pelagic fishes are subject to the same laws regarding the development of colouring and light-organs as the adults. In the uppermost 150 metres the young are quite transparent, and many of them possess light-organs in very early stages.

Early stages of *Argyropelecus* (see Fig. 534) develop the silvery

shen peculiar to the adults, and the young Alepocephalidæ (see Plate IX.) have the black pigment peculiar to the fish-



Young fish from all Stations
FIG. 533.

fauna of deep water. The genus *Gonostoma* is in this respect specially interesting, for the young of the deepest living species,

Gonostoma grande (see Chapter IX. and Plate II.), occur in deep water, and even when only 3 or 4 centimetres long are of



FIG. 534.
Argyropelecus, sp. juv. Nat. size, 0.8 cm.



FIG. 535.
Gonostoma grande, Collett. Nat. size, 3.7 cm.



FIG. 536.
Aceratias macrorhinus indicus, A. Br., juv. Nat. size, 1.8 cm.

a deep black colour (see Fig. 535), while the young of *Gonostoma denudatum* are colourless and live in the surface waters. Fig. 536 represents the young of the dark species, *Aceratias*

macrorhinus indicus, 1.8 cm. long. So few of these were captured that I cannot attempt to define their vertical distribution.

These instances suffice to show that in the ocean the vertical distribution of young stages varies greatly in different species. Certain forms pass the whole of their life-cycle in deep water beyond 500 metres; others live in deep water only in the adult stage, or at least spend their early life in the upper water-layers; others, again, pass the whole of their life in certain clearly defined intermediate layers; while others live in the surface waters all their lives. All these groups are holopelagic forms, but we meet with a group of genuine deep-sea fishes,

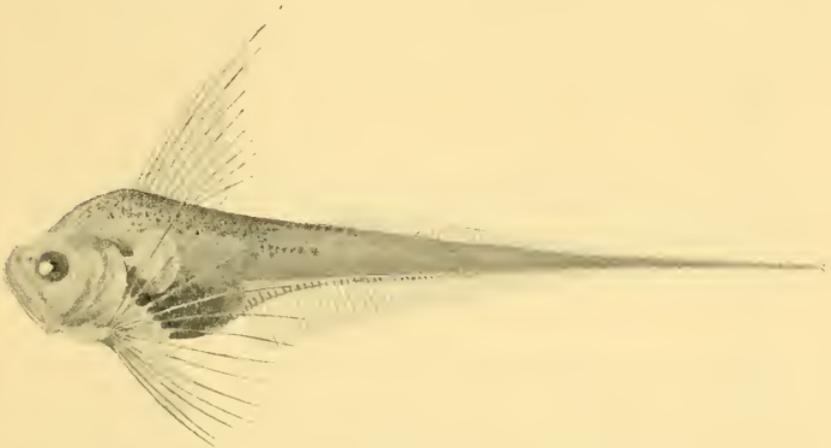


FIG. 537.

Young of *Macrurus*. Nat. size, 4.6 cm. Station 101.

which in the adult stage live along the ocean-floor, while the eggs and fry occur in the water above, at depths varying in different species. These forms remind us of the fishes of the coast banks, from which they have probably been derived. Of special interest is the fact that we found the pelagic young of *Macruridæ* (see Fig. 537) south of the Azores and at Station 101, between Rockall and the west coast of Scotland, though we have been unable to determine the species.

The majority of the young fish collected by us belong to the biological group of transparent surface forms, but some of the minute stages may have escaped our notice or may have been damaged beyond recognition by the coarse cloth employed in some of our gear. The various forms contained in our collections have yet to be systematically examined, so

that I can here only with great reserve say something about my preliminary impressions. It seems as if most of the specimens belong to the family Scopelidæ, which is represented in great numbers. Even young stages develop light-



FIG. 538.
Myctophum rissoi, Cocco. Nat. size, 11.5 mm.

organs (see Fig. 538), the arrangement and numbers of which, according to Brauer, are so regular that specific distinctions

may be based upon them. Secondly, there are many interesting and peculiar forms, stalk-eyed larvæ (see Fig. 539) of



FIG. 539.
Stalk-eyed fish larva. Nat. size, 0.9 cm.

various species being present. We have also excellent series of perfectly transparent forms with large telescopic eyes (see



FIG. 540.
New fish, resembling *Dysomma*. Nat. size, 8.5 cm.

Fig. 540, representing one of a series of stages belonging to a near ally of the genus *Dysomma*).

I was very anxious during our cruise to see if the pelagic appliances would yield any widely distributed young fish

belonging to the large edible types of pelagic fishes known from the coast banks, such as the mackerel, but our preliminary examination has not revealed many of these. At Station 42 one young individual belonging to the genus *Scomber* was taken, but this station is not far from the Canaries. The only young belonging to larger fishes of any economic importance taken by us in great numbers were those of the Saury pike (*Scombresox saurus*; see Fig. 541) and of the horse mackerel (*Caranx trachurus*). The young of both these forms have obviously a wide distribution, occurring abundantly in the open ocean even at the greatest possible distance from the coast; the eggs of *Scombresox saurus* were taken in the Sargasso Sea.

Geographical
distribution
of young fish.

The list of pelagic fishes in Chapter IX. shows that the majority were taken on our southern track, which agrees with the results of previous expeditions. Lütken says in his *Spolia*



FIG. 541.

Scombresox saurus, Walb. Nat. size, 6.2 cm.

Atlantica that the young of *Scombresox* were the most numerous fishes in his collections from the open Atlantic, having been obtained from no less than ninety different localities situated in two belts between latitudes 11° or 12° and 40° on both sides of the equator. They are typical surface forms, distinguished by a dark-blue colour on the back, while the sides are silvery and mirror-like. They pass through a typical metamorphosis, like the young of the gar-pike, the long jaws appearing only at a more advanced age (see Fig. 542, reproduced from Lütken). Related to *Scombresox* is the genus *Exocoetus*, which includes the typical flying fishes; I have indicated in Chapter III. that the young of these flying fishes (see Fig. 543) were taken by us at several localities in various stages. *Scombresox*, *Caranx*, and *Exocoetus* were thus the most important young fish belonging to large surface forms taken in our Atlantic cruise. In the chart (Fig. 544) I have indicated the quantities of young fish captured by us in various localities, though these quantities have in my opinion no other value than showing that great numbers of larvæ may be captured during summer in the open ocean as

well as near the coast banks. Our methods of capture were not designed for the purpose of obtaining detailed information

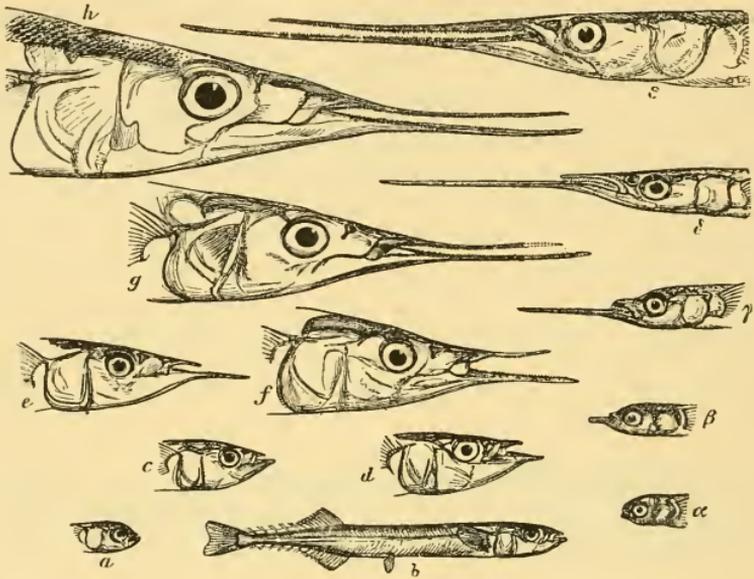


FIG. 542.

a-h, heads of *Scombrosox saurus* in different stages of development; *b*, a young fish. The younger stages somewhat enlarged, the older somewhat reduced in size. *a-e*, heads of *Belone vulgaris*. (From Lütken.)

as to the quantities occurring in different areas of the ocean; but in the present state of our knowledge it is very interesting

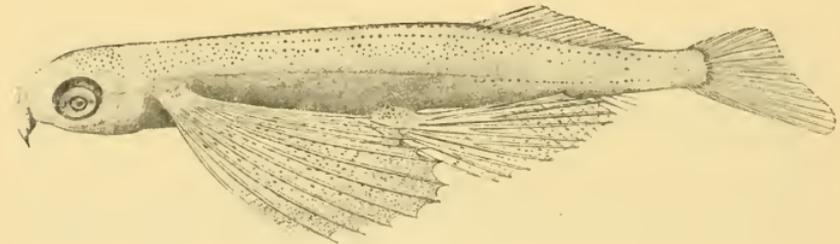


FIG. 543.

Young flying fish (*Exocoetus*). Nat. size, 2 cm.

to note that such large numbers of larvæ and young fish really occur all over the ocean.

Eel-larvæ
(leptocephali).

I will here restrict myself to giving some information as to an isolated group, viz. the larvæ of the eel-like fishes (lepto-

cephali). We see from Fig. 533 that about 200 individuals of this group were taken by us, belonging to some 20 species, and I have represented in Chapter III. some of the most peculiar new forms. Like most Atlantic fish-larvæ these forms are difficult to classify, because our knowledge of the different developmental stages is deficient, and also because these larvæ pass through a remarkable metamorphosis before assuming the ultimate shape of the adult. In a number of cases we are therefore quite ignorant as to what larval forms develop into

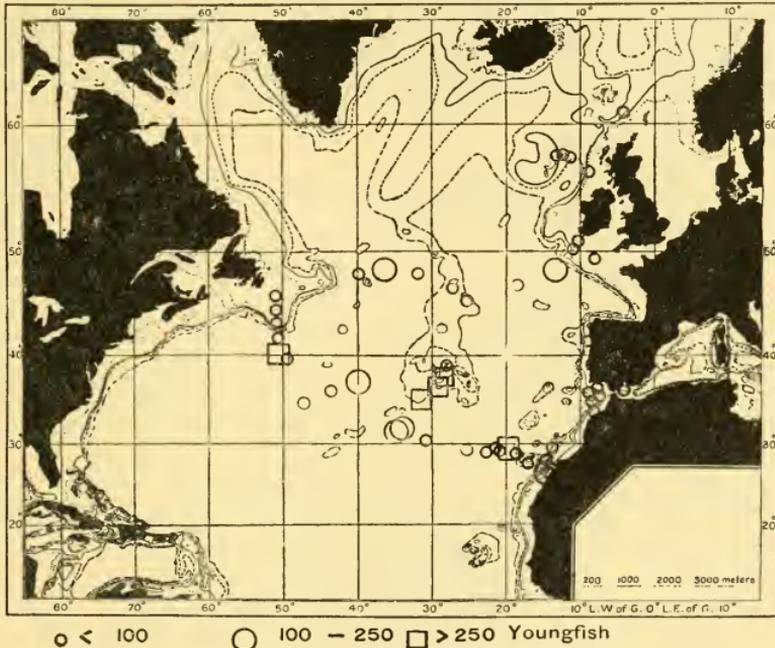


FIG. 544.—DISTRIBUTION OF YOUNG FISH.

the various known species belonging to the group of Apodes. Our material is being examined by Einar Lea, and will probably help to clear up some of the difficulties mentioned above. The stages belonging to *Gastrostomus bairdii* (repeatedly mentioned in Chapters III. and IX.; see Fig. 83, *a*, p. 97) form a very interesting series, the stages *a* and *b* (see Fig. 545) obviously being the transition stages between leptocephalus and adult; figure *a* plainly exhibits characters peculiar to the leptocephalus as well as to the adult, and evidently forms a more advanced stage of the transition. Another interesting transition stage in leptocephali is exhibited by the form repre-

sented in Fig. 546, taken at Station 53 in 1300 metres. The head has been much transformed, but the body still retains much of the leptocephalous character, while on the ventral side pigment has been developed.

