

# Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N): distribution strategies of calanoid copepods

Claudio Richter

Richter, C. 1995. Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N): distribution strategies of calanoid copepods – ICES J. mar. Sci., 52: 533–539.

Seasonal changes in the vertical distribution of zooplankton abundance and biomass are described for a 3000 m water column in the Greenland Sea basin, covering late fall, winter, spring, early and late summer. Three different distribution strategies, exemplified by calanoid copepods, are highlighted: (1) Seasonal migrants: herbivorous species undergoing diapause at great depths and surfacing in summer (*Calanus* spp., *Pseudocalanus minutus*); (2) mesopelagic residents: omnivores with broadly overlapping but stationary depth distribution throughout the year and vertical partitioning of the water column among the species (*Chiridius obtusifrons*, *Gaidius tenuispinus*, *Aetideopsis multiserrata*); (3) bathypelagic residents: large omnivorous species with broadly overlapping but stationary depth distribution throughout the year and vertical partitioning of the deepest layers (*Gaidius brevispinus*, *Aetideopsis rostrata*). No epipelagic residents appear to have evolved in this open ocean high latitude ecosystem, underscoring the potential role of deep water as a refuge for plankton in periods of low or nil surface production.

© 1995 International Council for the Exploration of the Sea

Key words: Aetideidae, Arctic, *Calanus*, copepods, distribution strategies, Greenland Sea, *Pseudocalanus*, seasonality, vertical migrations.

Claudio Richter: Institut für Polarökologie, Universität Kiel, Wischhofstr. 1–3, Gebäude 12, 24148 Kiel, Germany. (Present address: Zentrum für Marine Tropenökologie, Klagenfurterstr, GEO 28359, Bremen, Germany).

## Introduction

Calanoid copepods dominate mesozooplankton abundance and biomass in the high Arctic (Longhurst, 1985; Longhurst *et al.*, 1989; Hirche and Mumm, 1992), the subarctic (Smith *et al.*, 1985; Hirche *et al.*, 1991), and boreal regions of the Greenland and Norwegian seas (Wiborg, 1954; Østvedt, 1955). The bulk is made up of predominantly herbivorous forms of similar morphology but different adult size, namely *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, and *Pseudocalanus* spp. (Fig. 1). The females of these species occupy distinct and quasi non-overlapping size intervals of >4.5 mm, 3.2–4.5 mm, 2.4–3.2 mm, and <1.4 mm prosome length, respectively (compiled from Frost (1989), Unstad and Tande (1991), and Hirche *et al.* (1994)). This situation is different from the one encountered in the Antarctic, where considerable size-overlap occurs between the dominant calanids *Calanoides acutus* and *Calanus propinquus* (Schnack-Schiel and Hagen, 1994). However, while morphologically similar, these latter species display markedly different distribution patterns, feeding

habits, and lipid storage mechanisms (Hopkins and Torres, 1989; Hagen *et al.*, 1993; Kattner and Hagen, 1995; Schnack-Schiel and Hagen, 1995). To what extent differences in size, trophic level, biochemistry, spatial and temporal distribution are important segregation mechanisms that allow the co-existence of Arctic calanoids is virtually unknown.

The present study highlights the vertical and seasonal distribution patterns of the three reportedly herbivorous calanoid copepods in the Greenland Sea Gyre (GSG), *C. hyperboreus*, *C. finmarchicus*, and *Pseudocalanus minutus* and contrasts them with the distributions of some lesser known representatives of the omnivorous Aetideidae *Aetideopsis multiserrata*, *A. rostrata*, *Chiridius obtusifrons*, *Gaidius brevispinus*, and *G. tenuispinus*.

## Material and methods

Zooplankton material for this study was collected on repeated cruises to the GSG (75°N), covering late fall, winter, early and late summer of 1988/1989 and spring

Table 1. Station data for deep multinet hauls in the Greenland Sea Gyre, sampling the depth strata 3000–2000–1500–1000–500–400–300–200–100–0 m.

