

## INTERRELATIONS BETWEEN MICROZOOPLANKTON AND OTHER PLANKTON ORGANISMS

By

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### *Abstract*

Microzooplankton are believed to be a vital link between very small primary producers and larger secondary producers, but only the zooflagellates seem to be capable of ingesting bacterial-sized particles in sufficient quantity to meet their energetic requirements in oceanic waters. Ciliates and most other protozoans, as well as most metazoans in the sea, are poorly adapted to capture particles less than 1 or 2 microns in dimension. Hence, there may be one or more trophic links within the microzooplankton community itself. Food habits and feeding mechanisms of most microzooplankters are poorly known, but the use of flagellae, cilia, cirri, and direct phagocytosis of particulate matter are all practised. Feeding rates are probably size dependent and also regulated by quantity and quality of food. Microzooplankton animals are preyed upon by a wide variety of larger zooplankton. Some herbivorous zooplankton can ingest protozoans and their presence seems to improve the nutritional quality of detritus. A number of microzooplankton species fall into the size range of preferred foods of first feeding larval fishes and thus their distribution could conceivably directly effect the year-class strength of certain commercial species. However, the role of this enigmatic group of

### *Résumé*

#### **Relations entre le microzooplancton et les autres organismes planctoniques.**

Le microzooplancton est considéré comme un maillon vital entre les très petits producteurs primaires et les producteurs secondaires de tailles plus importantes; mais seuls les zooflagellés semblent capables d'ingérer des particules de la taille d'une bactérie en quantité suffisante pour assurer leurs besoins énergétiques dans les eaux océaniques. Les ciliés et la plupart des autres protozoaires, aussi bien que la plupart des métazoaires marins, sont mal adaptés à la capture de particules de moins de 1 à 2 microns. Ainsi il peut y avoir un maillon, ou davantage, à l'intérieur de la communauté microzooplanctonique elle-même. L'alimentation et les mécanismes de nutrition de la plupart des microzooplanctontes sont mal connus, mais l'usage de flagelles, de cils, de cirres et la phagocytose directe de matière particulaire sont pratiqués. Les taux d'ingestion dépendent probablement de la taille et sont également régulés par la quantité et la qualité de la nourriture. Les animaux du microzooplancton sont consommés par une grande variété d'organismes du zoo-

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organisms is still largely speculative; the requirement for more and better quantitative data to support our hypotheses regarding their pivotal position in pelagic food chains is emphasized.

plancton. Le zooplancton herbivore peut dans certains cas ingérer des protozoaires dont la présence améliore la qualité nutritive des détritus. Un certain nombre d'espèces du microzooplancton se trouvent dans la gamme de taille préférentielle dont se nourrissent à leurs premiers stades les larves de poisson et il est concevable que leur distribution pourrait ainsi affecter directement l'importance des classes d'âge annuelles de certaines espèces commerciales. Cependant le rôle de ce groupe énigmatique d'organismes est encore beaucoup affaire de spéculation; la nécessité de données quantitatives plus nombreuses et meilleures pour appuyer nos hypothèses concernant leur position de pivot dans les chaînes trophiques pélagiques est souligné.

## INTRODUCTION

The microzooplankton are a heterogeneous assemblage of animals generally defined by the interstices of the net used to sample them. I will follow the example of BEERS & STEWART (1967) and consider any recognizable animal material passing a 202  $\mu\text{m}$  net as belonging to the microzooplankton, although by some classifications animals between 2 and 20  $\mu\text{m}$ , such as certain protozoans, might be termed ultra-microzooplankton following DUSSART (1965) or nanozooplankton after SIEBURTH *et al.* (1978). Systematically the microzooplankton include a wide range of Protozoa and the developmental stages of many pelagic and benthic animals, but very few adult metazoans. In *Fig. 1* I have tried to show the trophic position of representative microzooplankton with a typical food web diagram. The arrows entering or leaving the area under the magnifying glass indicate the interrelationships which will be the primary concern of this paper.

I have put these organisms under the lens to emphasize their pivotal position in pelagic communities rather than to emphasize particular morphological features. Recent research has shown the quantitative importance of the animals in a variety of

marine environments and at all seasons (CHESTER, 1978; SOROKIN, 1979; TAGUCHI, 1976; TAKAHASHI & HOSKINS, 1978; TUMANTSEVA, 1981) and their potentially significant dynamic role has long been emphasized (JOHANNES, 1964, 1965; CONOVER, 1964; POMEROY, 1974). Even so most of what we know concerning the feeding interactions of this assemblage comes from rather casual qualitative observations of gut contents or is inferred from the behavior of taxonomically related forms from a different environment.

The animals making up the microzooplankton are relatively small and presumably all eat even smaller food. In this sense all are fine particle feeders, but it is by no means certain that all are non-perceptive suspension feeders as well. Those that have been studied show classical saturation responses to increasing food supply generally of the Holling Type II (*Fig. 2*). The animals which appear under the glass in *Fig. 1* use either cilia, flagellae or cirri to capture their food. Other protozoan microzooplankton, for example, radiolarians and foraminiferans, use phagocytosis and/or some form of pinocytosis to obtain nourishment.

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FIG. 1. — *Trophic relations involving the microzooplankton. Heavier arrow indicates greater importance of pathway.* CI, ciliate; CF, colorless flagellate; PF, pigmented flagellate; N, nauplius; DT, diatom; DF, dinoflagellate; DP, detritus particle; FCB, Free-living cyanobacteria; CCB, clumped cyanobacteria; FB, free-living bacteria; PT, pelagic tunicate; SS, small chaetognath; LS, large chaetognath; CP, copepod; CT, ctenophore; LF, larval fish; H, grazing fish.

FIG. 1. — *Relations trophiques mettant en cause le microzooplancton. L'épaisseur des flèches correspond à l'importance plus ou moins grande de la liaison.* CI, cilié; CF, flagellé sans pigment; PF, flagellé pigmenté; N, nauplius; DT, diatomée; DF, dinoflagellé; DP, particule détritique; FCB, cyanobactéries libres; CCB, cyanobactéries agglomérées; FB, bactéries libres; PT, tunicier pélagique; SS, petit chétognathe; LS, grand chétognathe; CP, copépode; CT, cténo-phore; LF, larve de poisson; H, poisson s'alimentant.