Fig. 547 shows the number of leptocephali of every description taken during our cruise, and we see that the majority were taken south of a line from Newfoundland past the Azores to



FIG. 545.

a. Larva of *Gastrostomus bairdii* (?). Nat. size, 4 cm. Station 64.

b. *Gastrostomus bairdii*, Gill and Ryd. Nat. size, 7.5 cm.

North Africa. The ones taken north of this line belong, according to Lea, to the following species:—

Leptocephalus brevirostris, the larva of the common eel.

Leptocephalus Congri vulgaris, the larva of the conger eel.

Leptocephalus Synaphobranchi pinnati, the larva of *Synaphobranchus pinnatus*.

Leptocephalus amphioxus, larva of an unknown species.



FIG. 546.

Transition-stage from leptocephalus to "young fish." Station 53, 1300 metres.

Only one specimen of the last mentioned was taken at Station 81 off Newfoundland, so that we may say that the three first mentioned are the only ones observed north of the line indicated. The majority of individuals as well as of species were thus taken south of the Azores.

The interest attached to this peculiar distribution of the leptocephali is greatly increased when we examine their dis-

tribution according to size and consequently according to age. We then find that the earliest stages of all the leptocephali

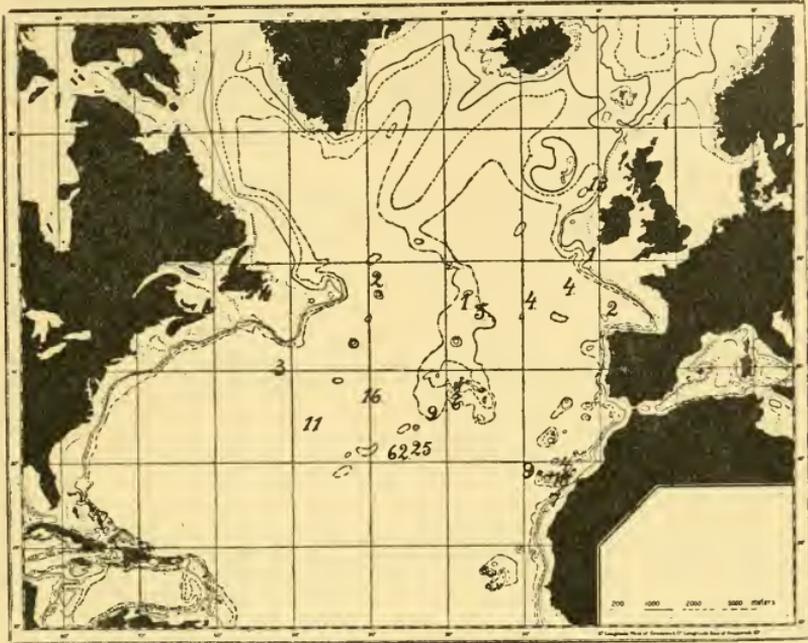


FIG. 547.—NUMBER OF LEPTOCEPHALI OF ALL SPECIES CAUGHT AT EACH STATION.



FIG. 548.

Young Leptocephalid, only 1.7 cm. long. Station 64.



FIG. 549.

Leptocephalus Synphobranchi pinnati. Nat. size, about 5 cm. Station 62.

captured were also taken in our southern section, south of the Azores. As mentioned in Chapter III, we took, in the Sargasso Sea at Station 64, very small leptocephali between 1 and 2 cm.

long (see Fig. 548). In this locality we also captured small

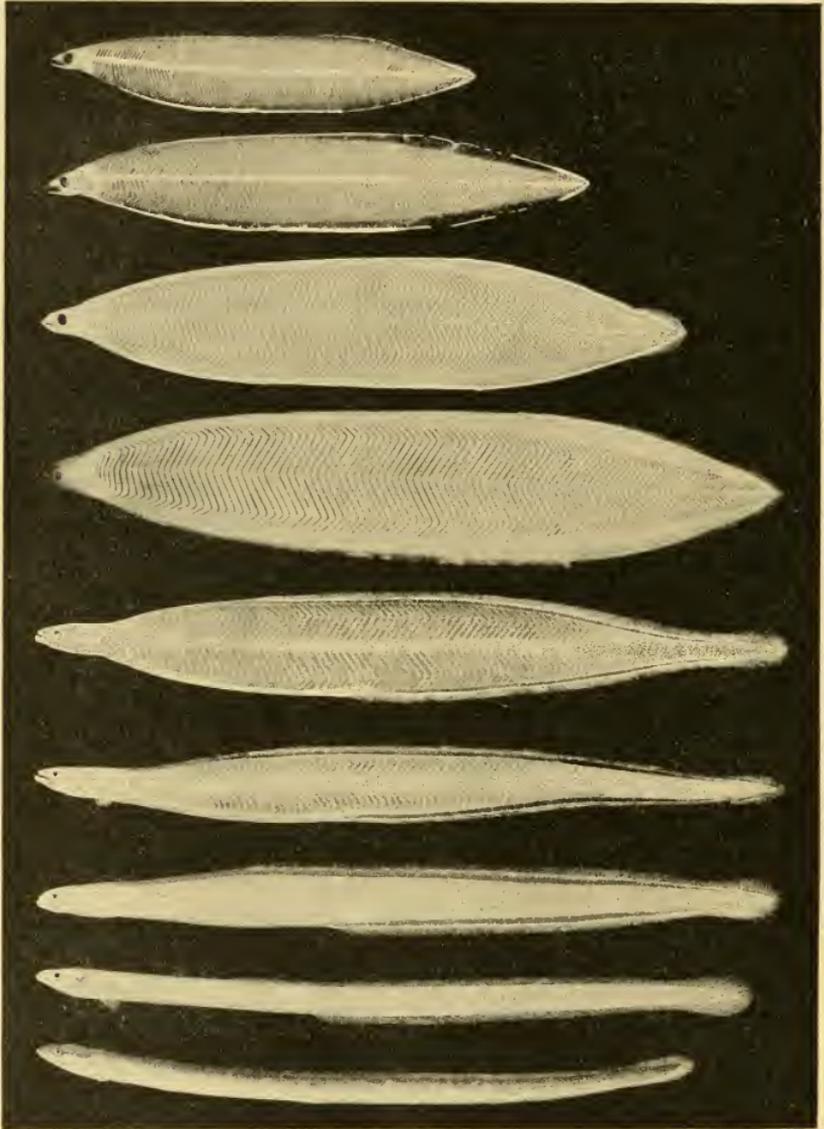


FIG. 550.

Stages of development of the common eel (*Anguilla vulgaris*, L.). ($\frac{1}{4}$.)
(The five lower figures from Schmidt.)

stages of leptocephali belonging to the common eel and to *Synphobranchus pinnatus* (see Fig. 549). North of the line from

Newfoundland to the Azores and Morocco only essentially larger (and older) stages of these species were taken, as shown in the case of the larvæ of the common eel (*Leptocephalus brevirostris*). It has long remained a mystery where the common eel spawns. No sexually mature individual has ever been found among the millions of eels annually captured in the waters of Europe, nor have the eggs or minute larvæ ever been found. The autumnal migration of the eel has, however, been known for ages. During this migration the eels leave the rivers, lakes,

Larvæ of the common eel.

and closed waters of the sea and make for open water, and certain naturalists, like C. G. J. Petersen, concluded that the eel was actually an oceanic deep-sea species. This idea seemed all the more obvious as the Italian scientist Grassi had, in the Mediterranean, proved *Leptocephalus brevirostris* to be the larva of the eel. A marked advance in the solution of this mysterious problem was made when Johs. Schmidt¹ succeeded in capturing quantities of leptocephali along the Atlantic slope of the coast banks of western Europe. Schmidt here found the fully developed larvæ, mostly exceeding 6 cm. in length, and all the transition stages before the leptocephali become "glass eels" or elvers, which in spring invade all the coasts of northern Europe, where they are well known.

During our cruise we found essentially smaller stages,² down to 4 cm. long, and we have thus been able to trace the series shown in Fig. 550. In this figure the five lower stages are taken from Schmidt's excellent account, the upper four stages having been drawn from specimens captured by the "Michael Sars," all magnified 1.4 time. The three upper figures

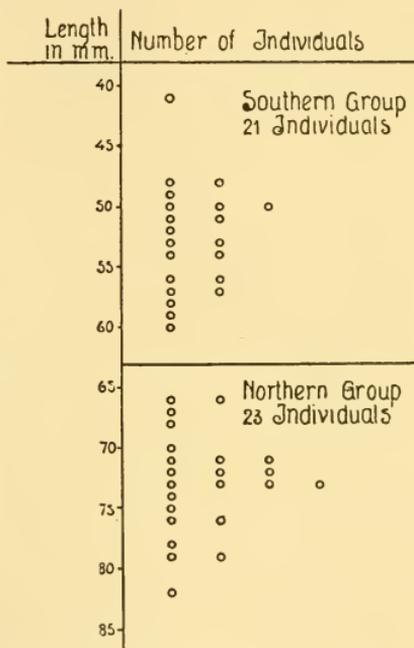


FIG. 551.—MEASUREMENTS OF LARVÆ OF THE COMMON EEL (*ANGUILLA VULGARIS*).

¹ See Schmidt, "Contributions to the Life-History of the Eel," *Rapports et Procès-verbaux du Conseil international*, vol. v., 1906.

² See Hjort, "Eel-larvæ from the Central North Atlantic," *Nature*, vol. lxxxv, p. 104, 1910.

represent stages prior to the fully grown leptocephalus, the five lower figures representing stages of the "metamorphosis." Without entering into the voluminous literature of the subject, we may state that we found a certain regularity as regards the geographical distribution of the various stages. Measuring the forty-four specimens taken by the "Michael Sars," and arranging them according to size (see Fig. 551), we see that they may be divided into two groups, one ranging from 41 to 60 mm., and

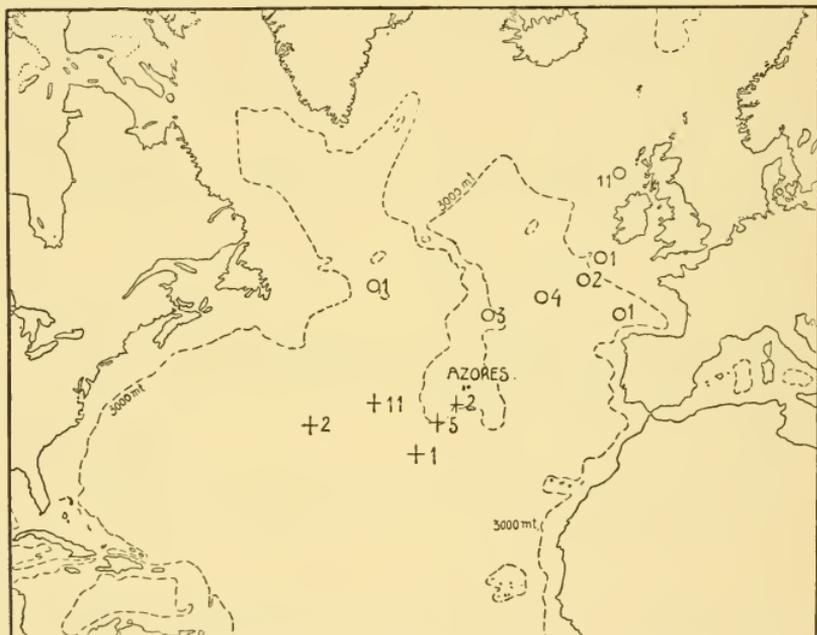


FIG. 552.—NUMBER OF LARVÆ OF THE COMMON EEL CAUGHT DURING THE EXPEDITION. ○ full grown larvæ ; + smaller larvæ.

the other exceeding 60 mm., in length. All the individuals of the former group were taken south of the Azores as denoted by crosses in Fig. 552, while all the specimens longer than 60 mm., *i.e.* the full-grown leptocephali, were taken north of the Azores as denoted by circles.

