



Zooplankton Distribution in Four Western Norwegian Fjords

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A multi-instrumental array constructed in the Laboratoire d'Ecologie du Plancton Marin in Villefranche sur mer, France, named the Underwater Video Profiler (UVP), was used to investigate the vertical distribution of zooplankton in four western Norwegian fjords in the summer 1996. Six distinct zoological groups were monitored. The fauna included: (a) small crustaceans (mainly copepods), (b) ctenophores (mainly lobates), (c) siphonophores (mainly physonects), (d) a scyphomedusa *Periphylla periphylla*, (e) chaetognaths and (f) appendicularians.

The use of the non-disturbing video technique demonstrated that the distribution of large zooplankton is heterogeneous vertically and geographically. Furthermore, the abundance of non-migrating filter feeders in the deep basins of the fjords indicates that there is enough food (living and non-living particulate organic matter) to support their dietary needs. This adaptation may be considered as a strategy for survival in fjords. Specifically, living in dark, deep water reduces visual predation and population loss encountered in the upper layer due to advective processes.

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Introduction

Fjord environments constitute a wide variety of glacier-excavated inlets. Their marine communities are influenced by the open sea, the surrounding coastal terrain, and freshwater runoff. Fjords are steep-sided and often contain basins that are deeper than water columns along the adjacent continental shelf (Farmer & Freeland, 1983). In these semi-enclosed basins, the sills act as barriers to the free interchange of deep oceanic water and deep basin water of the fjords (Matthews & Sands, 1973). As a consequence the exchange of zooplankton populations between the open sea and the inner fjord basin is restricted. A thin, low salinity, surface layer, derived from freshwater runoff from the neighbouring terrain, generally flows out of the fjord and exports some of the biological production of the fjord. The intermediary layer below the surface and above the sill depth is subject to import or export of phyto- and zooplankton by advection (Reigstadt & Wassmann, 1996). In fjords, as in other coastal zones the mixed layer

biological production, shore erosion, fluvial discharge and deposit re-suspension are the main sources of particulate matter. These processes influence the particle dynamics in semi-enclosed basins, such as fjords, more strongly than in the open sea (Eisma, 1993). Above the sill, water masses can undergo rapid changes. Beneath the sill depth, the water mass is much more stable (Eiane *et al.*, 1998). The photic zone (spanning the superficial brackish water and some of the intermediary layer) is generally supposed to be the feeding zone and thus constantly or temporarily (via migratory zooplankton) harvested by different components of the local food web. In contrast, the deeper aphotic zone is considered as a haven, minimizing visual predation and allowing space dilution to make non-visual predators less effective (Ohmann *et al.*, 1983). However, these deep layers are also considered as energetically deficient. Accordingly, many organisms only migrate to deeper layers during the period of high predation risk in the photic zone (Stich & Lampert, 1981; Lampert, 1989; Ohmann, 1990; Houston *et al.*, 1993). Moreover, avoidance of advective losses is important for the recruitment success of a population (Wroblewski, 1982). In this regard the vertical migration by some species may result in

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transport from the fjord by advective processes (Eiane *et al.*, 1998).

Most of the research concerning the distribution of zooplankton in the Norwegian waters has been conducted using net or acoustic techniques. These methods sample crustaceans and fish more successfully than gelatinous fauna. In this investigation, the Underwater Video Profiler (UVP) was used (Gorsky *et al.*, 2000), to determine the vertical distribution of zooplankton (mainly gelatinous forms) in four different south-western fjords of Norway. This sampling method does not disturb fragile zooplankton and allows for quantification of the gelatinous components of the food chain.

Materials and methods

The study was conducted during daytime, between 8 and 12 July 1996, using the Underwater Video Profiler for vertical profiling of four fjords on the western coast of Norway (Figure 1). The UVP (Gorsky *et al.*, 2000), is an instrument equipped with two video cameras (6 and 12 mm lenses) connected to two Hi8 recorders. A Seabird SBE 19 CTD and a fluorometer (Chelsea Instruments Ltd.) were coupled to the system. The imaged area was 425×325 mm for the 6 mm camera and 190×140 mm for the 12 mm camera. Four spotlights (Birns Ltd.) illuminated a volume of approximately 70 l in front of the cameras with white light.