RV	Cruise	Station	Position		Season	Date	Depth (m)
"Meteor"	8/1	613	74°45'N	01°04'E	Late fall	08 Nov 88	3777
"Meteor"	8/2	653	74°06'N	03°02'W	Late fall	27 Nov 88	3655
"Valdivia"	78/1	8	74°45'N	08°01'W	Winter	07 Feb 89	3400
"Polarstern"	ARK VI/3	91	74°45'N	01°02'E	Early summer	15 Jun 89	3770
"Valdivia"	86	177	74°45'N	01°04'E	Late summer	18 Aug 89	3780
"Polarstern"	ARK IX/1b	61	75°00'N	02°38'W	Spring	09 Apr 93	3688

of 1993 (Table 1). All stations were located in the ice-free and weakly stratified waters centred on Greenland Basin, where lateral advection is negligible, usually  $< 1 \text{ cm s}^{-1}$  (Visbeck, 1993). Details on the hydrography of the area are given in GSP Group (1990), Visbeck (1993), Budéus *et al.* (1993), and Schott *et al.* (1993).

Sampling was carried out with a Kiel Multinet (0.25 m<sup>2</sup> mouth area, 150 µm mesh) equipped with five nets in two successive vertical hauls covering nine depth strata from 3000 m to the surface. Sampling intervals were 3000–2000–1500–1000–500–0 m for the deep hauls and 500–400–300–200–100–0 m for the shallow casts. Samples were preserved in 4% borax-buffered formaldehyde and sorted in a Bogorov plate. As a rule, the entire sample was counted for the larger plankton ( $> 1 \text{ mm}$  prosome length), and only occasionally was the sample split with a Folsom splitter (1:4 at most) for enumerating very abundant species or stages. For *Pseudocalanus* ( $\leq 1 \text{ mm}$  prosome length) an aliquot (1:2, 1:4 or 1:10) of the sample was examined after fractionation with a Folsom or Wiborg splitter.

Based on the abundance data (Richter, 1994), percentile depths of distribution were calculated and depicted as box plots, each box encompassing 50% of total numbers, the whiskers 95% of the population in question (Figs. 1 and 2). The line within each box gives the 50-percentile or median depth of occurrence in terms of abundance ( $z_{50}$  depth henceforth), i.e. the depth separating the upper and lower half of the population in the water column. Calculations are based on the assumption of random distribution of individuals within each sampling interval.

## Results

Figure 1 reveals very different distribution patterns for the main calanoid herbivores in the Greenland Sea. The largest species, *Calanus hyperboreus* undergoes pronounced seasonal vertical migrations. The bulk of the population descends into the bathypelagial ( $> 1000 \text{ m}$ ) during the dark season, attains a residence  $z_{50}$  depth of about 1500 m by mid-winter, rises in spring, and crowds into the surface by early summer. The surface period is

fairly short and in late summer the descent to wintering depths is already underway. Descent and ascent do not appear to be strictly synchronous for the entire population, judging by the wide-ranged vertical distributions during late fall and spring. Narrower vertical ranges occur at the height of the dark and light seasons in February and June, respectively, i.e. once the population has reached its winter and summer residence levels.

The smaller congener *C. finmarchicus* shows a very different seasonal distribution. The population is confined to the epi- and mesopelagial ( $< 1000 \text{ m}$ ) throughout the year. Seasonal vertical migrations are only weak, scarcely exceeding 300 m in terms of the vertical displacement of the  $z_{50}$  depths. The ascent from the wintering depths appears to occur later than in *C. hyperboreus*. In fact, in April there is no sign of a spring rise, as yet. However, by June the entire population has moved into the surface layer, where it remains for a brief period. By August the bulk of the population is on its way down again.

*Pseudocalanus minutus* occupies a somewhat intermediate position between the two former species. It overwinters in the lower mesopelagial, between about 500 and 1000 m. A spring rise is already discernible in early April but it is not as evident as in *C. hyperboreus*. By early summer the entire population has gathered in the epipelagial. In contrast to the two preceding species, *P. minutus* remains at the surface through summer. From the early November distribution, it can be deduced that a considerable portion of the population remains at the surface through the fall. While the ascent occurs in a relatively narrow band (as compared to *C. hyperboreus*), the descent appears to be rather asynchronous for this species, spanning about four months between the first and last wintering stages, leaving the surface in August and end-November, respectively.