I presume that this peculiar distribution can only be explained by supposing that the eel spawns south of the Azores, and that the eggs and larvæ pass through their early stages there, being later carried into the northern North Atlantic and towards the coasts of northern Europe by the Gulf Stream. If this be correct, the majority of the young eels found in Europe

have been carried there by the currents from distant spawning grounds, just as the herrings are carried to the coasts of northern Norway from distant spawning grounds on the North Sea coast, or as the young cod of northern Iceland have drifted from the south coast of that island. This result is in itself of great importance, contributing to our knowledge of the mysterious life-history of the eel, especially when viewed together with similar facts pertaining to other leptocephali (conger, *Synaphobranchus*), and to forms like *Argyropelecus*, Scopelidæ, etc., which were far more numerous on our southern than on our northern track. Just as all the tropical and warm water forms, from foraminifera and copepoda to fishes, occur mainly south of the 40th degree, so also is the spawning of warm water fishes limited to this same area. I therefore believe that the eel probably belongs to this "intermediate" group, of which one is reminded by the large eyes and the silvery sheen of migrating "ripe" eels (compare, for instance, *Serrivomer*).

I am inclined to explain the fact that we did not obtain many of the remarkable larvæ and young fish collected by other expeditions from the surface of the ocean, as recorded for instance by Lütken in his *Spolia Atlantica*, by supposing that we did not go far enough south. Lütken states that his small young swordfish were all captured in tropical localities, and in regard to the mackerel he quotes Captain Andrea thus: "The Bonito is the oceanic fish which I have most frequently seen and captured; it is seen everywhere in the North and South Atlantic between the tropics, increasing in abundance as one approaches the equator. In the Indian Ocean I have not seen it south of lat. 26° S. nor east of long. 70° E. In the Java Sea, the China Sea, the Yellow Sea, and the Japan Sea I have never observed it."

In this place I have limited my remarks to the fishes alone, but similar results would probably appear in most animal groups if their vertical and horizontal distribution were studied; this must be reserved for the future, when the material collected by the expedition has been examined in detail.

AGE AND GROWTH

It has long been recognised that there is a certain correlation between the size and the age of animals belonging to the same species, and that a definite increment in size takes place within

a certain law-bound space of time, which varies in different species. These facts form the basis of an important branch of marine research, which possibly more than any other will help us to understand the life conditions of animals. The foundation of this branch of science is mainly due to C. G. J. Petersen¹ and H. Heincke.

Fish measure-
ments.

In his first investigations Petersen aimed at defining the age of the fish-species occurring in a restricted area, and for



C. G. J. PETERSEN.

this purpose he selected a small Danish fjord, the Holbaek fjord, where he attempted to capture all sizes of the various fishes, and measured the length of each one; he then tabulated these length-measurements for each species in order to study the frequency of the various sizes. Fig. 553 shows the results of his measurements of the common viviparous blenny (*Zoarces viviparus*). The scale is in Danish inches, and each dot denotes a specimen measured; males and females were measured separately, where the sexes could

be distinguished. I quote Petersen's description of this graphic representation: "If we now consider the females, we undeniably find remarkably few of a length between 8 and 10 inches; also there is a marked gap between the largest of the fry and the smallest females. Something similar is seen though less plainly in the males. The latter are, however, too few to let the gaps appear quite plainly. Alternating with these gaps certain sizes occur as it were in heaps, where many fish have almost the same length. The blennies may, to put it shortly,

¹ C. G. J. Petersen, *Beretning fra den danske biologiske Station*, No. 1, 1890, Kjöbenhavn, 1892.

be classified in three groups: (1) the large ones, (2) an intermediate group, and (3) the small ones or fry, and when fishing we will very seldom be uncertain as to which group we may refer the fishes captured. It is impossible to apply the rule to both sexes, but the males seem on the average to be somewhat smaller than the females, and also less numerous. Among the larger sizes of the blennies, the longest ones seem to be sparingly represented. Notwithstanding all my exertions in various localities, I have never been able at this time of the year (summer) to find blennies of less length than the ones recorded under the head of fry, that is, about 3 to 4 inches. As the fry, when born, are actually $1\frac{1}{2}$ inch long, I cannot doubt that the group of small blennies, which at this time of the year differ so considerably in size from the large ones, really are the fry of the year, which during the last six months have grown to this size, that is, have added a couple of inches to their length. It appears equally natural to consider the intermediate group of blennies, between 6 and 8 inches, as the fry of the previous year. The direct consequence is that all the large blennies between 10 and 12 inches are of an age exceeding one year and a half by one year at

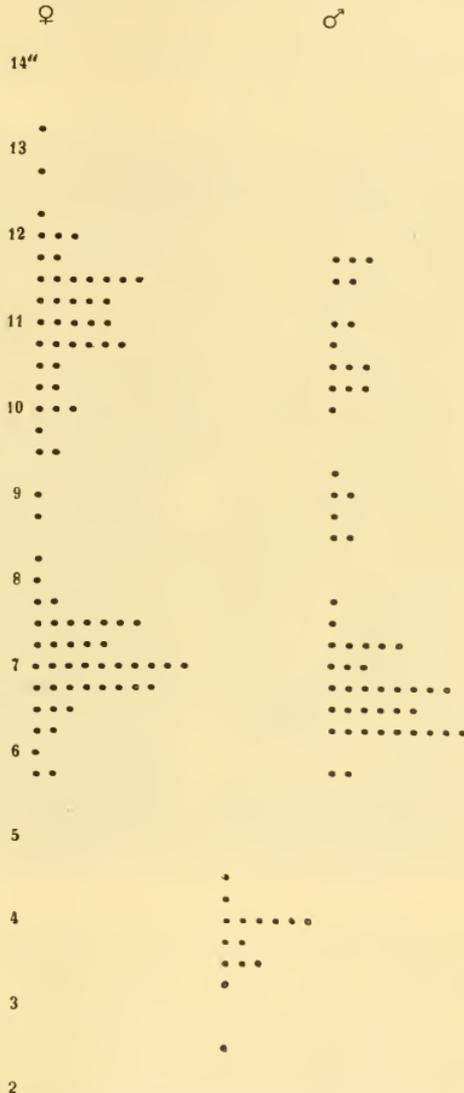


FIG. 553.—PETERSEN'S MEASUREMENTS OF *ZOARCES VIVIPARUS*.

least, and as only very few individuals grow to a large size, this group must be considered as 'full-grown' blennies. In other words, it takes the blennies $2\frac{1}{2}$ to 3 years to become 'full-grown.'

This account contains the foundation of this branch of science and a programme for further investigations, which have been employed in many recent researches, and will in future be employed along with more modern methods.



H. HEINCKE.

Another important series of investigations was inaugurated by Heineke, who endeavoured to employ the methods of anthropology by recording various dimensions of the organisms in order to characterise variations in growth peculiar to a species in different areas of the sea. Heineke measured the length and height of body, length of head, etc., in a great number of herrings from various marine areas, and he found the relations between these dimensions to be so characteristic that he

supposed the herring to be subdivided into various races, each constituting a peculiar type of growth.

These two methods are, however, useful only as long as one can operate with great numbers of measurements according to the principles of the statistical method, and it proved in many cases impossible to determine the age and the type of growth of each individual by these methods. As regards the study of age alone this proved a great obstacle, especially in regard to the older animals. It was therefore very important to find a method which would give the age of each individual and define its particular type of growth.

It has been discovered that in various boreal fishes the seasonal changes in their growth leave certain traces in all the osseous structures, such as vertebræ, gill-covers, otoliths, and scales, a difference being plainly seen between the parts formed during rapid growth (in summer), and the parts formed during feeble growth (in winter). In this way visible rings or zones are formed in the structures mentioned, varying according to summer and winter, thus enabling us to count the number of winters and summers passed by the fish in question, and to ascertain its growth in various phases of life. This was first discovered by Hoffbauer in the scales of the carp (1899), and has also been observed to hold good in the case of the otoliths of the plaice (Reibisch), and of the scales of gadoids (Stuart Thomson), while Heincke and others have proved various bones to be good indicators of growth. A voluminous literature¹ has accumulated as the result of these methods, which assumed greater importance when in 1904, upon the recommendation of Heincke, the international fishery investigators adopted them and applied them to many special and general problems. In recent years during the fishery investigations of several countries the growth and age of various commercial species have been subjected to analysis.

Age and growth of fishes denoted by their scales.

In Norwegian fishery work the scales have mostly been employed for age assessments, and in this way a number of species belonging to the cod family have been treated by Damas, while Sund has studied the age of the sprat, Broch, Dahl, and Lea the age and growth of the herring, and Dahl of the salmon and trout.²

Fig. 554 represents a series of scales of saithe, ranging from 17 to 67 cm. in length, taken on the west coast of Norway. They have been represented in proportion to the size of the

¹ See Knut Dahl, "The Assessment of Age and Growth in Fish," *Internationale Revue der ges. Hydrobiologie u. Hydrographie*, Bd. II., 1909, containing review of literature.

² Désiré Damas, "Contribution à la biologie des Gadides," *Rapp. et Proc.-verb. de la com. perm. pour l'expl. de la mer*, vol. x., Copenhagen, 1909.

Hjalmar Broch, "Norwegische Heringsuntersuchungen während der Jahre 1904-1906," *Bergens Mus. Aarbog*, 1908, No. 1.

Oscar Sund, "Undersökelsener over Brislingen i Norske farvand," *Aarsberetning vedk. Norges Fiskerier* 1910, Bergen, 1911.

Knut Dahl, "The Scales of the Herring," *Report on Norwegian Fishery and Marine Investigations*, vol. ii. No. 6, Bergen, 1907; "Age and Growth of Salmon and Trout in Norway," Salmon and Trout Association, London, 1911.

Johan Hjort, "Report on Herring Investigations until Jan. 1910," *Publications de Circonstance*, No. 53, Copenhagen, 1910.

Johan Hjort and Einar Lea, "Some Results of the International Herring Investigations, 1907-1911," *Publ. de Circonstance*, No. 61, 1911; "Einige Resultate der internationalen Heringsuntersuchungen," *Mitteilungen des Deutschen Seefischerei-Vereins*, No. 1, 1912.