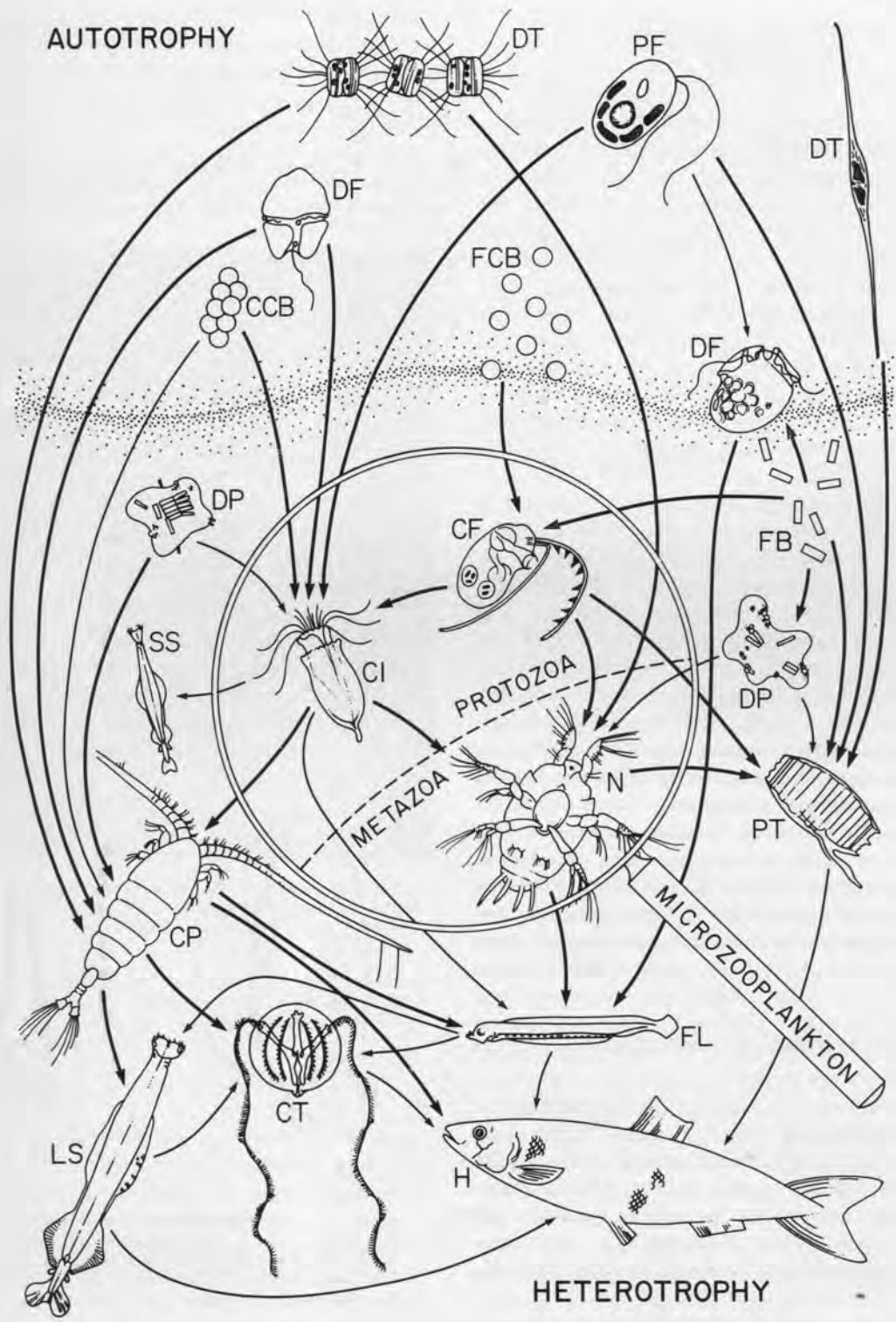


FIG. 1.

## FUNCTIONAL RESPONSE

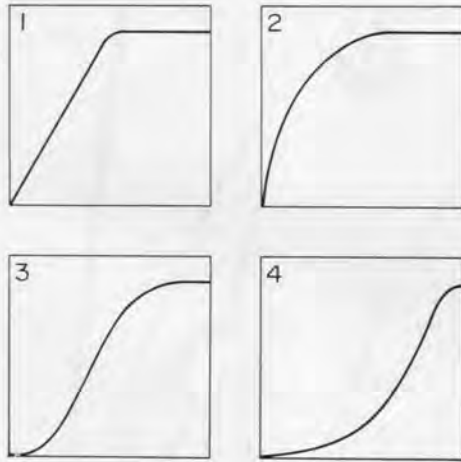


FIG. 2. — Functional response curves. 1 : rectilinear (HOLLING, 1959, Type I); 2 : negatively accelerated or hyperbolic (Type II); 3 and 4 : sigmoid (Type III), but with different slopes.

FIG. 2. — Courbes de réponse fonctionnelle. 1 : rectilinéaire (HOLLING, 1959, Type I); 2 : accélérée négative ou hyperbolique (Type II); 3 et 4 : sigmoïde (Type III) avec différentes pentes.

## FEEDING MECHANISMS

## 1. Ciliates

While a great deal is known about the feeding of certain protozoans, we are frustrated by the lack of information on truly planktonic forms. FENCHEL (1980 *a*) described in detail feeding for several benthic forms from which we can generalize about those in the pelagic zone. In the higher ciliates, feeding currents are maintained by ciliary membranelles, which may be as few as three, but can be many more in the Polyhymenophora, the class which includes the tintinnids and other oligotrichs. These membranelles transport water parallel to their orientation by a succession of metachronal waves. Generalized feeding currents are shown in Fig. 3 (left) for a typical oligohymenophoran such as *Tetrahymena*. The currents are directed into the mouth region then upwards and anteriorly through a single row of cilia (haplokinety) forming a paroral or undulating membrane. Dimensions of the interstices between the cilia are generally less than  $0.5 \mu\text{m}$  and these forms are predominantly bacterial feeders (FENCHEL, 1980 *a*).