In contrast to the herbivores, the omni- and carnivores belonging in the calanoid family Aetideidae show a vertical distribution that is largely unaffected by season. Each species occupies a distinct depth stratum that, in turn, leads to a vertical partitioning of the water column among the family members (Fig. 2). *Chiridius obtusifrons* populates the topmost layer in the upper

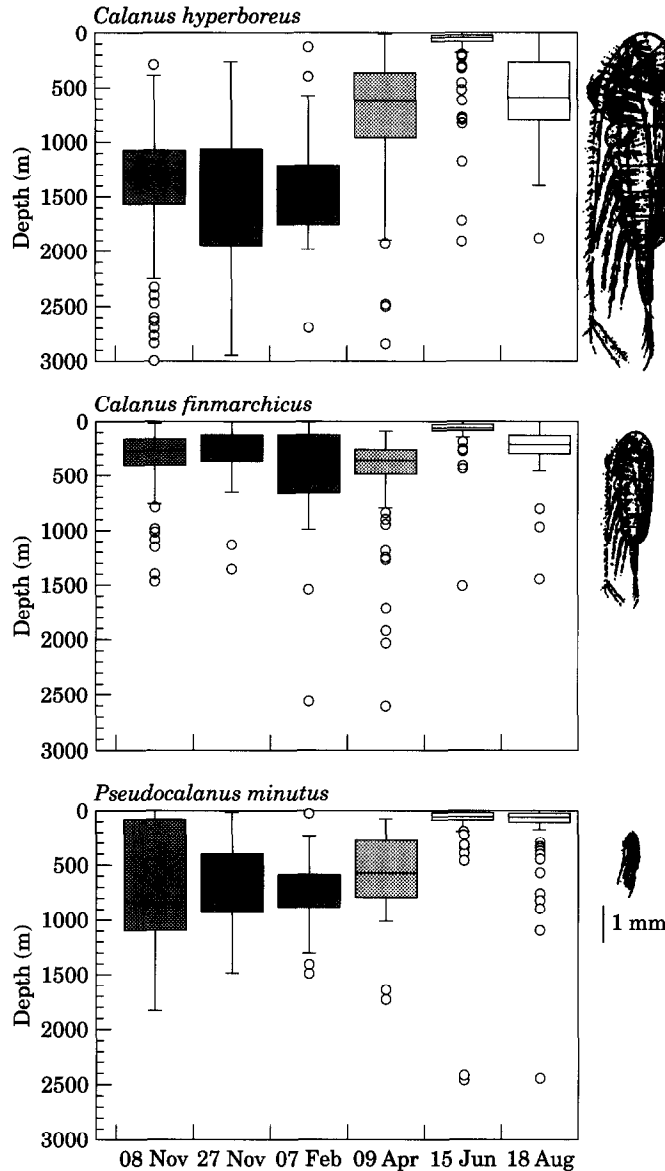


Figure 1. Seasonal vertical migration patterns of the dominant calanoid herbivores, with illustration of females, drawn to the same scale (after Sars (1903)). Boxes encompass 50%, whiskers 95% of the population in terms of number of individuals (all stages). Shading illustrates dark and light season.

mesopelagial with  $z_{50}$  depths at  $550 \pm 200$  m. It is followed by *Gaidius tenuispinus* in the lower mesopelagial ( $700 \pm 300$  m). *Aetideopsis multiserrata* is centred in the meso-bathypelagic transition zone ( $1000 \pm 200$  m). The larger congeners of the two latter species, *G. brevispinus* and *A. rostrata*, inhabit the bathypelagic zone at  $1200 \pm 200$  m and  $2200 \pm 500$  m, respectively.

There is some overlap in the distribution ranges of the named aetideid species and also some smaller scale features (such as the apparent rise of *A. rostrata* in winter/spring) that cannot be resolved with the wide sampling intervals employed in the lower reaches of the

bathypelagial. However, the maintenance of a specific level in the water column over time is a recurrent feature in all aetideids investigated and, as such, stands in striking contrast to the changing depth preferences of the migratory species.