Einar Lea, "On the Methods used in the Herring Investigations," *Publ. de Circonstance*, No. 53, 1910; "A Study on the Growth of Herrings," *Publ. de Circonstance*, No. 61, 1911.

fish, and we therefore easily see how the number of annual rings increases proportionately with the growth of the fish. By counting the winter-rings we can ascertain how many winters each fish has lived, and by examining a great number

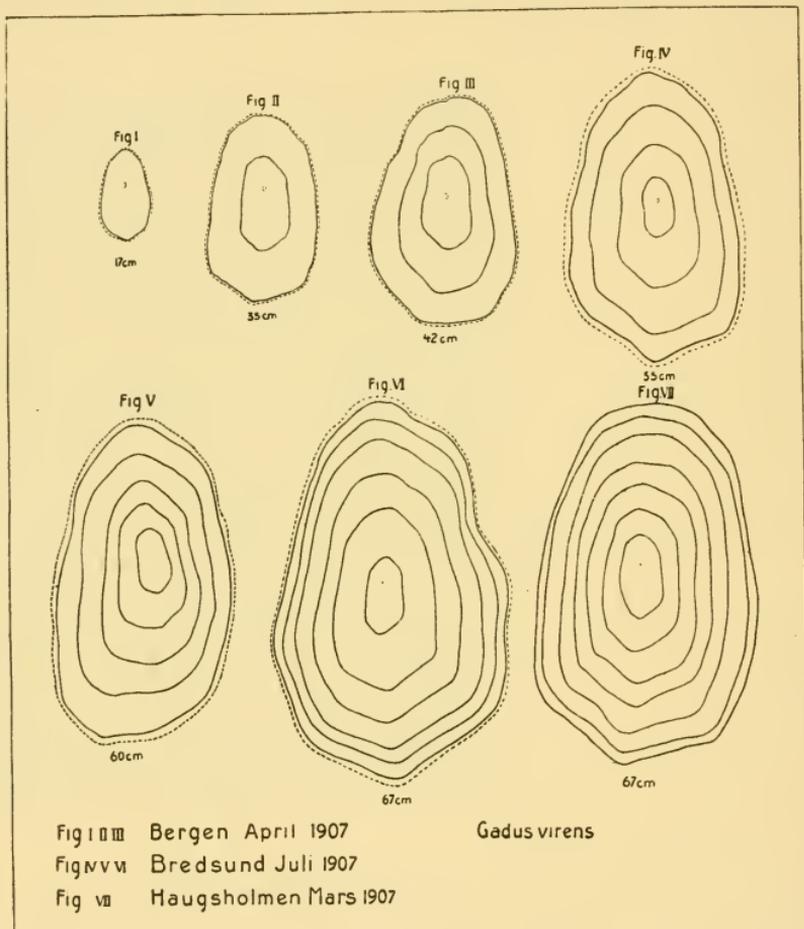


FIG. 554.

Scales of saithe (*Gadus virens*) of different sizes (size of the fish noted below each scale).
(From Damas.)

of individuals from a definite catch we may ascertain the number of individuals belonging to each annual class. In this way we may obtain an idea of the age-composition of the catch. The next step is to examine a large number of catches, and to form an estimate regarding the age-composition of the

fish-stock. Fig. 555 represents an analysis of the age-composition of a catch of saithe; it is of course not representative of

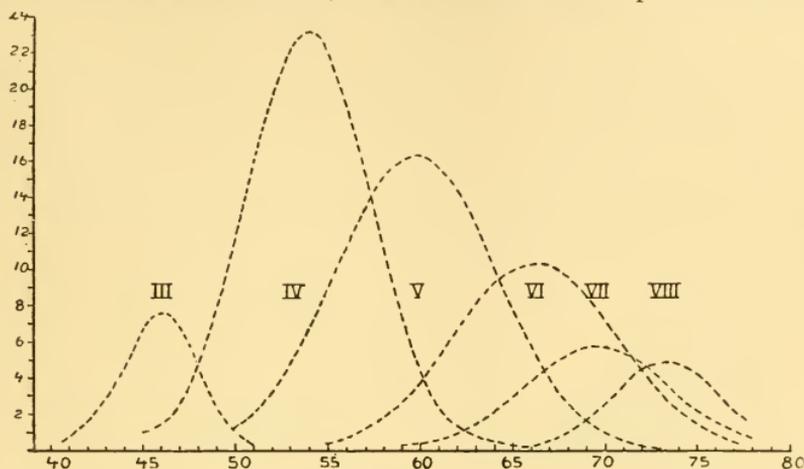


FIG. 555.

Age distribution of the saithe (*Gadus virens*) from an examination by Damas of the scales of 654 fishes caught in Söndmör (Norway) in July 1907. The age-groups that were poorly represented have been left out.

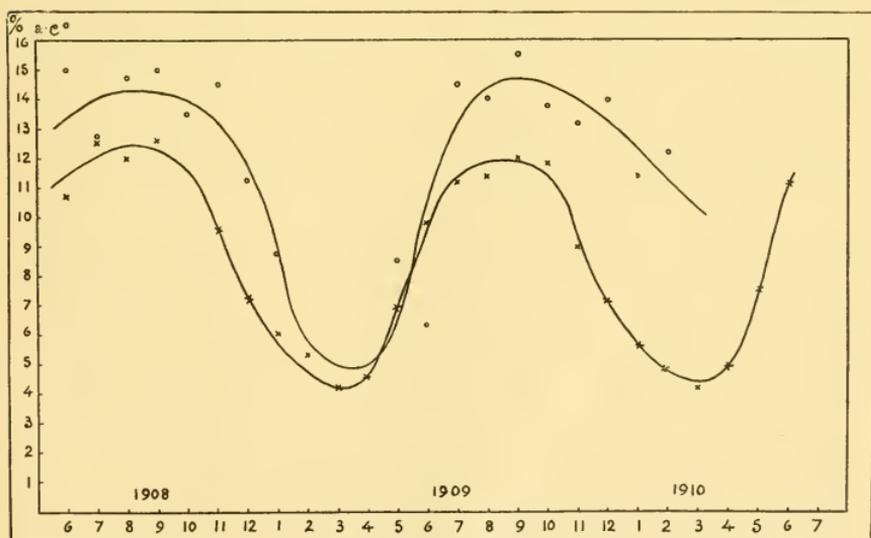


FIG. 556.

° Percentage of fat in sprats caught off the Norwegian west coast in different months.
 x Average temperature of the surface of the sea, off Bergen, in each month of the year.
 (From Sund.)

the saithe-stock, but might perhaps have been so in regard to the special shoal of saithe from which it was taken.

Growth
dependent
on external
conditions.

Some of the general results obtained by these investigations are of great interest; for instance, the growth of fishes has proved to be largely dependent on the temperature. Some chemical investigations corroborate this. Fig. 556 shows the fat-contents of the sprat as determined by H. Bull, compared by Sund with the surface temperature of the sea off western Norway in various seasons of the year. The fat-contents of the sprat increase during summer, when there is a rise in temperature, while both decrease towards the end of the year; it follows from this that the growth of the fish must be influenced by the prevailing temperatures in different waters.



FIG. 557.

Scale of *Gadus callarias*, L. Nat. size of fish, 55 cm. Station 72.

The investigations on the scales of fishes have now given us numerous facts confirming and elucidating this. Thus Damas says that the age of first maturity in the cod undoubtedly varies greatly according to local conditions. Generally the growth of cod-species may be said to decrease, and the age of first maturity to increase, the farther north we go. Thus on the Skagerrack coast a saithe may be 30 cm. long at the end of its first year, while a saithe of corresponding age in northern Norway is not, as a rule, more than 10 cm. in length. In northern waters, therefore, the winter-rings in the scales are much more marked than in more southern waters, for instance, in the North Sea. The duration of the warm season also differs in different waters, and the time when it sets in varies in different localities as well as at different depths (see Fig. 509, which shows that at 200 or 300 metres the highest temperatures do not occur in the summer, but late in the autumn). An examination of cod scales from the Barents Sea proved that in August summer growth had not yet commenced in that area, where the winter season is of very long duration, while the summer is short. It is interesting to compare this with certain observations which we had the opportunity of making during our Atlantic cruise on the banks of Newfoundland, where, as mentioned on pp. 109-114, the cod spawn in July. We here observed cod with large ripe ovaries and found the recently hatched larvæ at the surface. The scales of these

cod (see Fig. 557) plainly show winter-growth along their edges, that is to say, vigorous summer-growth had not yet set in, and as a matter of fact the temperatures were low (between 2° and 4° C., see Station 72, Fig. 95, p. 110) just where the cod were taken.

These variations of growth put their stamp on the fish, the shape of which depends on its growth-history. And in waters, like those off the Norwegian coast, subject to great variation and extending south and north through so many degrees of latitude, an infinite variety in growth-types appear as a natural consequence. Some of these types may perhaps, through generations, be subjected to the accumulating influence of surroundings, thus possibly giving rise to races. Other and minor variations in growth may perhaps be considered as

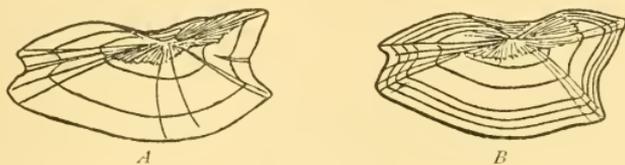


FIG. 558.

Interpericulum of plaice (*Pleuronectes platessa*). A, ♂ 21 cm. long, North Sea, three years old; B, ♀ 21 cm. long, Baltic Sea, six years old. (From Heincke.)

temporary or individual variations due to surroundings only, and not subject to the laws of heredity.

The way in which individuals vary according to surroundings might profitably be studied by experiments in transplantation and marking of various types. Heincke¹ has made some very interesting investigations on the growth of the plaice, and found that in waters so widely different as the North Sea and the Baltic the growth of the plaice varied greatly. Fig. 558 shows the gill covers of two plaice of the same size, both 21 cm. long; the North Sea plaice is only 3 years old, while the Baltic plaice is no less than 6 years old. Similar distinct types of growth have been discovered in the herring during the international investigations, Dahl having first drawn attention to the existence of such types; Lea continued these investigations with a large amount of material, and claims that among others two growth-types may be recognised, one belonging to the north-eastern part of the North Sea (the Norwegian west coast), and the other to the Kattegat (see Fig. 559).

¹ *Die Beteiligung Deutschlands an der internationalen Meeresforschung, IV.-V. Jahresbericht*, Berlin, 1908.

Both the scales represented belong to herrings six winters old and represent true averages of growth, which has obviously been very different in the two types.

While studying the growth of Gadidae, Damas conceived the idea that by examining the growth-history of single individuals, as depicted in their scales, one should be able to determine the localities, or at least the conditions, in which the individuals had grown up, in other words that this study should afford a key to the migrations of the fishes; thus he considers it probable that a certain saithe captured on the west coast of Norway may be recognised as having spent its infancy on the north coast of Norway. Similar ideas have

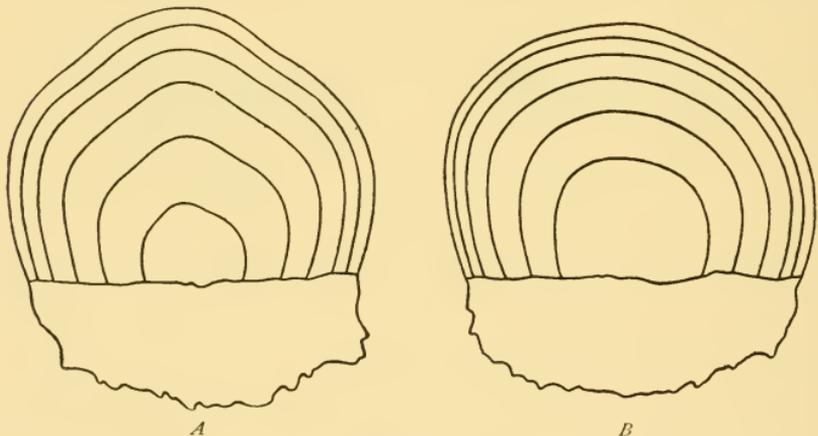


FIG. 559.

Diagram of herring scales of average growth. *A*, from the north-eastern part of the North Sea; *B*, from the Kattegat.

been expressed by Lea after studying the scales of herring. He discovered that among the fat-herrings of northern Norway the ones born in 1904 could be seen to have had an exceedingly poor growth during their third year, the summer-belt in the scales being strikingly small in that year (see Fig. 560). This peculiar feature was in that year limited to a certain part of the coast. The individuals thus "marked" were, however, in subsequent years when increasing in age found to have a much wider distribution, extending to the west coast of Norway and other localities. He considers this as significant of migration, and even attempts to calculate the percentage of the herrings taken on the west coast that had spent their infancy in northern Norway.