Study site

The studied fjords, Sognefjorden, Lurefjorden, Herdlefjorden and Korsfjorden are located in the zone between $60^{\circ}08'$ and $61^{\circ}05'N$ and $4^{\circ}31'$ and $5^{\circ}14'E$ in the vicinity of Bergen.

Sognefjorden was the deepest fjord studied with maximum depth of 1300 m (the deepest and longest fjord system in the world), separated from the open sea by a 150 m deep sill. The Norwegian Trench, a trough cutting into the continental shelf along the western coast, has maximum depth of only 400 m. Thus, Sognefjorden has an isolated, deep sea environment (Christiansen, 1993). The maximum depth of Lurefjorden is 450 m but its sill is only 20 m deep and some 200 m wide, making it almost landlocked fjord. Herdlefjorden has an even shallower (10 m), but wider sill at its NW-end, but communicates freely (down to 400 m) with another fjord at its SE-end. In contrast, Korsfjorden is a large fjord situated about 25 km south of Bergen with a 690 m deep main basin, a 3000 m wide inlet and 180 m deep sill towards the North Sea and deep communications with other fjords

to the north and to the south. Whereas the salinity of the intermediary and deep layers of Lurefjorden is lower and characteristic of shelf or coastal water (Golmen, 1991), the salinity of the intermediary and deep layers of the other examined fjords are typical of oceanic (Atlantic) water (Matthews & Sands, 1973; and this study). Matthews and Sands (1973) presume that in Korsfjorden the renewal of deep water by superficial oceanic water occurs in the first months of each year.

Sampling

From 8 to 12 July 1996, the Underwater Video Profiler (Figure 1) was used to videotape the zooplankton in the four fjords. The vertical casts were performed on board the RV *Hans Brattström* from the surface to approximately 50 m above the bottom. In Sognefjorden the UVP was deployed to the depth of 1000 m. The lowering speed was 0.5 m s^{-1} and the lighting continuous. The tapes were examined on board and in the laboratory. The macrozooplankton belonging to six distinct zoological groups were identified visually and their abundance integrated in 10 m layers. Our estimations of zooplankton abundance are not exhaustive and the sampled volume was not sufficient for a reliable quantitative description of zooplankton communities inhabiting the fjords. Only the dominant groups are presented here and the quantitative indications should be used with precautions. The rapid swimming behaviours of small crustaceans were used to quantify their abundance. Nevertheless, the study of deep layers with non-destructive video techniques is new and some of the results we are showing here can be obtained only by this method. For better reliability of zooplankton estimation, the UVP is now provided with a programmed, repetitive profiling option. This option allows the execution of a series of vertical deployments without the necessity to lift the UVP onboard. The image acquisition is performed only during the descent.

Results

In all four fjords the minimum salinity was found near the surface (see Figures 2–5). The lowest superficial salinity was observed in Herdlefjorden (<29). The lowest superficial fluorescence, as well as the lowest salinity and temperature values in deeper waters were found in Lurefjorden. The fluorescence maximum was the deepest in Korsfjorden (30 m deep), while in Sogne- and Lurefjorden the fluorescence maximum was located at the depth of 10 m. In Herdlefjorden a

strong fluorescence maximum was observed at the surface layer and was inversely correlated to the salinity.

The vertical distributions of the zooplankton recorded by the Underwater Video Profiler were different in each fjord. In Sognefjorden, most of the small crustaceans (mainly copepods between 0.5–3 mm) were observed in the first 60 m with an average value of 16 individuals per m^3 . Below this depth their concentration was about one order of magnitude lower. The layer of highest crustacean concentration was situated above the siphonophore population (Figure 2). Siphonophores (primarily physonects, Animation 1) were the most numerous gelatinous predators in Sognefjorden during the studied period. Three hundred and fifty siphonophores m^{-2} were counted between 70 and 1000 m depth. The suspension feeding appendicularians constituted another important component of the Sognefjorden ecosystem. They had a peculiar vertical distribution. One population proliferated in the superficial layer, from the surface to 35 m deep, the second from 270 m to 1000 m with the integrated abundance of 3050 appendicularians m^{-2} for this deep population. A few lobate ctenophores (probably *Bolinopsis infundibulum*) were seen below 550 m as well as a small number of the polychaetae Tomopteridae (probably *T. helgolandica*) between 300 and 470 m (Animation 1). No Scyphomedusae (= *Periphylla periphylla*) were observed in the two profiles conducted in Sognefjorden.