## Discussion

The present study confirms previous investigations in the Norwegian Sea, Greenland Sea, and Arctic Ocean which show that calanoid copepod species may carry out considerable seasonal vertical migrations (Sømme, 1934;

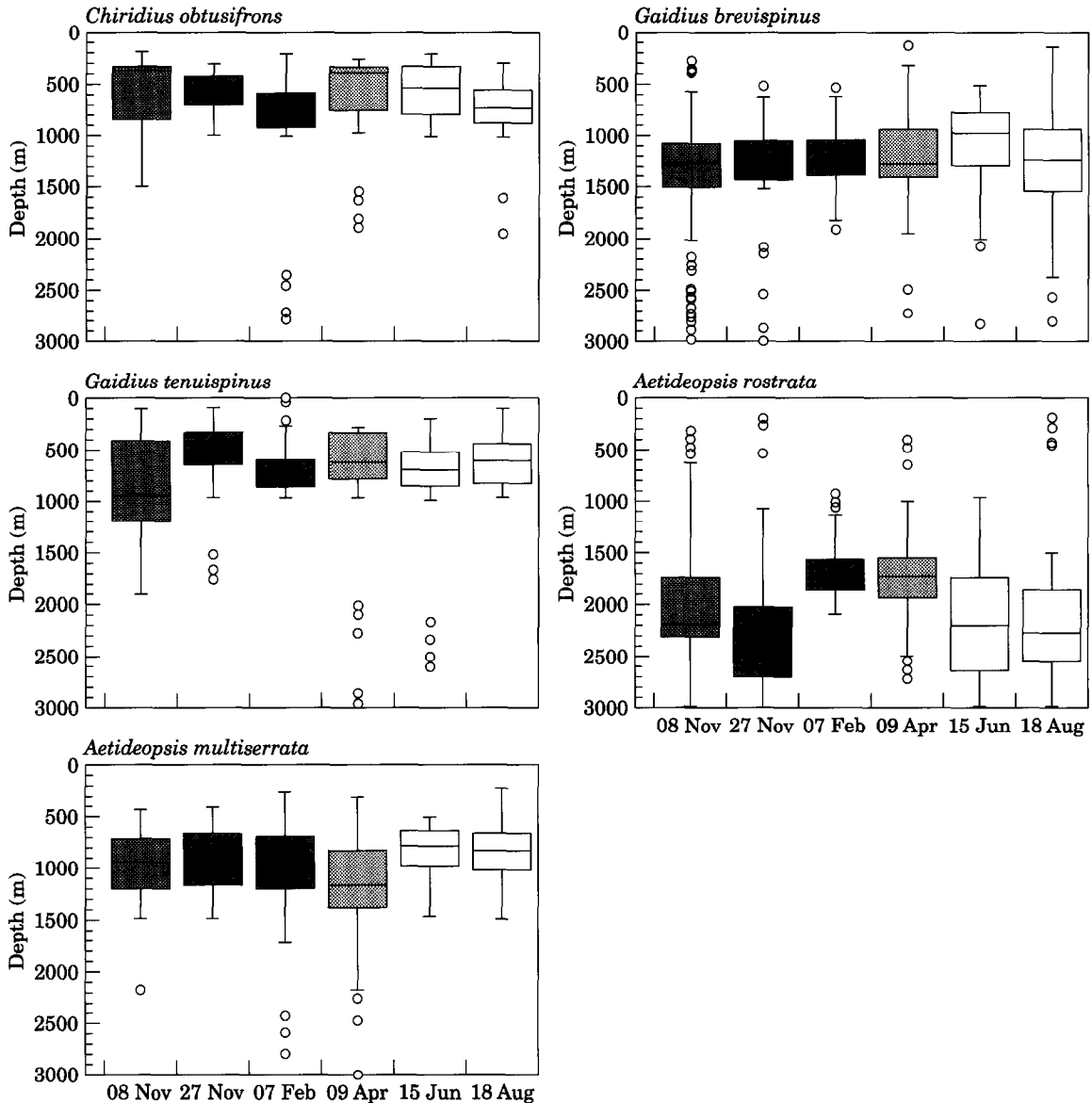


Figure 2. Seasonal vertical migration patterns of calanoid omnivores belonging in the family Aetideidae. Boxes encompass 50%, whiskers 95% of the population in terms of number of individuals (all stages). Shading illustrates dark and light season.