In the polyhymenophorans, the membranelles not only generate the feeding currents but act as the filter as well. They are usually arranged in a band, with membranelles oriented perpendicular to the

long axis as in the hypotrich *Euplotes* shown in Fig. 3, right; at the anterior end the water is driven posteriorly to propel the animal while more posteriorly the currents pass distally from the buccal

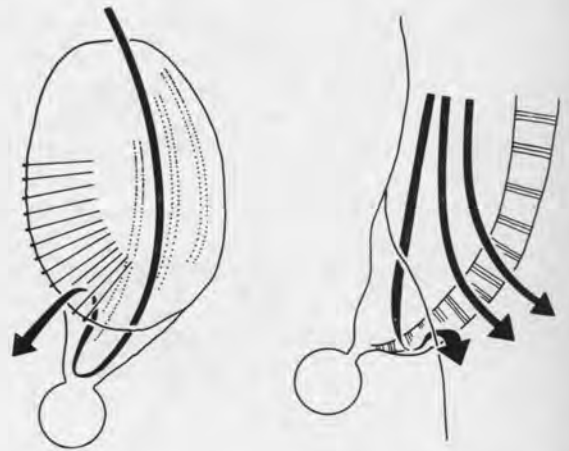


FIG. 3. — A generalized representation of the feeding currents in the mouth region of an oligohymenophoran (left) and a polyhymenophoran ciliate (right) (after FENCHEL, 1980 *a*. Reproduced by permission of VEB Gustav Fischer, Verlag).

FIG. 3. — Représentation schématique des courants servant à l'alimentation dans la région buccale d'un cilié oligohyménophore (à gauche) et d'un cilié polyhyménophore (à droite) (d'après FENCHEL, 1980 *a*. Reproduit avec l'autorisation de VEB Gustav Fischer, Verlag).

cavity through the membranelles and particles thus retained are transmitted to the cytosome where ingestion takes place. Membranelles in the tintinnids form helical adoral and paroral arrays (Fig. 4), but there have been virtually no observations on how these function to capture food since those of CAMPBELL (1927). Presumably metachronal motions of the longer adoral cilia propel the ciliate forward while



FIG. 4. — Peristomal view of ciliary membranelles in a species of *Tintinnopsis* showing the helical organization (Kenneth Gold, unpublished. Reproduced by his permission).

FIG. 4. — Vue péristomiale des membranelles ciliaires dans une espèce du genre *Tintinnopsis* montrant la disposition en hélice (dessin original de Kenneth Gold reproduit avec son autorisation).

directing currents into the peristome and out between the bases of the membranelles. Captured particles would then be directed along the paroral membranelles in helical fashion toward the cytostome. Morphological and experimental studies suggest that tintinnids, similar to other polyhymenophorans, cannot utilize the small free-living bacteria characteristic of most marine environments. While presumably differing in details, the feeding mechanisms of the remaining marine oligotrichs probably function along similar lines.

## 2. Flagellates

Heterotrophic flagellates, primarily Zoomastigophorea, are characteristic of many aquatic systems, including both eutrophic and oligotrophic parts of the ocean (SCROKIN, 1979), but again their feeding behavior must be largely inferred from laboratory studies of organisms from a much different environment. *Bodo saltans* was isolated from a freshwater pond by BROOKER (1971) and investigated with light and electron microscopy. The ovoid body supports two flagellae of unequal length emerging from an anterior flagellar pocket (Fig. 5). The shorter interior flagellum imparts a rotary motion in swimming while, in this species, the longer trailing flagellum may be used as a means of attachment. The anterior flagellum bears bundles of hair-like projections called mastigonemes along one side only. These structures are presumed to facilitate the generation of feeding currents which would bring bacteria into the vicinity of the buccal cavity and the buccal lappets. Whether they actually bring food particles to the mouth is unclear, but such behaviour has been described by SINTON (1912) cited in BROOKER (1971) for another species of *Bodo*. Once seized by the buccal lappets a bacterium is moved rapidly down the cytopharynx where it passes into a food vacuole (Fig. 5). Cytoplasmic bacteria, presumably sharing some kind of commensal relationship, are also seen. *Bodo saltans* is 5-8  $\mu\text{m}$  long by 2-5  $\mu\text{m}$  wide and can be cultured in 0.1 % liver infusion of bacteria which must be several orders of magnitude more concentrated than the environment of open ocean zooflagellates.

## 3. Digestion in *Tetrahymena*

Details of the digestive process in ciliates have been summarized by ELLIOT & CLEMMONS (1966) (Fig. 6). The food vacuole expands as it fills, eventually sealing off and sliding into the cytoplasm. In the meantime, primary lysosomes are formed along the rough endoplasmic reticulum and then budded off into the cytoplasm where they seem to merge with pinocytic vacuoles invaginated from undifferentiated areas of the pellicle and plasma membrane. This secondary lysosome element apparently contains the necessary digestive enzymes to lyse the bacteria after fusing with a food vacuole. Digestion proceeds

as the vacuole moves posteriorly. Small evaginations, containing digested food, drift off into the cytoplasm and are absorbed, while the particulate wastes are excreted at the cytopyge. In some species dissolved organic matter, when available in high concentration, may be directly absorbed into autophagic

#### 4. Cirral feeding by copepod nauplii

The first two naupliar stages of *Calanus finmarchicus* do not feed but otherwise there are no important morphological or behavioral changes before