The study of numerous samples taken from the fish-stock of a certain area may aim at ascertaining the age-composition of that stock, and from the results the following main points in the natural history of the fish may be elucidated: (1) the age at which maturity occurs; (2) the

Age-composition of the stock of fishes.

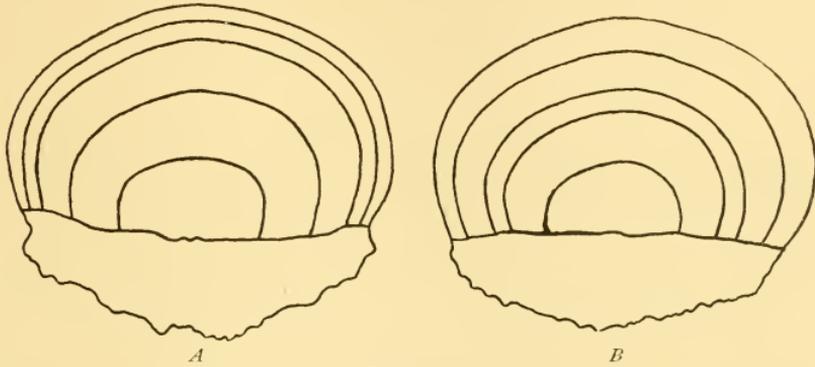


FIG. 560.

Two scales of five-year-old herrings. *A*, growth under normal conditions; *B*, abnormal growth in the third zone.

duration of life; and (3) the variations in the age-composition and magnitude of the fish-stock.

Studies of this kind have shown us that various species

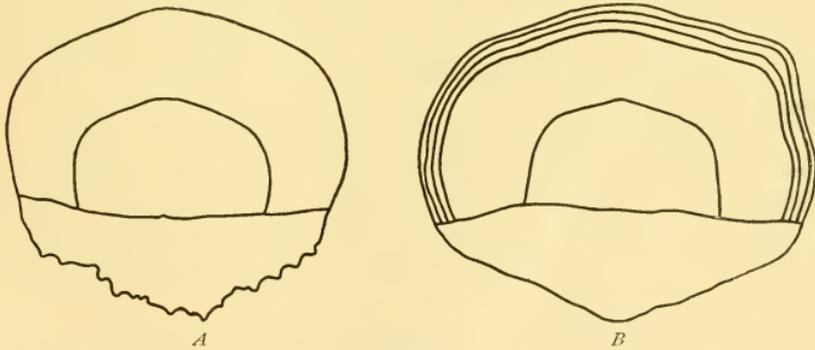


FIG. 561.

Scales of *A*, herring (*Clupea harengus*); *B*, sprat (*Clupea sprattus*). Both fishes 16 cm. long.

are distinct even in this respect. Nothing shows this more clearly than a comparison between the two closely related species: the sprat and the herring. Fig. 561 represents scales of a herring and of a sprat, both 16 cm. long, the herring being only $1\frac{1}{2}$ year old and the sprat 4 years. The

age-composition of spawning shoals in the two species appears from the following examples :

	Annual Class.													
	2	3	4	5	6	7	8	9	10	11	12	13	14	
Percentage of sprat . . .	30	42	19	8	1	
Percentage of herring	2	22	19	15	13	19	3	2	2	1	1	...	

Sund found that the majority of sprats spawn when two to four years old, while Dahl found that the herrings spawn from the 3rd to the 14th year, the majority between four and eight years old. This difference is fundamental in the life-history of the two species. The life-cycle of the sprat is rapid, indicating a rapid renewal, while the herring lives much longer, spawns for a great number of years, and spawning commences two years later than in the sprat. The herring is a typically boreal fish, its southern limit to the south-west of Britain conforming to that of all the boreal bottom-fishes (see Chapter VII.). Herrings live, at least sometimes, at considerable depths, depositing their eggs on the bottom of the coast banks during winter and spring, now in shallow, now in deeper water.

The sprat is distributed far south in the Atlantic, occurring, according to Day, round the Iberian Peninsula. It is a surface fish occurring in boreal waters mainly where high summer temperatures prevail; it spawns during summer, the eggs being pelagic.

From the study of the age of fishes I was induced to hope that the variations in the magnitude of the fish-stock might be estimated, and my collaborators have made very extensive investigations with most important results. This applies to the cod family as well as to the sprat and the herring. I will here only review some of our results from the herring investigations.

For a number of years samples for age-analysis have been collected during the various herring fisheries on the coast of Norway, the analysis of which has proved that the age-composition of immature herrings, as well as the shoals of spawning herrings, vary considerably from year to year. These variations are mainly due to the fact that certain annual classes are exceedingly prolific, while others are very poorly represented. The following table records the results of an analysis of

samples representing immature fat-herrings from northern Norway in the years 1907-1910,¹ the frequency of each annual class being given in percentages of the total sample for each year:—

	Annual Classes.						
	1	2	3	4	5	6	7
1907 . . .	11.5	36.8	51.3	0.4
1908 . . .	0.4	51.4	10.3	37.8
1909 . . .	3.1	61.0	13.3	5.0	16.9	0.7	0.2
1910 . . .	0.2	50.7	42.0	0.9	1.7	4.5	0.1

This table shows that the fat-herrings in 1907 consisted mainly of fish two and three years old, in 1908 they were mainly two and four years old, and in 1910 again the majority were two and three years old. This apparent irregularity has an enhanced interest when we remember that the herrings, which in 1907 were three years old, in 1908 were four years old, and so on. The annual classes born in 1904 and in 1907 are printed in heavy type, and the table shows a decided regularity in the abundance of certain annual classes. The same regularity appeared when older herrings were studied. When four years old the fat-herrings begin to "migrate" away from the shoals of immature herrings, and mingle with the "spring-herring" shoals (the spawners). In such spawning shoals from western Norway the year class born in 1904 proved to have the occurrence shown in the following table in percentages of the total sample analysed each year, comprising sixteen annual classes:—

	Year.			
	1908.	1909.	1910.	1911.
Percentage of total samples born in 1904 . . .	34.8	43.7	77.3	70.0

Among the great number of annual classes composing the

¹ J. Hjort and E. Lea, "Some Results of the International Herring Investigations, 1907-1911," *Publ. de Circonstance*, No. 61, Copenhagen, 1911.

herring stock, one single annual class may thus be enormously prolific, the individuals exceeding in number those of all other annual classes taken together.

These facts naturally lead to the following conclusions touching questions of interest to general biology as well as to practical fisheries. The age-composition of a fish-stock varies exceedingly; there are good and bad years, producing annual classes rich or poor in individuals. Favourable and unfavourable conditions must thus vary in nature, and seem to affect specially the earlier phases in the life of the fish, inasmuch as we perceive that in advanced years the numerical preponderance of an annual class is equally perceptible for a number of years.

The variations caused by the influence of one year will therefore not always perceptibly influence the number of individuals of the total stock, and in practical fishery its influence will as a rule only be felt some years later, when the annual class in question plays an important part in the catches of fishermen. If favourable years have occurred just before or after the birth of the class in question its influence may perhaps not be felt at all. All this of course applies only to species with many annual classes of spawners, for where few annual classes spawn (or perhaps only one) conditions will be different.

The influence of one year may, however, appear in the quality of the whole stock, for instance in the fat-contents (see Fig. 556 representing the growth of the sprat).

Wherever there is a good opportunity of obtaining representative samples showing the age-composition of a fish-stock, it should be possible to predict the composition of that stock for the following years. We may thus, for instance, count upon the possibility of annual classes containing a marked abundance of young individuals reappearing, after the lapse of a definite time, as equally abundant shoals of older and more valuable fish.

The results here mentioned have been obtained through laborious investigations occupying many years, involving the study of the fishes at all seasons, in order to prove that the various growth-rings of the scales really correspond to seasonal changes.

As far as I know, no systematic investigations as to growth have ever been made in the open ocean, but I may point out that in tropical waters and at all depths in the ocean the same biological problems, which we have just described from boreal waters, present themselves for study and solution. In this connection I consider it interesting to cite some instances from

our preliminary investigations, showing that periodic growth may be traced even in the ocean, but as to the nature of this periodicity I dare not at present express an opinion.

Fig. 562 represents a scale taken from the abyssal fish *Macrurus (Nematonurus) armatus*. As indicated in Chapter VII. this species lives in depths beyond 2000 fathoms, and at

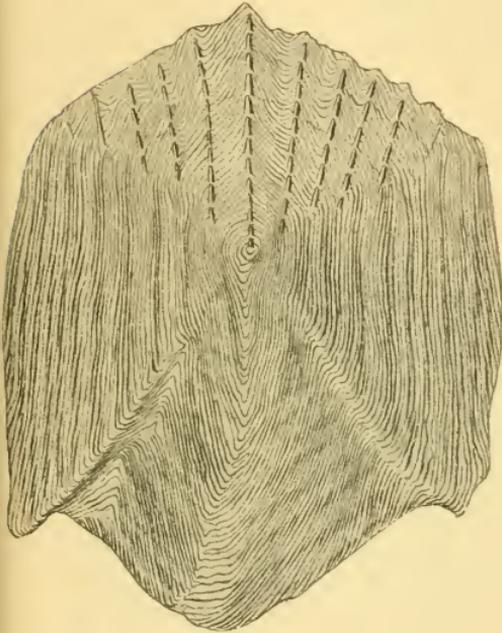


FIG. 562.

Scale of *Macrurus (Nematonurus) armatus*, Hect. (about $\frac{1}{4}$).
Fish from Station 88. Length, 52 cm.

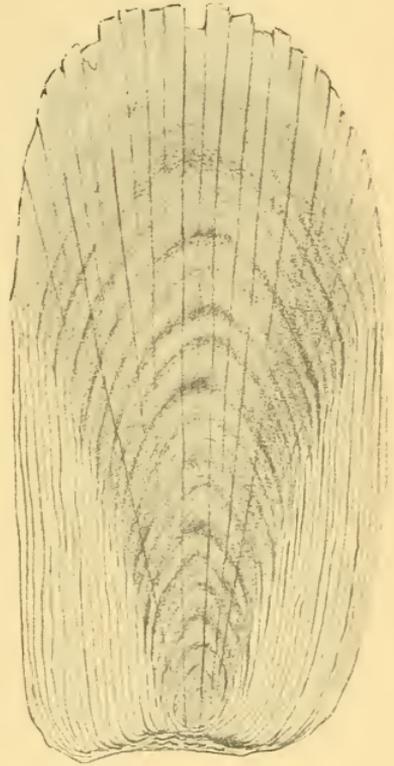


FIG. 563.

Scale of *Bathygadus melanobranchus*, Vaill.
Nat. size of fish, 42 cm. Station 41,
1365 metres.

a temperature of 1° to 3° C. The specimen from which this scale was taken was captured at Station 88 in 3120 metres, and was 52 cm. long. The figure shows the presence of rings, which remind one of the rings found in the scales of the cod family, but they do not continue round the entire area of the scale. The number of rings present appears to be more than ten, but I am unable to decide this with accuracy.

Fig. 563 shows a scale from *Bathygadus melanobranchus*,

42 cm. long, taken at Station 41 in 1365 metres. We see here a great number of rings, perhaps twenty in all, but these rings

are in many respects essentially different from the annual rings in the scales of boreal fish. In the latter the central rings are as a rule very large, the subsequent rings becoming narrower as the fish grows older. If the rings in the scale of *Bathygadus* signify periods of growth, these would seem to be of a peculiar character.

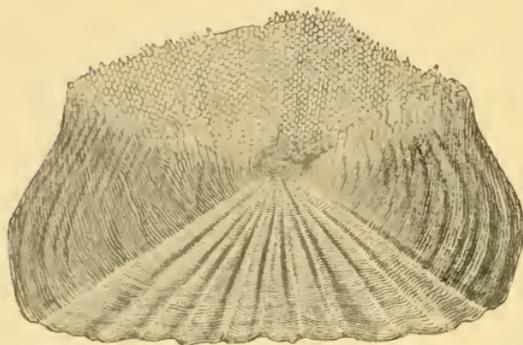


FIG. 564.
Scale of *Cantharus lineatus*, Montagu (White).
Length of fish, 42 cm.