Østvedt, 1955; Kosobokova, 1982; Hirche, 1991), while others maintain their vertical position relatively unaffected over time (Østvedt, 1955; Grainger, 1989), reflecting differences in feeding modes (Raymont, 1983). Indeed, from eight species (out of five genera and three families) presented, all three seasonally migrating species are (predominantly) herbivorous (Marshall and Orr, 1972; Corkett and McLaren, 1978), whereas all non-migrating ones belong to the omnivorous family Aetideidae (Harding, 1974; Hopkins, 1985, 1987). The question is: How does feeding mode translate into distribution type? Given the observed variations in the distribution patterns within the migrant and resident

groups, further questions to be answered relate to the timing and spatial extent of seasonal vertical migrations (SVM), and to the nature and consequences of spatial segregation for non-migrating species. Perhaps a key to the understanding of seasonal distribution patterns in the GSG is the observation that none of the calanoid species remain in the near-surface during the dark season, raising the question: Why is there a fall migration at all? This is, of course, equivalent to: Why are there no epipelagic resident species in the Greenland Sea Gyre?

Given the limited food resources in high latitude ecosystems, it is of vital importance for a herbivore to be

in the right place at the right time. During the short growing season the right place unquestionably is the sun-lit surface layer, where high primary production and heavy grazing enable growth (Legendre *et al.*, 1993), lipid-accumulation and, eventually, survival during the dark season (e.g. Kattner and Hagen, 1995). Not surprisingly, this is the period when highest concentrations of all three herbivorous species occur in the surface layer (Richter, 1994). It is less obvious, on the other hand, why the surface should be the “wrong” place to be during the unproductive season, as again is unanimously perceived by the GSG herbivores, which all leave the surface by the end of the growing season (or even in anticipation of the end, as suggested by the early leave of *Calanus* spp.; cf. also Kaartvedt (in press)). One of the often overlooked facts is that the fall descent is counter to the positive buoyancy of the early overwintering stages (Køgelier *et al.*, 1987), which by late July in the Greenland Sea have grown so fat as to float (Richter, unpubl. observations). As such, the fall migration is an active rather than a passive process, requiring an unknown amount of energy. What then are the gains to be expected from overwintering at depth? Bioenergetic advantages (McLaren, 1963) and population retention mechanisms (Russell, 1927) can be ruled out because both vertical temperature differences and lateral advection are negligible in the GSG (Quadfasel and Meincke, 1987; Visbeck, 1993). Predator avoidance has become a fashionable explanation for (diel) zooplankton migrations, especially in response to visual predators (Gliwicz, 1986; Frost, 1988; Bollens and Frost, 1989a, b, 1991; Bollens *et al.*, 1992) and is likely to play a major role in determining the overwintering depth of *C. finmarchicus* in Norwegian Fjords (Kaartvedt, in press). However, in the Greenland Sea, sizeable fish stocks are confined to the frontal areas of the periphery and do not occur in the centre of the gyre, as well as mesopelagic fish which seem to avoid waters of negative temperatures (Sameoto, 1989; Giske and Kaartvedt, pers. comm.). It is therefore very unlikely that vertebrate predation is a major factor influencing the vertical distribution of zooplankton in the GSG.