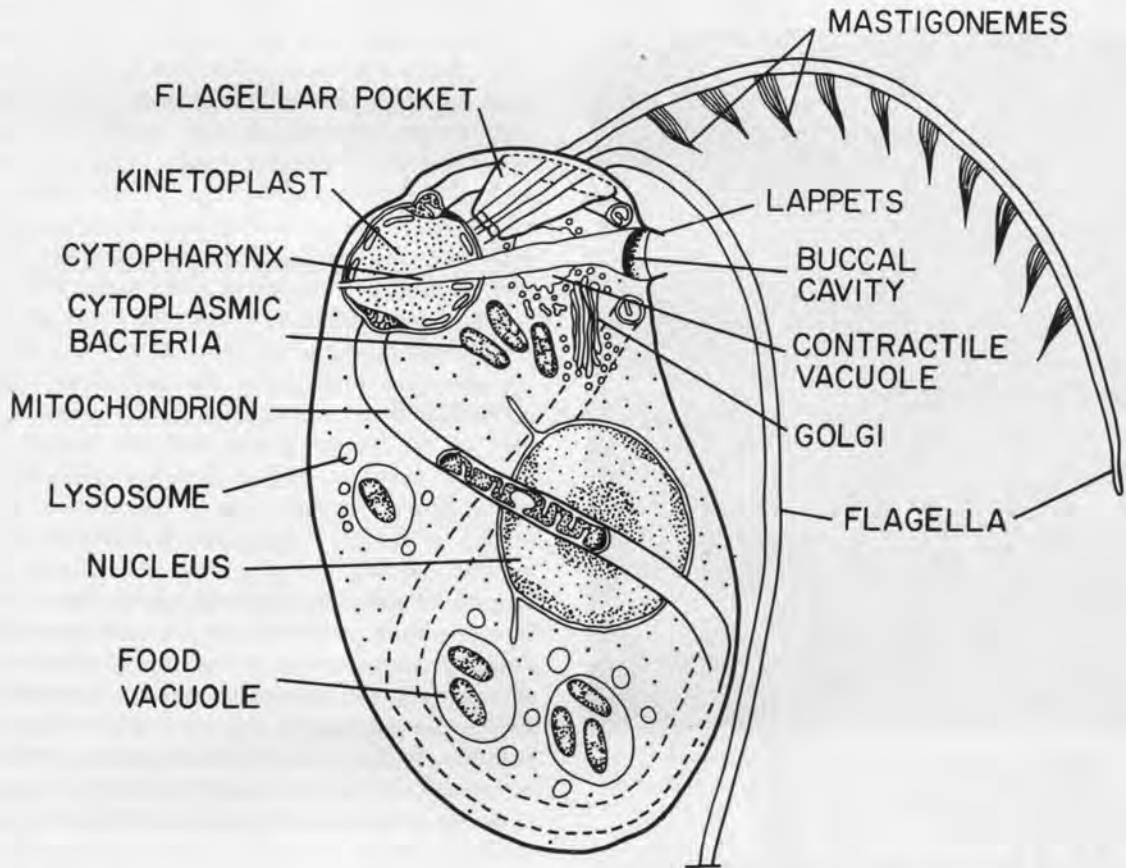


FIG. 5. — Diagram of *Bodo saltans* showing the arrangement of the main organelles (after BROOKER, 1971. Reproduced by permission of the Trustees of the British Museum of Natural History).

FIG. 5. — Diagramme de *Bodo saltans* montrant l'arrangement des principales organelles (d'après BROOKER, 1971. Reproduit avec l'autorisation des « trustees » du « British Museum of Natural History »).

vacuoles. Food vacuoles, sometimes in considerable abundance, can be seen in planktonic marine ciliates in culture (LAVAL-PEUTO *et al.*, 1979). Cytoplasmic events involved in digestion probably limit protozoan ingestion rates; for example, CURDS & VANDYKE (1966) have described how empty food vacuoles may alternate with full ones when certain ciliates are fed on high bacterial concentrations.

metamorphosis to the first copepodid stage. As shown in Fig. 7, there are three pairs of appendages: the first antennae, which seem to be involved in rapid movement, but which are motionless during feeding; the second antennae, which are primarily responsible for motion during feeding; and the mandibles that actually capture and process food particles (GAULD, 1959). Swimming motions of the second