Fig. 564 is the scale of a fish 42 cm. in length from the coast banks of Africa, *Cantharus lineatus*, taken in shallow water at a high temperature. This scale also shows rings which are very distinct, especially towards the periphery of the scale.

In Fig. 565 I have represented a scale from a surface fish, *Polyprion americanus*, 49 cm. in length, taken in the surface waters at Station 56.

In the scales of all these fishes, taken under such various conditions, we observe peculiarities of structure, resembling the rings produced by the periodicity of growth in the scales of fish from boreal waters. There seems thus to be every reason for subjecting the growth of the scales and other organs of

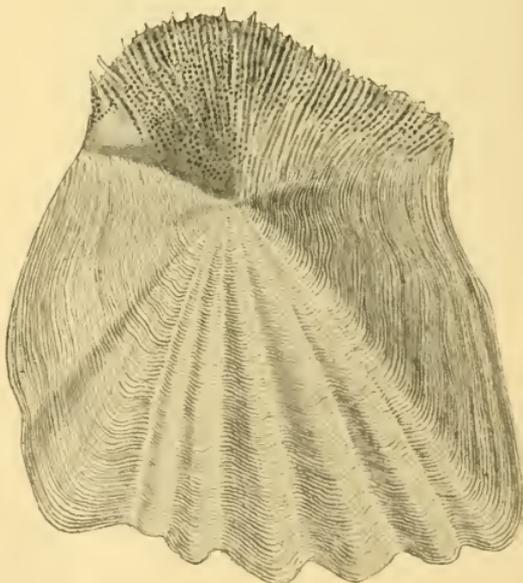


FIG. 565.
Scale of *Polyprion americanus*, Bl. and Schn.
Length of fish, 49 cm.

warm-water and oceanic fish-species to a closer investigation, and for studying them at various seasons. As a means of control and comparison, measurements on a large scale, according to Petersen's method, would be very important. Although our material is very abundant, it is insufficient for the purpose of distinguishing various size-groups among the fishes. That such groups occur among the deep-sea fishes is plainly indicated by our measurements of *Cyclothone* (see Fig. 473, p. 620), which show a binodal curve for individuals of *Cyclothone signata* from 500 metres, and a multinodal curve in the case of *C. microdon*. At 500 metres the average size is about 35 mm., and at 1500 metres about 60 mm. Perhaps there is another group in depths between the two mentioned. Regarding the meaning of the nodes in these curves I must confess myself ignorant.

From the coast banks of Africa we have a series of measurements of *Dentex macrophthalmus*, which for the sizes between 17 and 24 cm. show a very regular size-distribution of the fish captured.

Future investigations of the fish-fauna of the coast banks may lead to good results by starting from the study of such forms as occur also in the North Sea, for instance the hake (*Merluccius vulgaris*). Their growth might then be subjected to a comparative study on a long stretch of coast through many degrees of latitude and under exceedingly various conditions. The same method might also be applied in the case of the southern pelagic clupeidæ: the sprat, the pilchard, and the anchovy.

ABUNDANCE OF MARINE ANIMALS

On dry land we can, to a large extent, examine the yield of the soil, weighing and measuring the crops, and keep count of animals of economic importance. As regards the yield of the sea our experience is merely of a relative kind. From generation to generation a certain amount of knowledge has been accumulated as to the quantities of various fish that have been captured, but the number of animals actually living in the sea is unknown.

Many scientists have undoubtedly often had to acknowledge that biology would be raised to an essentially higher level, if it were possible to arrive at absolute figures denoting the numbers of individuals inhabiting the sea, instead of merely the relative figures which are now obtained through the study and comparison of various catches.

A first attempt in this direction was made by Sir John Murray during the cruise of the "Challenger," by calculating the amount of calcium carbonate in the form of living organisms per square mile of the ocean by 100 fathoms in depth.

Quantitative estimations of organisms in the ocean.

No one has devoted more time and thought to this problem than V. Hensen, who has been indefatigable in his endeavours to devise methods for an absolute determination of the quantities of organisms contained in the ocean, his avowed intention being to ascertain the quantities of "primitive food for marine animals."¹ From theoretical considerations he concluded that the primitive food of marine animals necessarily consisted of the microscopic plants living in the surface waters of the ocean, and that the effect of currents would be to distribute these minute plants quite regularly and uniformly. He held the idea that a hoop-net hauled vertically from bottom to surface would filter a column of water with a diameter very nearly corresponding to the diameter of the net, and that in this way it was possible to calculate the catch per square metre of surface. The volume of the catch might be measured, and the number of individuals belonging to all the species might be counted. Definite figures might thus be obtained representing the abundance of each species per square metre of surface, and the area of the water being known, the aggregate quantities might be calculated. In order to count all the micro-organisms he invented a method based on the principle employed in physiology for the purpose of counting blood corpuscles, viz. to dilute a sample of known volume with a known volume of liquid in which the organisms become evenly distributed. With a specially devised instrument a small sample (say 1 c.c.) is taken out and its contents counted.

This method has added greatly to the practical working of biological ocean research, and will undoubtedly increase in importance in future. Like all other means of research it must be employed with judgment, and the special nature of the investigations must decide whether it may be applied and at what stage with advantage. The application of the method has led to much discussion, the enthusiastic advocates of the method considering it imperative that it should be used in all "truly scientific" investigations on the micro-organisms of the ocean, while its opponents have looked upon it as a means of

¹ V. Hensen, "Über die Bestimmung des Planktons," *V. Bericht der Commission zur wiss. Untersuchung der deutschen Meere in Kiel*, 1887.

investigation to be applied, like all other means, according to circumstances.

Hensen invented his method for the purpose of investigating the floating or suspended life in the sea, which he termed "plankton." This plankton is, however, very difficult to define, for among the profusion of organisms, ranging from the minutest plants, the coccolithophoridæ, to large crustaceans and fishes, there is an enormous variety in size, in activity, and consequently in the faculty of avoiding the appliances of capture. In many investigations, therefore, the word plankton may be taken to signify practically "the catch made in the hoop-net constructed by Hensen, when new and in perfect working order." But does this selection among the organisms of the sea correspond to an arrangement peculiar to the organisms in nature? All our experience shows that the catching power of the Hensen net is restricted, firstly, because, as shown in Chapter VI., an important group of plants (the coccolithophoridæ) may pass through the meshes of even the finest silk nets, and secondly, because the selection of animals actually taken is very limited, consisting of unicellular animals, minute crustaceans, sagittidæ, etc., while the large crustaceans, schizopoda, decapoda, and even small fish-fry, mostly avoid the net. This limited power of capture alone is apt to affect our ideas of marine life in a perfectly arbitrary manner; but another objection to the universal application of the Hensen method arises from the fact that in large areas the conditions do not correspond to the theoretical conditions on which the method is based, for in theory the distribution of the organisms is regarded as something like the even distribution of the molecules of a gas encased in a box or aquarium.

In 1885 Hensen made an expedition in the "Holsatia" and in 1889 another in the "National," during which vertical hauls were made with his nets in shallow water from bottom to surface, and in the ocean mostly from 200 metres to the surface. The volumes of organisms taken during these cruises have been represented graphically in Fig. 566, reproduced from Steuer's text-book. In this figure the track of the cruise has been used as horizontal axis, and lines have been drawn vertically (as ordinates) to show the relative volumes taken per square metre of surface. These volumes are very great in the Irminger Sea and in the North Sea (amounting to 166.9 c.c.), and very small in the Sargasso Sea as well as in

the open ocean on the whole. In all or most of these samples the numbers of individuals have been counted after the return of the expedition,—a laborious and painstaking piece of work,

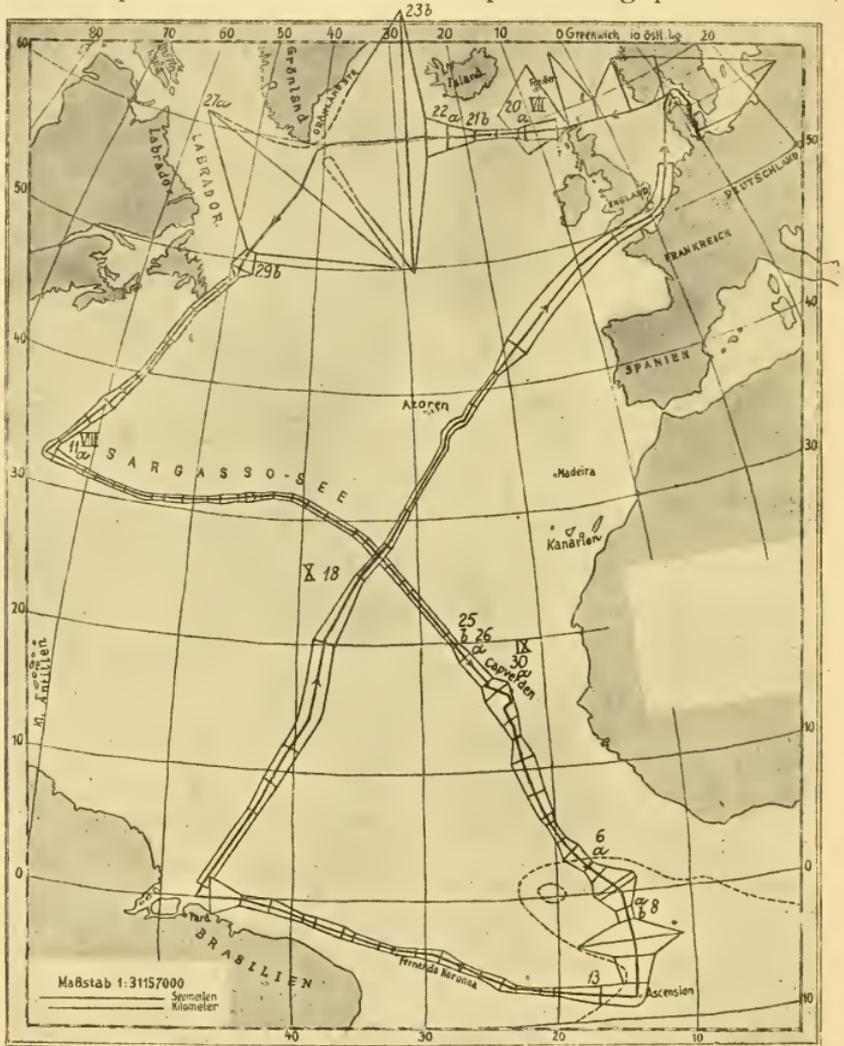


FIG. 566. — VOLUMES OF "PLANKTON" IN THE ATLANTIC AND IN THE NORTH SEA, ACCORDING TO THE INVESTIGATIONS OF THE "HOLSATIA" IN 1885 AND THE "NATIONAL" IN 1889. (After Hensen, from Steuer.)

which has added greatly to our knowledge of marine biology. In Chapter IX. I have had occasion to refer to many important facts for which we are indebted to these expeditions, but I

doubt whether the method of work adopted has resulted in a correct idea of the quantities of organisms which these hoop-nets can capture per square metre of surface, and whether this method recommends itself for adoption in the present state of our knowledge.