Invertebrate predation, by contrast, might indeed have a measurable effect, although it has rarely been invoked to explain SVM in the sea, to date. One line of evidence comes from upward-looking Acoustic Doppler Current Profiler (ADCP) measurements that were carried out in the same investigation area and period, showing an almost invariable sound scattering layer (SSL) of macroplankton-sized acoustic targets in the top 150 m throughout the dark season (Fischer and Visbeck, 1993). The authors speculate that the SSL might be due to the euphausiid *Thysanoessa longicaudata* gathering in its “feeding horizon”, which complies with earlier observations on the vertical distribution of this omnivorous species (Mauchline and Fisher, 1969;

Mauchline, 1980). A second likely candidate is the hyperiid amphipod *Themisto* spp., as deduced from incidental catches in mesoplankton samples in the area (Richter, 1994). Both groups are known to feed on copepods (Mauchline and Fisher, 1969; Falk-Petersen *et al.*, 1987), potentially threatening any wintering population in their range. The second line of evidence comes from the discovery in the GSG of a biomass-rich omnivorous and carnivorous mesozooplankton community, located somewhat deeper in the water column (Richter, 1994). It is made up mainly of chaetognaths and ostracods which are centred in the mesopelagial (300–800 m). Individuals escaping predation in the epipelagial thus face continued risk of predation by large *Eukrohnia hamata* capable of taking large copepod prey (Sullivan, 1980; Øresland, 1990), while traversing the mesopelagial. The bathypelagial, finally, by virtue of its sparse population and decreasing percentage of carnivores (Vinogradov, 1970), may be regarded as a refuge, not only for the wintering herbivore stocks, but also for the young of some mesopelagic species (e.g., the ostracod *Boroecia borealis*; Richter, 1994). Herbivores undergoing deep vertical migrations are likely to experience lower mortality than others wintering at shallower depths, and this indeed appears to be the case when comparing *Calanus* spp. and *Pseudocalanus* population declines over winter (Richter, 1994).

Mesopelagic Aetideidae, while capable of taking small copepods in the size range of a wintering *Pseudocalanus* (Harding, 1974; Hopkins, 1985) are subject to the same potential threat of chaetognath predation as migrating herbivores. However, they occur in low numbers, thereby reducing encounter probabilities with their predators. The large bathypelagic representatives of this group are probably least affected by predating losses. Moreover, they might take advantage of the seasonal occurrence of *Calanus hyperboreus*, which overwinter as copepodite stage III within their range (Hirche, 1991; Richter, 1994). This is suggested by the co-occurrence of *Gaidius brevispinus* with *C. hyperboreus* during the dark season, and by the apparent “inverse” SVM of *Aetideopsis rostrata* from the lower into the upper bathypelagial during the late winter period. However, the diets of these two species are unknown, let alone their seasonal variations. Aetideidae appear to be year-round opportunistic feeders, feeding on a variety of food items (Hopkins, 1985, and references therein). Lack of food specialization is believed to have resulted in a vertical partitioning of the limited resources and in a stepwise arrangement of species with depth (Raymont, 1983; cf. also Mauchline, 1995), allowing for a large generic radiation within the Aetideidae (Razouls, 1993). Their layered occurrence observed during this investigation confirms previous findings from the Norwegian Sea (Østvedt, 1955) and the North Atlantic (Grice and Hülsemann, 1965). How these species maintain their

vertical position within the unstratified waters of the GSG is one of the mysteries to be unravelled.

Clearly, more work needs to be done to obtain a finer vertical and temporal resolution of the distribution of Calanoida in the Greenland Sea, including the deep sea, which is a likely zone of interaction between resident and a transient faunas of active and overwintering species.

## Acknowledgements

This research would not have been possible without the excellent cooperation of Dr H.-J. Hirche and co-workers in the Greenland Sea Project, who provided samples and *Calanus* abundance data for the 1988/1989 expeditions. Dr W. Hagen provided additional samples in 1993 and reviewed an early draft of the manuscript. Professors G. Hempel and S. Kaartvedt gave valuable suggestions. This work was supported by a fellowship from the federal state of Schleswig-Holstein, the Deutsche Forschungsgemeinschaft (DFG) through Sonderforschungsbereich (SFB) 313 of Kiel University, and the German Ministry for Research and Technology (BMFT) grant 03PL009A9.