In the almost land-locked Lurefjorden the composition and distribution of the studied zooplankton (Figure 2) were quite different. It was the only fjord where siphonophores were not recorded and the only fjord where the *Periphylla periphylla* jellyfish were found (Animation 2). The vertical distribution of the zooplankton in Lurefjorden was strongly stratified. High concentrations of small crustaceans occupied the superficial 90 m averaging about 60 individuals m^{-3} . From 90 to 230 m this group was rare. Below this depth the abundance of small crustaceans increased, but remained low when compared to the superficial population. Lobate ctenophores (1 individual m^{-3}) were located in the superficial 200 m. In deeper layers a few cydippid ctenophores were observed. The appendicularian population was located below the lobate ctenophores community. These oikopleurid appendicularians occupied the water column between 220 and 320 m. Their standing stock, about 380 individuals m^{-2} , was not very high. This low density was possibly related to the presence of the chaetognath population recorded from 170 m to the depth of the cast with about 310 indi-

viduals m^{-2} (Animation 1). Several *P. periphylla* were also observed in the interval between 270 and 330 m.

In Herdlefjorden (Figure 3), small crustaceans (33 individuals m^{-3}) dominated the superficial 80 m. From 90 to 190 m, their abundance strongly declined. and Below 190 m the standing stock of crustaceans averaged 7 individuals per m^3 . Appendicularians occurred in the water mass below 260 m (Animation 1). The concentration of appendicularians averaged 10 individuals m^{-3} . Ctenophores were observed in low concentrations during several profiles in this fjord but not during the deepest one showed here. Other gelatinous predators appeared in low numbers.

In Korsfjorden (Figure 4), the six zooplankton groups occurred mainly below 200 m depth. Only copepods showed a superficial maximum with a standing stock of about 15 individuals m^{-3} . Their abundance decreased with depth between 110 and 190 m. In deeper layers an increase in their concentration was observed, up to 10 individuals m^{-3} . The appendicularian population (1336 individuals m^{-2}) was found from the depth of 300 m to 640 m. The depth distribution of lobate ctenophores (Animation 2) overlapped that of appendicularians, but their abundance was an order of magnitude lower. Between 330 m and 550 m we recorded 50 physonect siphonophores. The chaetognaths appeared in low numbers throughout the water column.

Discussion

According to Farmer and Freeland (1983), the fjord coastline provides an excellent laboratory to study different flow systems. In semi-enclosed basins, such as fjords, the main water column can be divided vertically into two flow systems. An advective system above the sill and stable water body below the sill depth. The effects of wind stress, solar heating and fresh water discharge are concentrated at the surface. Kaartvedt and Nordby (1992) showed that freshwater discharge affects the abundance, horizontal and vertical structure of the zooplankton community in the upper 20 m. While brackish water species are flushed out the fjord as fresh water discharge increases, some marine species modify their migratory behaviour and maintain their population density in the fjord.

According to Eiane *et al.* (1998), the adaptation of zooplankton to a given environment is constrained by the agents of mortality. These agents are starvation, predation, and losses due to advection. The superficial layer is generally considered to be the feeding zone and thus constantly or temporarily (via migrators) harvested by different components of the local food web. Above the sill depth the risk of being advected is

higher than in deeper strata and increases the loss rate. According to Eiane *et al.* (1998), the strategies of vertical positioning in zooplankton should be corrected for risk of advective loss. They consider that the vertical migration is an optimal adaptation reducing this risk.