It is evident that the quantity of organisms present at any given moment does not afford any gauge as to the "primitive food" contained in the ocean. The quantity of such food depends on the intensity of reproduction, which is entirely unknown, from coccolithophoridæ to fishes. For this reason the volumes of plankton shown in Fig. 566 convey no idea of the actual production of the ocean, a fact of which Hensen was fully aware. The abundance in boreal waters only lasts a short time, and during that time production is probably not by any means so rapid as in the warm ocean. While the Hensen nets thus capture only an arbitrary selection of organisms, the depths from which the nets were hauled were also chosen in an arbitrary manner. Hensen¹ himself says, when describing the copepoda: "The figures show that the copepoda usually live still deeper than 200 metres, their density being, however, insignificant." The results seem to have given rise to some doubt in his mind as to the latter opinion.

In Chapter IX., and when speaking of nutrition, I have mentioned some of the investigations made on board the "Michael Sars" regarding the capture of minute crustaceans in closing-net hauls from various depths. The catches have been classified in regard to number of species as well as to volume, and the characteristic feature was that the greatest number of species and the greatest volumes of these crustaceans did not occur in the upper water-layers, but at certain intermediate depths. In the Sargasso Sea the greatest volumes were captured between 1000 and 500 metres, off Newfoundland between 500 and 200 metres, and in the Norwegian Sea (Station 113) between 1000 and 500 metres. In the Sargasso Sea a greater number of species (51) was found in the deep hauls between 1000 and 500 metres than in the "surface" hauls between 200 metres and the surface (22). Certain species occurred at all depths, others only in the deepest hauls. Our horizontal hauls showed that besides these minute forms taken by the closing-nets there is a prolific community of large crustaceans, prawns, etc., in deep water, where many litres could be taken in each haul, while higher up

¹ "Das Leben im Ozean," *Erg. d. Plankton-Expedition*, Bd. v., Kiel, 1911.

these animals are absent, and the volume is obviously at a minimum.

We may therefore assert that the small nets actually capture a purely accidental selection of the animals present, and that the use of the nets only above 200 metres gives a merely casual selection, which is by no means a characteristic gauge as to the quantity of organisms living beneath a square metre of surface even at the moment.

Is the idea of a certain quantity per square metre of surface on the whole of any value whatever as regards the ocean? We may speak about the quantities produced per hectare or per square metre of soil, and we may also classify the production of a pond; but is there in the ocean any connection whatever between the different layers of a column of water 5000 or 6000 metres deep by 1 metre square in regard to the vertical exchange of nutritive substances? Is it not probable that this exchange takes place in an oblique direction and at various angles at different depths? At the surface of the North Atlantic the Gulf Stream in many places runs with great velocity, but how deep this current extends, or, to put it more correctly, at what depths it runs in the same direction and with the same velocity, is indeed as yet almost unknown. Below this current there are perhaps in places powerful reaction currents, running in opposite or other directions, probably with a considerable vertical range (see current measurements described in Chapter V.), and these would have to be passed through before reaching depths where the water layers move very slowly or not at all. Bodies sinking from the productive plant-stratum at the surface must, therefore, be supposed to be carried far away in a horizontal direction before reaching deep water. The nutriment of the deep layers of any locality is thus not derived from a point situated exactly above it, but has probably come from some very distant point, and the fact that boreal forms are found in deep water below the warm waters of the south may be a corroborative proof of this.

Notwithstanding my admiration for Hensen's methods, I have always held that before these methods can be applied in nature we must make a qualitative investigation, to be followed by an investigation as to the relative quantities of the organisms present, in order to define the selection which must be made if we wish to determine the absolute quantities. To define the quantity of something perfectly casual is indeed of little

Qualitative investigations must precede quantitative estimations.

importance, but to determine the exact quantity of something clearly defined, as, for instance, the number of individuals of certain definite species living in a sharply limited water-layer, is of the highest interest.

When planning the Atlantic cruise of the "Michael Sars" I considered it our first duty to investigate in a qualitative way what organisms live at the various depths. For this purpose we made many determinations of quantity (see Chapter IX.), for instance, in order to illustrate the abundance of certain species in each of the appliances towed at different depths. This method made no pretence of giving absolute figures, but it gave us certain ideas regarding the relative quantities of organisms living at different depths, and the figures obtained by counting the fishes in our trawlings are of a similar kind. My opinion is that these estimates represent the natural conditions better than the ideas regarding animal life in the Atlantic gained by the German Plankton Expedition; this ocean, being inhabited by organisms at all depths, is very far from being as poor as shown by the nettings of the Plankton Expedition. At the surface reproduction must be exceedingly rapid, or else it would be perfectly inconceivable that so many animals could live in the deeper water, unless, indeed, their nourishment were derived from distant localities, a question that future investigations must answer. Further, the peculiar difference between the quantities of organisms occurring in the deep water of boreal and of warm oceanic waters will have to be more closely studied. In the ocean we find first a minimum just below the surface, then a pronounced maximum, with probably a minimum again in the deeper waters (see Chapter IX. on capture of *Cyclothone* in closing-nets at Station 63). I suggest as a working hypothesis that this is due to the peculiar distribution of specific gravity and viscosity, which is quite different in boreal and in warm oceanic waters.

When speaking of floating, I mentioned how the distribution of temperature, and consequently of specific gravity and viscosity, affected the geographical distribution of species, and in Chapter IX. I drew a limit between boreal and warm-water forms, which on the whole, horizontally and vertically, coincided with the isotherm of 10° C. In thus employing temperature alone as a means of dividing animal-communities my idea has only been to consider the temperature as an indicator of certain climatic conditions on which animal life is dependent. From this point of view let us inspect a section of the Atlantic along

the 30th meridian west (Fig. 567). We see that the water-layer limited by the isotherm of 10° C. is relatively thin in proportion to the depth of the ocean. The genuine warm-water layers with temperatures exceeding 15° C. reach only to 30° south and north, and are only 200 to 300 metres thick. The whole layer above 10° C. has a thickness varying between 300 and 700 metres (or between $\frac{1}{10}$ and $\frac{1}{9}$ of the depth of the ocean). Now it was only a part of this small layer which was examined by Hensen's expeditions, and consequently the results must necessarily be incomplete.

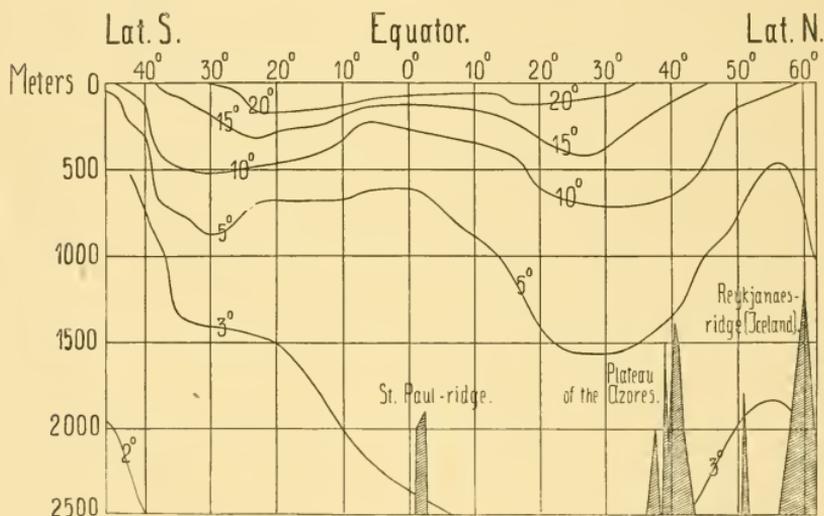


FIG. 567.—DISTRIBUTION OF TEMPERATURE IN THE ATLANTIC ALONG THE THIRTIETH MERIDIAN OF WEST LONGITUDE. (From Schott.)

Distribution
of whales.

In order to understand the abundance of animal life in various parts and at various depths of the Atlantic, it is very useful to review our knowledge of the distribution of whales in that ocean. I agree with Eschricht in dividing the whales into different biological groups according to the food on which they live. One group feeds on "plankton," another on both plankton and fishes, and a third group on squids.

Genuine "plankton whales" are the arctic "right" whale (the Greenland whale, *Balena mysticetus*, see Fig. 568), and the boreal blue whale (*Balenopectera musculus*, Fig. 569). By the aid of their enormous tongues they press the water out of their mouths between the whalebone lamellæ, thus filtering the water and retaining the minute organisms (see Fig. 570).

Another group of whalebone whales, the fin-whale (*Balænoptera physalus*), the humpback whale (*Megaptera boops*,

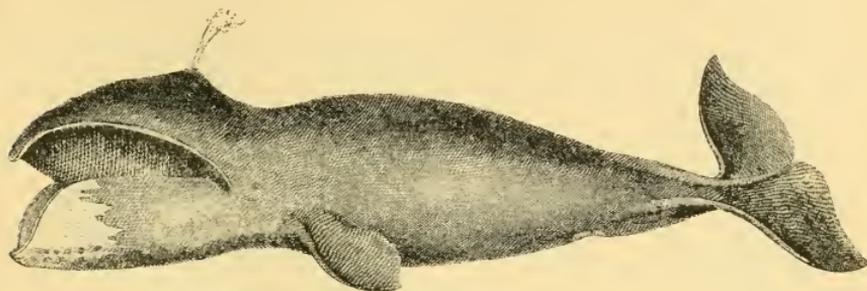


FIG. 568.

Greenland whale (*Balena mysticetus*). (From Scoresby.)

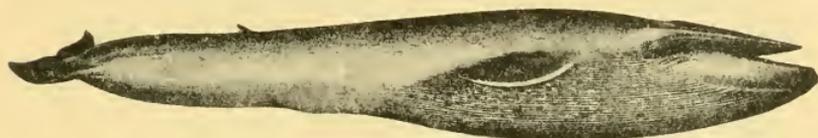


FIG. 569.

The blue fin-whale (*Balænoptera musculus*). (From G. O. Sars.)

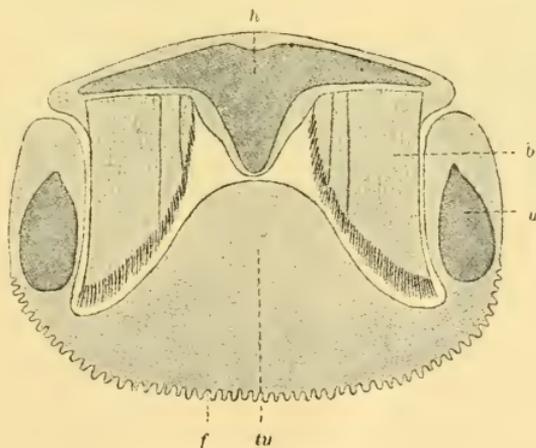


FIG. 570.

Cross-section of head of a fin-whale (*Balænoptera*). (From Boas.)

h, Head; *u*, lower-jaw; *b*, whalebone; *tu*, tongue; *f*, furrows of the skin.

Fig. 571), and the "saithe" whale (*Balænoptera borealis*) feed on plankton as well as on pelagic fishes, mainly capelan and herrings, which also constitute the main food of the small tooth-whales of the porpoise description.

The cachalot or sperm-whale (*Physeter macrocephalus*, Fig. 572) and the bottle-nose (*Hyperoodon diodon*) feed mainly on squids.¹

Howard Clark² has published an interesting chart recording the various whaling areas, in which he has separated areas fished in 1887 from areas previously fished but then abandoned. The whales fished in various areas are denoted by letters:—

- B. = Greenland whale.
- R. = Other Right whales (*Balæna*).
- F. = Fin-whales (*Balænoptera*).
- H. = Humpback whales (*Megaptera*).
- S. = Cachalots or Sperm-whales.

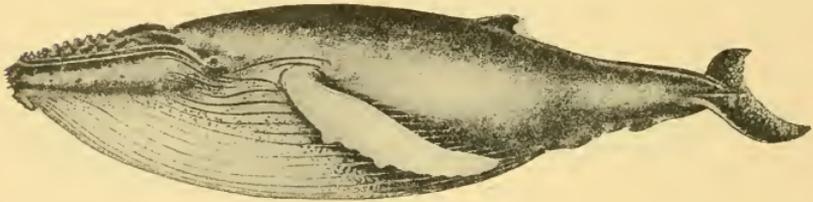


FIG. 571.
The Humpback (*Megaptera boops*). (From G. O. Sars.)