## References

- Bollens, S. M., and Frost, B. W. 1989a. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, 34: 1072–1083.
- Bollens, S. M., and Frost, B. W. 1989b. Predator-induced diel vertical migration in a planktonic copepod. *Journal of Plankton Research*, 11: 1047–1065.
- Bollens, S. M., and Frost, B. W. 1991. Diel vertical migration in zooplankton: rapid individual response to predators. *Journal of Plankton Research* 13: 1359–1365.
- Bollens, S. M., Frost, B. W., Thoreson, D. S., and Watts, S. D. 1992. Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis. *Hydrobiologia*, 234: 33–39.
- Budéus, G., Maul, A.-A., and Krause, G. 1993. Variability in the Greenland Sea as revealed by a repeated high spatial resolution conductivity-temperature-depth survey. *Journal of Geophysical Research*, 98(C6): 9985–10000.
- Corkett, C. J., and McLaren, I. A. 1978. The biology of *Pseudocalanus*. *Advances in Marine Biology*, 15: 1–231.
- Falk-Petersen, S., Sargent, J. R., and Tande, K. S. 1987. Lipid composition of zooplankton in relation to the sub-Arctic food web. *Polar Biology*, 8: 115–120.
- Fischer, J., and Visbeck, M. 1993. Seasonal variation of the daily zooplankton migration in the Greenland Sea. *Deep-Sea Research*, 40: 1547–1557.
- Frost, B. W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. *Bulletin of Marine Science*, 43: 675–694.
- Frost, B. W. 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Canadian Journal of Zoology*, 67: 525–551.
- Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature*, 320: 746–748.
- Grainger, E. H. 1989. Vertical distribution of zooplankton in the central Arctic Ocean. In *Proceedings of the sixth conference of the Comité Arctique International*, 13–15 May 1985, pp. 48–60. Ed. by L. Rey and V. Alexander. E. J. Brill, Leiden. 637 pp.
- Grice, G. D., and Hülsemann, K. 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the northeast Atlantic. *Journal of Zoology*, 146: 213–262.
- GSP Group 1990. Greenland Sea Project – A venture towards improved understanding of the oceans' role in climate. *EOS*, 71: 750–751.
- Hagen, W., Kattner, G., and Graeve, M. 1993. *Calanoides acutus* and *Calanus propinquus*, antarctic copepods with different lipid storage modes via wax esters or triacylglycerols. *Marine Ecology Progress Series*, 97: 135–142.
- Harding, G. C. H. 1974. The food of deep-sea copepods. *Journal of the Marine Biological Association of the United Kingdom*, 54: 141–155.
- Hirche, H.-J. 1991. Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biology*, 11: 351–362.
- Hirche, H.-J., Baumann, M. E. M., Kattner, G., and Gradinger, R. 1991. Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea. *Journal of Marine Systems*, 2: 477–494.
- Hirche, H.-J., Hagen, W., Mumm, N., and Richter, C. 1994. The Northeast Water Polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biology*, 14: 491–503.
- Hirche, H.-J., and Mumm, N. 1992. Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep-Sea Research*, 39 (Suppl 2): S485–S505.
- Hopkins, T. L. 1985. Food web of an Antarctic midwater ecosystem. *Marine Biology*, 89: 197–212.
- Hopkins, T. L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology*, 96: 93–106.
- Hopkins, T. L., and Torres, J. J. 1989. Midwinter food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep-Sea Research*, 36: 543–560.
- Kaartvedt, S. (in press). Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia*.
- Kattner, G., and Hagen, W. 1995. Polar herbivorous copepods – different pathways in lipid biochemistry. *ICES Journal of Marine Science*, 52 (this issue).
- Køgel, J. W., Falk-Petersen, S., Kristensen, Å., Pettersen, F., and Dalen, J. 1987. Density- and sound speed contrasts in sub-Arctic zooplankton. *Polar Biology*, 7: 231–235.
- Kosobokova, K. N. 1982. Composition and distribution of the biomass of zooplankton in the central Arctic Basin. *Oceanology*, 22: 744–750.
- Legendre, L., Gosselin, M., Hirche, H.-J., Kattner, G., and Rosenberg, G. 1993. Environmental control and potential fate of size-fractionated phytoplankton production in the Greenland Sea (75°N). *Marine Ecology Progress Series*, 98: 297–313.
- Longhurst, A. R. 1985. The structure and evolution of plankton communities. *Progress in Oceanography*, 15: 1–35.
- Longhurst, A. R., Platt, T., Harrison, W. G., Head, E. J. H., Herman, A. W., Horne, E., Conover, R. J., Li, W. K. W., Subba Rao, D. V., Sameoto, D., Smith, J. C., and Smith, R. E. H. 1989. Biological oceanography in the Canadian High Arctic. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 188: 80–89.
- Marshall, S. M., and Orr, A. P. 1972. The biology of a marine copepod, *Calanus finmarchicus*. Springer, Berlin. 195 pp.