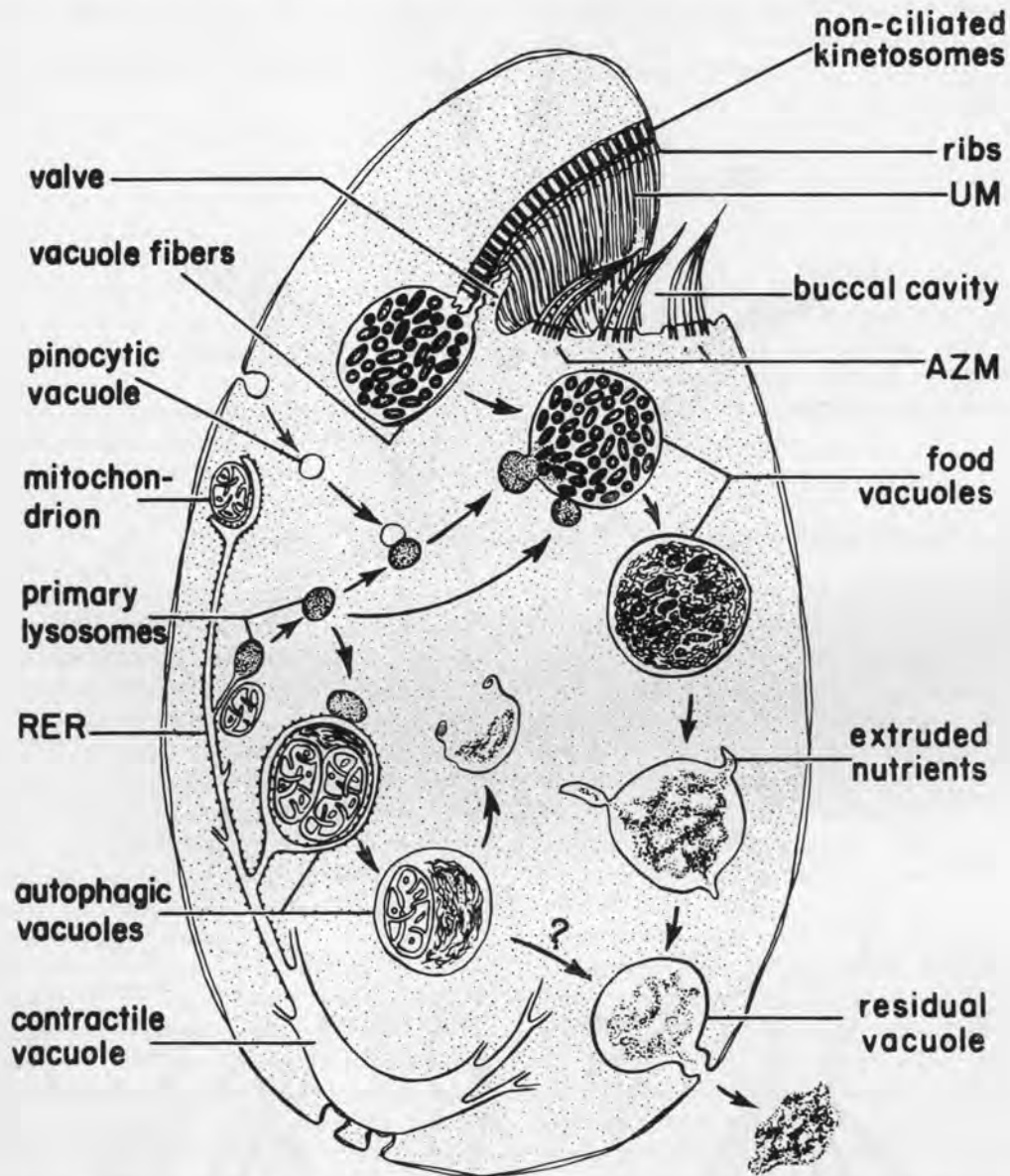


FIG. 6. — Schematic representation of the possible structural pathways of intracellular digestion in *Tetrahymena pyriformis*. UM, undulating membrane; AZM, adoral membranelles; RER, rough endoplasmic reticulum (after ELLIOTT and CLEMMONS, 1966. Reproduced by permission of the Society of Protozoologists).

FIG. 6. — Représentation schématique des liaisons structurales possibles dans la digestion de *Tetrahymena pyriformis*. UM, membrane ondulante; AZM, membranelles adorales; RER, reticulum endoplasmique grossier (d'après ELLIOTT et CLEMENS, 1966. Reproduite avec l'autorisation de la Société des Protozoologistes).

antennae and mandibles direct lateral and vertical currents posteriorly along the body. Particles contained in this essentially « u-shaped » stream can only be captured if contacted by the setae on the mandibular endopods. In forward position, the mandibles make an angle of about 80° with the long axis

of the body and the setae are nearly normal to the ventral surface. As the limb moves posteriorly and medially the setae become opposed lying parallel to the ventral surface, thus forming a « basket » just posterior to the mouth. To be seized by this mechanism a particle must be 15 or 20 µm in one dimen-

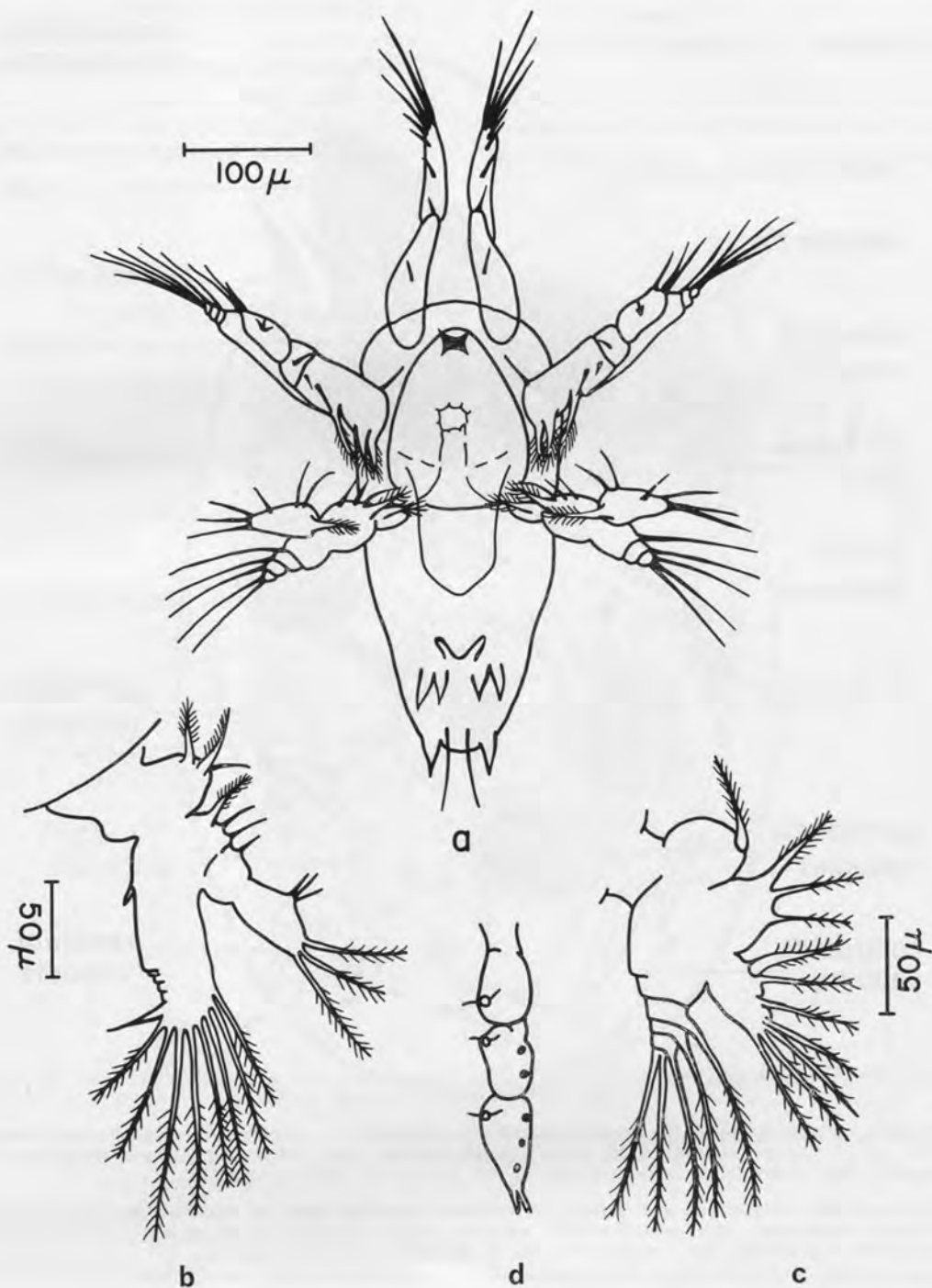


FIG. 7. — Naupliar stage 3, *Calanus finmarchicus*. a, ventral view showing resting position of limbs; b, second antenna; c, mandible; d, diagram, showing arrangement of setules on mandibular endopod (after GAULD, 1959. Reproduced by permission of the Zoological Society of London).