FIG. 572.
Cachalot or Sperm-whale (*Physeter macrocephalus*). (From drawing in the Bergen Museum.)

The Chart (Fig. 573) gives his records from the Atlantic, and at the same time the temperature at 100 metres has been entered, from Fig. 312, p. 445, and from Schott's report on the "Valdivia" Expedition. The dense hatching shows areas where whales were fished in 1887, the open hatching areas then abandoned. In northern boreal waters, north of the isotherm of 10° C., only or mainly the Greenland whale, fin-whales, and humpbacks are found, the right whale of the North Atlantic (north-caper or Biscayan whale, *Balæna biscayensis*, Fig. 574) being a rare visitor. In antarctic waters, where the thermal

¹ See Turner, *Journ. Anat. and Phys.*, vol. xxvi.

² *The Fisheries and Fishery Industries of the United States*, Section V., Washington, 1887.

conditions correspond to those of boreal waters, right whales predominate; in recent years, however, large numbers of fin-

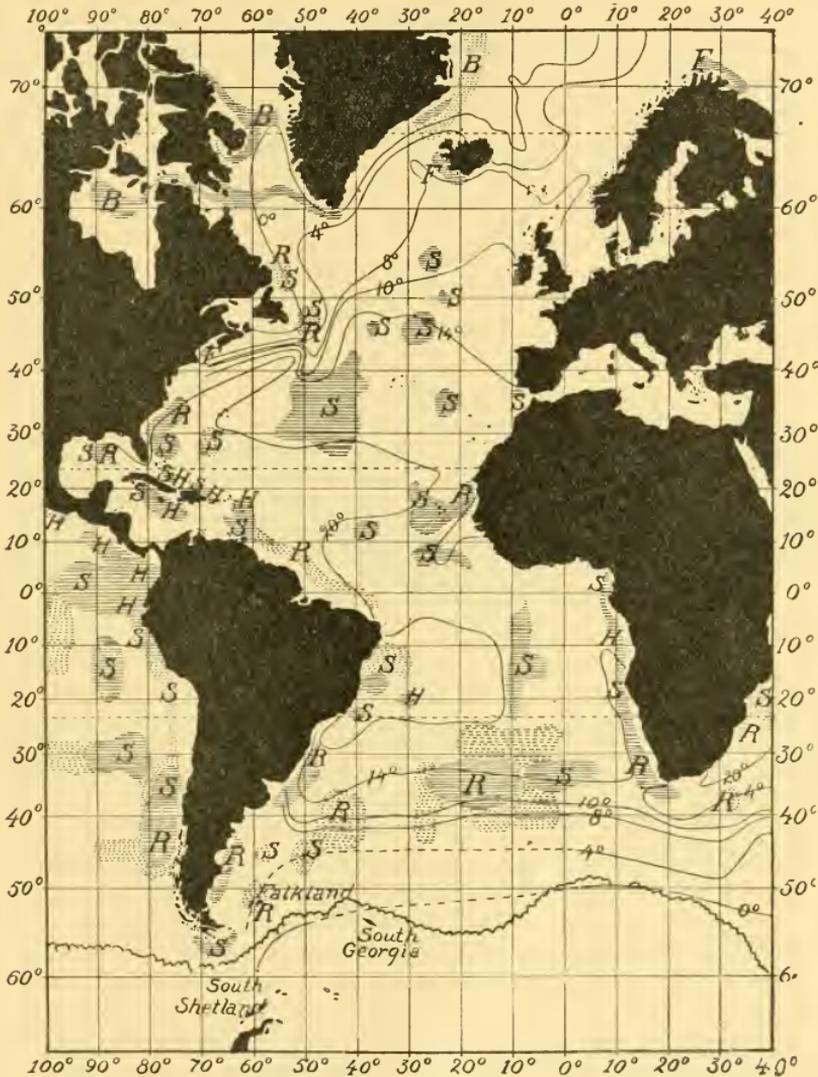


FIG. 573.—DISTRIBUTION OF WHALES, AND TEMPERATURE AT 100 METRES (see text).

whales and humpbacks have also been found there. In coast waters right whales and humpbacks predominate. In the open ocean between the parallels of 10° north and south,

the cachalot is the principal, if not the only, large species which has been the object of man's exertions in these parts.

The distribution of whales, here roughly outlined, seems to agree very well with what I have previously stated in regard to the distribution of pelagic animals. In boreal, and probably also in antarctic, waters the abundance of minute pelagic animals (plankton) in the upper layers is particularly characteristic of certain seasons of the year, and for this reason the whalebone whales have their habitat in these waters. In coast waters the plankton is equally rich in many places, along with quantities of small pelagic fishes, herrings, sprats, pilchards, etc., which are the food sought by humpback whales. Whether the various right whales, like *Balæna biscayensis*, in

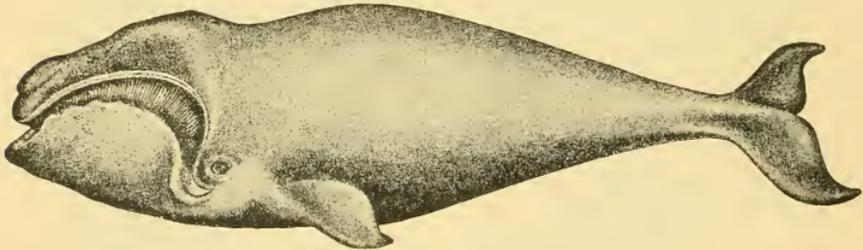


FIG. 574.
Balæna biscayensis. (From Guldberg.)

southern waters eat the small herring species besides the plankton is unknown to me; in boreal waters I am only aware that plankton has been found in their stomachs.

In the open ocean the plankton is scarce in the upper layers, but the deeper layers contain multitudes of large crustaceans and squids, and here only squid-hunting whales like the cachalot are found in numbers. Enormous diving power is peculiar to the cachalot and its ally, the bottle-nose. One of our most experienced bottle-nose whalers has told me how the whale "sounds" when struck by the harpoon, very often diving straight down, taking out as much as 400 fathoms of line in a perfectly vertical direction. It is very interesting to note that on our Atlantic cruise we found many proofs of the existence of quantities of squid in vast areas of the open ocean, partly belonging to the same species as the Prince of Monaco found in the stomachs of sperm-whales. The occurrence of these whales, and the importance of the sperm-whaling carried on in the open

oceans, seem to indicate that the oceans are not quite so poor as Hensen's results would imply. But the nature, reproduction, and vertical distribution of the "plankton" differ entirely in the warm part of the ocean and in boreal waters. The only thing we can do at present is to compare these two classes of conditions, and to compare the groups of phenomena regarding adaptation found in the ocean.

Generally speaking, I think our experience justifies the opinion that the scientific investigation of an ocean must commence with observations of a qualitative kind. A chemist, intent upon the investigation of a complex chemical compound, sets to work in the same way, first endeavouring to make out the nature of the single components of the compound, and in many cases he will find it practicable to make preliminary, merely relative, estimates as to the quantity of each component present before entering into an absolute quantitative analysis.

Hensen himself has shown how to make a definite selection in the case of the complex "plankton"-problem by taking up for quantitative investigation the occurrence of one single organism, viz. the pelagic egg of the plaice. In this case, of course, an infinitely more clearly defined and sharply limited problem presented itself, and Hensen endeavoured to solve it for certain areas of the North Sea and the Baltic, developing the very interesting idea that the number of spawning plaice might be arrived at by studying the number of pelagic eggs within a restricted area, and ascertaining the number of eggs spawned by the average female plaice. While studying the cod eggs of the Norwegian Sea I have very often had occasion to consider the same problem, but I have never ventured to attempt its solution. Even in this case I considered it necessary, first of all, to make qualitative investigations, commencing with a detailed study of the areas where the eggs of each species occur.

Pelagic
fish-eggs.

The Norwegian waters are peculiar in varying greatly in depth: in the course of a few miles one may find depths ranging from a few to a couple of hundred fathoms; they are very instructive although, compared with the North Sea or the Baltic, they exhibit extreme conditions.

Another point to be considered is the fact that eggs, as soon as spawned, are carried away by currents, the distance which they travel depending on various local conditions. The influence of these currents must, therefore, be ascertained, as the eggs cannot be considered as stationary.

A third and important point is that all the individuals of a species do not spawn at the same time. Hensen himself thinks that each fish spawns several times within a short period, and besides the spawning season of each species varies from place to place. At a definite moment it is thus impossible to find all the eggs in the earliest stage, for as a matter of fact in the Norwegian coast waters the same haul includes eggs in various stages as well as larvæ and more advanced young. As regards Norwegian waters it is therefore, as far as I can see, at present impossible to realise Hensen's idea of counting the fishes of the sea, or to cope with the problem of calculating the stock arising from the developed larvæ.

It is well known that in many countries a considerable amount of work has been devoted to so-called artificial fish-hatching, which consists in keeping the eggs until the minute larvæ have escaped. Hopes have been entertained of increasing the fish-supply by means of this hatching, the idea having prevailed that these larvæ had a better chance of growing up than the eggs. But when these minute larvæ are placed in the sea, where there are already great numbers of them, they disappear from view in a few minutes, and their subsequent fate is entirely unknown. All calculations as to how many of them grow up must be based on unknown and uncontrollable factors, and become all the more doubtful considering there is now ample proof that the abundance of different annual classes varies enormously in nature.

Quantitative investigations of an entirely different kind have in recent years been started by C. G. J. Petersen,¹ who constructed a bottom-sampler, or kind of gripper (see Fig. 575), which, like a dredging apparatus, brought up a large sample from the surface of the sea-floor. The bottom-sampler is intended to cut out a sample of one square foot from the bottom, which is passed through sieves, the sand and mud being sifted off, leaving the animals to be classified, measured, counted, weighed, and finally submitted to chemical analysis. These investigations on the abundance of bottom animals are simpler than those dealing with the pelagic organisms, which move so freely in a horizontal as well as in a vertical direction.

Petersen has also attempted to solve the problem of the quantity of fishes by experiment.² He captured great numbers

¹ *Report of the Danish Biol. Station*, No. xx., 1911.

² "The Labelling of Fish in the Sea," *Fishery Report for the Years 1888-1889*, and *Report from the Danish Biol. Station*, No. iv., 1893.

Artificial fish-hatching.

Quantitative investigations on the sea-floor.

of plaice, marked them, and let them go again. He then kept account of the percentage of marked plaice subsequently recaptured, and comparing this percentage with the total catch according to the fishery statistics he hoped to arrive

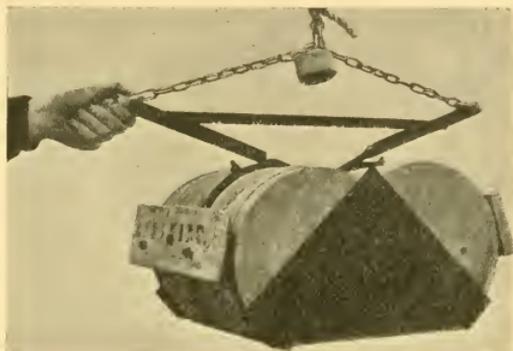


FIG. 575.—C. G. J. PETERSEN'S BOTTOM-COLLECTOR.

approximately at the proportion between the number of plaice caught by the fishermen and those living in definite regions. In restricted areas, where immigration and emigration are insignificant, his interesting experiments have yielded very good results, providing probably the only accurate knowledge at present available regarding the abundance of fishes in the sea.

J. H.

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