In Korsfjorden, large caridean and penaeidean decapods occur at depths of 300–400 m during the daytime (Matthews & Pinnoi, 1973). They migrate upward during the night. The above authors observed only one generation of *Pasiphaea sivado* and concluded that this species was recruited from outside. In this fjord, the relatively deep sill allows the exchange of planktonic organisms with the open sea. According to Matthews and Sands (1973), the seasonal effect of temperature in this fjord is apparent down to a depth of 300 m, below which the temperature shows only little variation. The four groups of macroplankton observed in Korsfjorden during the daytime, the ctenophores, siphonophores, chaetognaths and appendicularians, were found under the depth of 300 m. A deep distribution pattern of the same groups was observed also in Herdlefjorden. This fjord communicates at its SE-end with another fjord without any topographical restriction. In contrast, in the land-locked Lurefjorden the ctenophore population occupy the upper 300 m. The scyphozoan *P. periphylla* is normally a deep oceanic species that may perform extensive diurnal vertical migration (Thurston, 1977). In the past it was recorded in the studied fjords but not in as high densities as in Lurefjorden (for review see Fossa, 1992). High densities of *P. periphylla* have persisted here for 20 years. Fossa (1992) observed copepods and larger crustacean remains in its stomach. The pelagic fish community seems to be affected by the presence of this medusa. According to Fossa (1992), the shallow sill, narrow inlet and low freshwater input may enhance the population maintenance due to low advective loss from the fjord. As the recruitment is limited by the topographic conditions, it is possible that the jellyfish has out-competed the fish populations. These semi-enclosed systems may thus provide an environment where long term evolution of the local ecosystem is possible with little or no exchange of zooplankton populations between the open sea and the fjord.

We did not investigate the superficial and intermediate flow processes, but our observations indicate that the vertical distribution of the gelatinous zooplankton can be affected by the boundary properties of the fjords controlling these advective processes. The particulate organic matter (POM) has an important trophic role in fjords. It constitutes the major part

of the pelagic biomass in Masfjorden (Giske *et al.*, 1990). Its biomass is one order of magnitude higher than that of the zooplankton. According to Giske *et al.* (1990), the POM is the major food source of the euphausiid *Meganyctiphanes norvegica* (cf. Fisher & Goldie, 1959). Sognefjorden is also characterized by a high input of organic material of terrestrial origin supporting high population densities of benthic fauna (Christiansen, 1993).

The discovery of appendicularian populations adapted to the life in the deep sea is related to the progress in deep water technology (Barham, 1979; Youngbluth, 1984, 1990). The appendicularians feed on a broad range of particles, less than 1 μm to about 50 μm in size (Flood *et al.*, 1992; Flood & Deibel, 1998). They do not store energy in the form of lipid deposits (Deibel *et al.*, 1992) and rely on a constant food supply. Thus, the presence of permanent appendicularian communities in deep layers indicates the availability of a sufficient stock of food particles of ingestible size and quality. Runnström (1931) described seven appendicularian species from Herdlefjorden and Hjeltefjorden. *Oikopleura dioica* is considered as one of the most widely distributed species often collected on the western Norwegian coast. Paffenhöffer (1976) found that *O. dioica* ingests around 100–200% of its body weight each day at a particle concentration of $65 \mu\text{g C l}^{-1}$. This concentration corresponds to the POC concentration measured in Masfjorden by Giske *et al.* (1990). Thus, if the POC concentrations in the fjords studied here are similar to that found by Giske *et al.* (1990) in Masfjorden, the dietary needs of deep appendicularian populations can be satisfied by the POC standing stock alone.

We have observed two features that should be taken into consideration when dealing with behavioural strategies in zooplankton. (a) The superficial layer is not the only possible feeding zone, and (b) non-migratory residency in the deep basins may be considered as an useful strategy to reduce predation rates and the superficial advective loss and thus the mortality rate. The deep fjords are considered as refuges for the zooplankton. Future investigations will show if the populations adapted to this environment can play an ecological role in structuring the food webs in the adjacent basins by export of populations.

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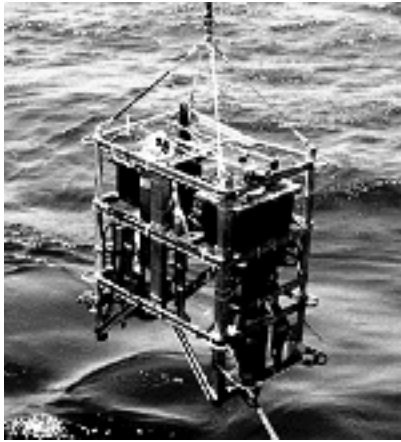


FIGURE 1. The Underwater Video Profiler (UVP). For details see Gorsky *et al.* (2000).