FIG. 7. — Stade nauplius 3 de *Calanus finmarchicus*. a, vue ventrale montrant la position au repos des appendices; b, antenne 2; c, mandibule; d, diagramme montrant l'arrangement des sétules sur l'endopodite mandibulaire (d'après GAULD, 1959. Reproduit avec l'autorisation de la Société Zoologique de Londres).



sion, the minimum distance between the setae. Hence, nauplii do not feed on appreciably smaller sized particles than the adults. Indeed, copepodid I is more

efficient in handling both larger and smaller particles than is the immediately preceding naupliar stage (FERNÁNDEZ, 1979 a).

## FEEDING BEHAVIOR

### 1. Selective feeding

Whether planktonic suspension feeders can discriminate between particles using criteria other than size and shape remains a contentious issue. Among benthic ciliates studies by FENCHEL (1980 b) the size range of acceptable latex spheres for a species is quite narrow and correlates well with the morphological and dimensional characteristics of the feeding apparatus. Certainly inert particles of suitable size seem to be consumed at about the same rate as natural foods, but it does not appear that any experiments have been carried out in which the ciliate was given a choice between an inert particle and a suitable food of the same size and shape. In a series of experiments where the large ciliate *Stentor coeruleus* was given a choice of food, RAPPORT *et al.* (1972) showed clear selection for animal particles (other ciliates) over plant cells (flagellates) independent of the relative size or concentration of each.

Among the tintinnids the minimum size of a consumable particle does not seem to have been determined, although SPITTLER (1973) observed consumption of yeast and activated carbon particles less than 2  $\mu\text{m}$  in diameter. Maximum size of starch granules ingested was 41.2 to 45 % of the diameter of the lorica which agrees well with the more recent observations of BLACKBOURN (1974) and HEINBOKEL (1978 a). SPITTLER also observed a marked preference for yeast cells over carbon particles by tintinnids when they were offered together. HEINBOKEL (1978 b) noted that *Eutintinnus pectinis* demonstrated a preference for the more concentrated cell type in a mixed food situation and « switching » was suggested for *Stenosemella ventricosa* from Coulter Counter studies with natural particles as food (RASSOULZADEGAN & ETIENNE, 1981).

The nauplius of *Calanus pacificus* selected algal cells in preference to plastic beads, pollen grains and detritus (FERNÁNDEZ, 1979 b) and they showed higher ingestion rates when fed the cell on which they had

been raised than when switched to a different species (FERNÁNDEZ, 1979 a). In contrast with this sophisticated behaviour, ALLAN *et al.* (1977) felt that the nauplii of *Eurytemora affinis* were less selective than the copepodid stages.

### 2. Factors controlling feeding

Theory suggests that metabolism, and presumably feeding as well, should be greater on a size-corrected basis for the microzooplankton than for larger filterers. In the ciliates studied by FENCHEL (1980 c) this hypothesis was generally supported, but a stronger, positive correlation was demonstrated between filtration rate and optimum particle size for a particular grazer. The physical and energetic constraints of passing a viscous fluid, water, through a filter containing very small apertures limits the clearance rate of ciliated bacteriovores and explains their scarcity in oligotrophic waters (FENCHEL, 1980 d).

Filtering rates for tintinnids feeding on particles greater than 1  $\mu\text{m}$  are highly variable and presumably are affected by particle size and concentration as in the benthic ciliates. Evidence that the feeding response sometimes saturates with increasing food is given by SPITTLER (1973), BLACKBOURN (1974) and HEINBOKEL (1978 a and b) in experiments with single food sources; however, BLACKBOURN (1974) did not see inhibition of feeding at high concentrations of natural particulate matter nor any change in electivity for *Tintinnopsis subacuta* as potential food became more abundant. There was no diel feeding periodicity shown by any tintinnid species during one field study described by HEINBOKEL (1978 a) nor was there a marked effect of temperature on feeding in BLACKBOURN's (1974) work.

Extrapolation of linear or curvi-linear plots of ingestion rates against available food have suggested the presence of a lower concentration necessary to initiate feeding in larger zooplankton (PARSONS *et al.*, 1967). Such estimates have proved highly variable,

with size of the food particle being among the contributing factors (FROST, 1975). A lower feeding threshold has been found for copepod nauplii (FERNÁNDEZ, 1979 *a*), and for tintinnids by BLACKBURN (1974) and HEINBOKEL (1978 *b*), but as in the work with copepods, no value for an absolute limiting concentration could be fixed. Values could be negative on occasions and were clearly influenced by the curve-fitting model chosen as previously shown by MULLIN *et al.* (1975). I suggest that the use of a sigmoid-model, such as the Holling type III (*Fig. 2*), eliminates the necessity to find an absolute threshold value while affording a stabilizing refuge to prey organisms against overgrazing.

### 3. Efficiency of zooplankton grazing

At the present time, there is a degree of controversy regarding the potential impact of various

groups of suspension feeders on primary production and on the available particulate resources in different types of pelagic regimes. The scientific dilemma is exaggerated by increasing evidence that some of the primary production can be returned to the water as dissolved organic matter (MAGUE *et al.*, 1980), presumably contributing to the support of free-living bacterial populations, while a larger fraction is packaged initially in small flagellates and coccoid cyanobacteria (JOHNSON & SIEBURTH, 1979; WATERBURY *et al.*, 1979; MALONE, 1980), all too small for efficient grazing by the majority of mesozooplanktonic herbivores. As I have tried to show in *Fig. 1*, the microzooplankton are believed to be the all important link between the apparently very productive small forms and the conspicuously dominant crustacean zooplankton. To better understand and compare the grazing potential of the micro- and larger zooplankton, I have assembled some data on the filtering capabilities of representative forms in *Table 1*.