- Mauchline, J. 1980. The biology of euphausiids. *Advances in Marine Biology*, 18: 372–623.
- Mauchline, J. 1995. Bathymetric adaptations of life history patterns in congeneric species (Euchaeta: Calanoida) in a 2000 m water column. *ICES Journal of Marine Science*, 52 (this issue).
- Mauchline, J., and Fisher, L. R. 1969. The biology of euphausiids. *Advances in Marine Biology*, 7: 1–454.
- McLaren, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada*, 20: 685–727.
- Øresland, V. 1990. Feedings and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctic Peninsula. *Marine Ecology Progress Series*, 63: 201–209.
- Østvedt, O.-J. 1955. Zooplankton investigations from weather ship “M” in the Norwegian Sea, 1948–49. *Hvalradets Skrifter*, 40: 1–93.
- Quadfasel, D., and Meincke, J. 1987. Note on the thermal structure of the Greenland Sea gyres. *Deep-Sea Research*, 34: 1883–1888.
- Raymont, J. E. G., 1983. *Plankton and productivity in the oceans*, 2. Zooplankton. Pergamon Press, Oxford. 824 pp.
- Razouls, C. 1993. Bilan taxonomique actuel des copépodes planctoniques marins et des eaux saumâtres. *Proceedings of the first European Crustacean Conference 1992*, 64: 300–313.
- Richter, C. 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Berichte zur Polarforschung*, 154: 1–87.
- Russell, F. S. 1927. The vertical distribution of plankton in the sea. *Biological Reviews*, 2: 213–262.
- Sameoto, D. 1989. Feeding ecology of the lantern fish *Bentosema glaciale* in a subarctic region. *Polar Biology*, 9: 169–178.
- Sars, G. O. 1903. An account of the Crustacea of Norway, 4. Copepoda Calanoida. Bergen Museum, Bergen. 171 pp.
- Schnack-Schiel, S. B., and Hagen, W. 1994. Life cycle strategies and seasonal variations in distribution and population structure of four dominant calanoid copepod species in the eastern Weddell Sea, Antarctica. *Journal of Plankton Research* 16: 1543–1566.
- Schnack-Schiel, S. B., and Hagen, W. 1995. Life cycle strategies of *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. *ICES Journal of Marine Science*, 52 (this issue).
- Schott, F., Visbeck, M., and Fischer, J. 1993. Observations of vertical currents and convection in the central Greenland Sea during the winter of 1988–1989. *Journal of Geophysical Research*, 98(C8): 14401–14421.
- Smith, S. L., Smith, W. O., Codispoti, L. A., and Wilson, D. L. 1985. Biological observations in the marginal ice zone of the East Greenland Sea. *Journal of Marine Research*, 43: 693–717.
- Sømme, J. D. 1934. Animal plankton of the Norwegian coast waters and the open sea. I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Fiskeridirektoratets Skrifter*, 4(9): 1–163.
- Sullivan, B. K. 1980. In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at ocean station “P”. *Limnology and Oceanography*, 25: 317–326.
- Unstad, K., and Tande, K. 1991. Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. *Polar Research*, 10: 409–420.
- Vinogradov, M. E. 1970. Vertical distribution of the oceanic zooplankton. Israel Program for Scientific Translations, Jerusalem. 339 pp.
- Visbeck, M. 1993. Konvektion im offenen Ozean. Interpretation von Beobachtungen aus der Grönlandsee und dem westlichen Mittelmeer. *Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel*, 237: 1–187.
- Wiborg, K. F. 1954. Investigations on zooplankton in coastal and offshore waters off western and northwestern Norway. *Fiskeridirektoratets Skrifter*, 11(1): 1–246.