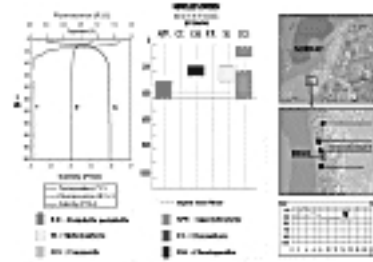


FIGURE 4. Herdlefjorden.. The depth scale of the plots is given in metres, except for the CTD/fluorescence plot, which is given in decibars (1 decibar *c.* 1 m). The adjacent open sea mean depth is shown by the red dotted line. For better comparison of the plots the scales of the deepest vertical cast (Figure 2) were maintained in all figures. The arrow points to the position of the deepest UVP cast.

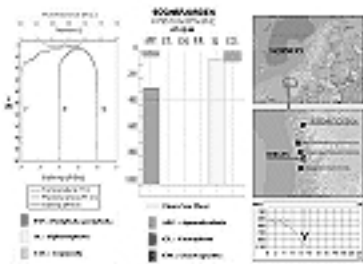


FIGURE 2. Sognefjorden. Study site, topography, selected zooplankton distribution and CTD/fluorometer profile. Depth scales are given in metres except for CTD/fluorescence plot, which is given in decibars (1 decibar *c.* 1 m). The adjacent open sea mean depth (370 m) is shown by the red dotted line. The arrow points to the position of the deepest UVP cast.

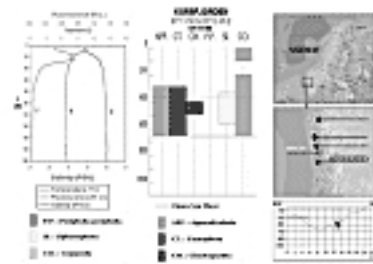


FIGURE 5. Korsfjorden. The depth scale of the plots is given in metres, excepted for CTD/fluorescence plot, which is given in decibars (1 decibar *c.* 1 m). The adjacent open sea mean depth is shown by the red dotted line. For better comparison of the plots the scales of the deepest vertical cast (Figure 2) were maintained in all figures. The arrow points to the position of the deepest vertical UVP cast.

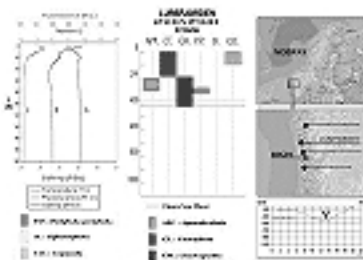
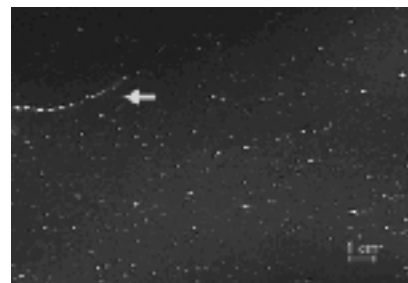
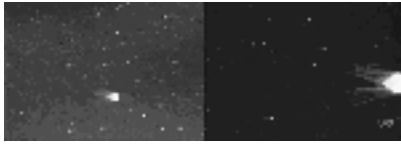


FIGURE 3. Lurefjorden. The depth scale of the plots is given in metres, except for the CTD/fluorescence plot, which is given in decibars (1 decibar *c.* 1 m). The adjacent open sea mean depth is shown by the red dotted line. For better comparison of the plots the scales of the deepest vertical cast (Figure 2) were maintained in all figures. The arrow points to the position of the deepest UVP cast.



ANIMATION 1. Examples of zooplankton (arrow) recorded in the four fjords using the Underwater Video Profiler. A physonect siphonophore from Sognefjorden (5 cm in size) at 700 m depth, a tomopterid polychaete (4.5 cm) from 450 m in Sognefjorden, a chaetognath (3.5 cm) recorded in Lurefjorden at a depth of 380 m and an appendicularian (1 cm in diameter) from Herdlefjorden, recorded at 390 m depth.



ANIMATION 2. Macrozooplankton from Lurefjorden recorded simultaneously by the 6 and 12 mm optics: *Periphylla periphylla*, a coronate scyphozoan jellyfish, (5.5 cm in length) at 320 m, and a lobate ctenophore (8 cm) at 60 m depth.