TABLE 1. — Weight-specific filtration and ingestion rates for some zooplankton. Data from various sources.

Group and species	Biomass or volume of grazers	Food source	Food concentration ( $\mu\text{g C l}^{-1}$ )	Environmental type	Filtration rate ( $\text{ml day}^{-1} \text{mg C}^{-1}$ )	Ingestion % body weight or % body carbon $\text{day}^{-1}$	References
Microzooplankton							
Zooflagellates							
<i>Parabodo attenuatus</i>	$67 \times 10^{-12} \text{ g}$ ( $100 \mu\text{m}^3$ )	Bacteria and dissolved organic matter	200-400*	Neritic	—	1,212	KOPYLOV <i>et al.</i> (1980)
Ciliates							
<i>Favella ehrenbergii</i>	$48 \times 10^4 \mu\text{m}^3$	Natural seston	ca. 250	Neritic	—	70	RASSOULZADEGAN (1978)
<i>Stenosemella ventricosa</i>	$7 \times 10^4 \mu\text{m}^3$	Natural seston	ca. 150	Neritic	—	43-223	RASSOULZADEGAN and ETIENNE (1981)
<i>Tintinnopsis cf. acuminatales</i>	$10^4 \mu\text{m}^3$	Cultured flagellates	ca. 170	Temperate coastal	$5.6 \times 10^4$	950	HEINBOKEL (1978 <i>b</i> )
Copepod nauplii							
<i>Calanus pacificus</i> N V	$2 \times 10^{-5} \text{ g}$	<i>Lauderia borealis</i>	49	Temperate coastal	$4.9 \times 10^4$	240	PAFFENHÖFER (1971)
<i>C. pacificus</i> N III	$1.2 \times 10^{-5} \text{ g}$	<i>Thalassiosira fluviatilis</i>	125	Temperate coastal	$0.4 \times 10^4$	50	FERNANDEZ (1979 <i>a</i> )
<i>Eurytemora affinis</i>	$10^{-5} \text{ g}$	Natural seston	630	Neritic	$0.19 \times 10^4$	120	ALLAN <i>et al.</i> (1977)
Larger zooplankton							
Copepods							
<i>Calanus pacificus</i> C V	$7.3 \times 10^{-4} \text{ g}$	<i>Lauderia borealis</i>	49	Temperate coastal	$1.1 \times 10^4$	54	PAFFENHÖFER (1971)
<i>C. cristatus</i>	$17.6 \times 10^{-3} \text{ g}$	Natural seston	212	Boreal oceanic	$0.03 \times 10^4$	6.4	TAGUCHI and ISHII (1972)
Salps							
<i>Pegea confederata</i>	0.5-30 g	<i>Thalassiosira pseudonana</i>	100	Tropical ocean	$1.93 \times 10^4$	190	HARBISON and GILMER (1976)

\* 1,500  $\mu\text{g C l}^{-1}$  bacteria and DOM combined.

TABLE II. — Estimates of the percentage of phytoplankton consumed by microzooplankton in several marine environments (GIFFORD, unpublished).

Taxon	Location	% Primary production consumed				References
		Time	Zone	Range	Mean	
Tintinnids	Southern California Bight Long Island Sound	All seasons	EZ	1-20 <sup>a</sup>	ca. 4 <sup>a</sup>	HEINBOKEL & BEERS, 1978
		June	S	9.8-20 <sup>b</sup>	14.9 <sup>b</sup>	CAPRIULO & CARPENTER, 1980
		Nov.	ca. 5-7 m 17 m	19.1-62.5 <sup>b</sup> 6.4-16.6 <sup>b</sup>	40.8 <sup>b</sup> 11.5 <sup>b</sup>	
Total ciliates	Peru	June	EZ	5-24 <sup>a</sup>	15 <sup>a</sup>	BEERS <i>et al.</i> , 1971
Total micro-zooplankton	Eastern tropical Pacific California Current	Feb.-April	EZ	39-104 <sup>a</sup>	70 <sup>a</sup>	BEERS & STEWART, 1971
		April-Sept.	EZ	7-52 <sup>a</sup>	23 <sup>a</sup>	BEERS & STEWART, 1971
Total ciliates + nauplii	Saanich Inlet	Winter	EZ		30 <sup>a</sup>	TARAHASHI & HOSKINS, 1989

EZ = euphotic zone.  
S = surface.  
a = of daily production.  
b = of standing stock.

If the very small particles are so important in the sea, and if the ciliates cannot use them as FENCHEL (1980 *d*) has argued, what happens to this production? Zooflagellates are an important link according to SOROKIN (1979) and the work of KOPYLOV *et al.* (1980) supports this contention. In culture *Parabodo attenuatus* can consume ten times its own biomass, but at rather high carbon concentrations for the open ocean (Table I). It is not clear whether this flagellate was capable of utilizing the dissolved organic matter in its environment directly but recent studies by HAAS & WEBB (1979), with unpigmented flagellates in culture, could not demonstrate DOM uptake. In a second study KOPYLOV & MOISEEV (1980) observed experimentally that the presence of zooflagellates reduced bacterial production in some coastal embayments on the Black Sea by 28 to 55%. Flagellate growth efficiency in this process was 14 to 44%. Regrettably we have as yet no information on zooflagellate performance from oligotrophic waters nor is there a measure of specific filtration rate for them which can be compared with that of other grazers. However, very recently a cyanobacterium has been identified in the food vacuoles of a neritic zooflagellate by PERKINS *et al.* (1981).

Ciliates of the tintinnid group can utilize efficiently particles in the 2 to 20  $\mu\text{m}$  range, which includes both zooflagellates like *Parabodo* and a wide variety

of autotrophic flagellates. Specific filtration rates are very high and the daily ration is probably about 0.5 to 3 times the organism's biomass, but is also heavily dependent on the concentration of suitable food (Table I). JOHANSEN (1976) has calculated on the basis of her grazing measurement that tintinnids can utilize 15 to 100% daily of the nanoflagellates in a Nova Scotia inlet, but in many environments the tintinnids may be only a small fraction of the total ciliate community. In Table II, for which I am indebted to Dian Gifford of Dalhousie University, are summarized a number of attempts to assess the role of microzooplankton, or that of certain components of that complex. In most cases, no grazing data were available for any species so that general estimates of microzooplankton performance from other locations had to be applied. Where some grazing data were available for certain forms, such as the tintinnids, the contribution by other ciliates and micrometazoa could only be estimated or was omitted from the calculation. In no case was the role of zooflagellates considered.

As for other microzooplankton components, only copepod nauplii and early copepodid stages have been seriously studied. Filtering rates on a desirable cultured alga are comparable to those found for the generally smaller ciliates (Table I). However, the range of particles which are acceptable to them is

quite narrow. They are probably in competition with their progenitors and would seem to be poor intermediates, particularly in oligotrophic food webs. Note that studies with natural particulates generally have lower ingested rations than studies with cultures, probably reflecting the lack of availability of much of the particulate matter to the grazers, either because it was the wrong size or shape or was otherwise unpalatable.

To date only a few meso- or microzooplankton have been shown capable of utilizing very small particles. Among these are the salps, larvaceans and other pelagic tunicates. As shown in *Table I*, the salp *Pegea confederata* is an extremely efficient filterer, especially considering its large size. However, salps in general, seem to be opportunists, responding quickly to favorable environmental conditions, using asexual reproduction to facilitate a high intrinsic rate of increase (HERON, 1972), but apparently contributing little to the next trophic level.

#### 4. Microzooplankton as prey

Assuming that very small living cells can enter the food web via the microzooplankton bridge, what is the next step in the food web? Much of the information we have about this link comes from the analysis of gut contents and, therefore, is strongly biased by those forms having recognizable hard parts such as the tintinnids. Hence, the following is probably only a partial list of microzooplankton predators: salps, polychaete larvae, copepods, other ciliates, rotifers, euphausiids, decapod shrimps, larval and juvenile fishes, cladocera, pteropods, and chaetognaths. Many of these observations are rather casual and some even a bit controversial. I will discuss only two linkages which appear to be important at the present time.

Among the most successful pelagic animals are the copepods which seem to have radiated into almost every niche in the sea, including adaptations for saprophagy, parasitism and commensalism. Gut analyses by HARDING (1974), VERONINA & SUKHANOVA (1976) and PERUYEVA (1977) show how widely utilized protozoans are by this group but give little quantitative information. On the other hand, most experimental investigations of omnivorousness among calanoid copepods have concentrated on the utilization of crustacean nauplii, LONSDALE *et al.* (1979) and PAFFENHÖFER & KNOWLES (1980) among recent examples. Saturation of the feeding response has

been demonstrated, as well as selective feeding, and a strong case made for the advantages of the use of animal food during periods of low phytoplankton production. However, as mentioned earlier, nauplii are in effect in the same niche as adult copepods and do not make direct use of food resources otherwise unavailable to the pelagic community.

The first experimental investigation known to me in which protozoans were linked to crustacean zooplankton was carried out by PAVLOVSKAYA & PECHEN (1971) in which  $C^{14}$ -labelled *Uronema* were fed to *Acartia clausi* and *Tigriopus brevicornis*, among other animals. For reasons that I have discussed elsewhere (CONOVER & FRANCIS, 1973), it is uncertain whether their methods were adequate, but they were unable to demonstrate that the protozoan was a sufficient food for *Acartia*, although it certainly was ingested. Neritic copepods, *Eurytemora affinis* and *Scottolana canadensis*, presumably occupying a similar niche to *Acartia*, grazed on and were benefited by the presence of protozoans in their diet, judging by their increased survival time (BERK *et al.*, 1977) and greater egg production (HEINLE *et al.*, 1977). Apparently protozoans, through their interactions with bacteria, further decomposition and render nearshore detrital resources more nutritious for zooplankton, thus linking decomposer and autotrophic-heterotrophic food webs. Analogous systems for fresh water have been described by PORTER *et al.* (1979) and FENCHEL (1975).

Microzooplankton are also frequently found in the guts of larval fish and, thereby, they are implicated in one of the most controversial of current fishery topics, the importance of first feeding success of the young larva to year class strength. For example, it has been shown by LASKER (1975) that about 30 nutritious particles of 40-50  $\mu\text{m}$  diameter must be in the vicinity of a first feeding larva of the anchovy to initiate feeding and the filling of the gut. The young larva is a feeble swimmer and relatively inefficient in prey capture. If it cannot find enough prey of the right size that it can capture, it soon dies. Gut analysis of young anchovy show a preponderance of copepod eggs and nauplii, but up to 20% of unidentified round objects (ARTHUR, 1976), but clearly all the food objects met the dimensional criteria for microzooplankton mentioned earlier. Other workers have found that fine-net zooplankton tows, fractionated to provide sufficient particles less than 100  $\mu\text{m}$ , made a suitable initial diet for the culture of several fish species (STEPIEN, 1976; HOUDE & SCHEKTER, 1980).

but only KORNIYENKO (1971), to my knowledge, has actually used protozoans as part of the diet in fish culture experiments. Whether or not fishery biolo-

gists can make use of first-feeding success in forecasting future fish stocks, the importance of microzooplankton at this critical life history stage is clear.

## CONCLUSIONS

The hypothesis that microzooplankton fill a trophic gap in pelagic food webs is certainly supportable in a qualitative way. At the same time, it is becoming clear that the microzooplankton are in reality a micro food web within the overall pelagic ecosystem structure, with perhaps two or three trophic steps being necessary to reintroduce dissolved organic matter to the system or to convert that fraction of the primary production generated by the so-called nanoplankton into what we traditionally misname secondary production. Such extra steps doubtless increase food

chain efficiency, in the sense that less material and energy are lost from the productive zone, but such a fine-grained community structure should not yield large standing crops, even though one line of theoretical reasoning (PIMM & LAWTON, 1977) advocates that it is population dynamics, not energetics, that limits the length of food chains. Regardless there is great need for observational and quantitative data. To be able to attach reliable rates and biomasses to just one of the pathways shown in *Fig. 1* would be a major achievement.

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