The Ecology of Arctic Deep-Sea Copepods (Euchaetidae and Aetideidae). Aspects of their Distribution, Trophodynamics and Effect on the Carbon Flux

---

Holger Auel

Ber. Polarforsch. 319 (1999)
ISSN 0176 - 5027

Anschrift des Verfassers:

Holger Auel
Hauptstraße 327
D-51465 Bergisch Gladbach

Die vorliegende Arbeit ist die inhaltlich unveränderte Fassung einer Dissertation, die 1998 der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel vorgelegt wurde.

Table of contents

"If we had had no other way of whiling away time on board the raft,
there would have been entertainment enough in lying with our noses
in the plankton net. Not for the sake of the smell, for that was bad.
Nor because the sight was appetising, for it looked a horrible mess.
But because, if we spread the plankton out on board and examined
each of the little creatures separately with the naked eye, we had
before us fantastic shapes and colours in unending variety."

Thor Heyerdahl (1948) The Kon-Tiki Expedition.

Summary

The present study focuses on the distribution, trophodynamics and reproductive strategies of Arctic deep-sea copepods of the families Aetideidae and Euchaetidae. Results from field work, analytical and experimental approaches are combined to assess the impact of these meso- and bathypelagic copepods on the carbon flux within Arctic deep-sea ecosystems. Furthermore, general concepts concerning pelagic biodiversity and interspecific competition are highlighted and discussed.

The regional and vertical distribution of Aetideidae and Euchaetidae was studied at 19 stations in the Greenland Sea, Fram Strait and the adjacent Arctic Ocean. Sampling was concentrated on three latitudinal transects from the East Greenland shelf to the central deep-sea basin at 75°, 81° and 81°35′ N. A fourth transect was conducted from the southern Nansen Basin (82°39'N; 1°25'E) onto Yermak Plateau (81°54'N; 7°42'E). A total of four euchaetid and seven aetideid species were identified. Within both families congeners were generally restricted to distinct depth strata, thus vertically partitioning the water column. In the central Greenland Sea *Chiridius obtusifrons* occupied the mesopelagial from 100 to 500 m depth, whereas *Aetideopsis minor* was concentrated in 500 to 1000 m and *A. rostrata* inhabited the bathypelagial below 1000 m. Correspondingly, *Gaetanus tenuispinus* dominated in 200 to 500 m depth, while *G. brevispinus* prevailed below 500 m. A vertical separation of congeneric species appeared also among Euchaetidae. *Pareuchaeta glacialis* and *P. norvegica* dominated from the surface to 500 m depth, whereas *P. barbata* inhabited the 500 to 1500 m layer and *P. polaris* dwelled at depths below 1000 m.

In the northern part of the investigation area the vertical ranges of most aetideid and euchaetid species were shifted upwards, thus supporting the widely established concept of a polar emergence. The multi-layered distribution pattern, however, remained principally the same. Boreal-Atlantic species, e.g. *Pareuchaeta norvegica*, *P. barbata* and *Gaetanus tenuispinus*, were absent from the polar NE Greenland shelf and Nansen Basin. Nevertheless, they occurred abundantly at 82°N over the Yermak Plateau, where their distribution reflected the inflow of Atlantic water masses into the Arctic Ocean. This supports the hypothesis that a branch of the West Spitsbergen Current extends northward along the western flank of Yermak Plateau.

With respect to reproductive strategies, strong differences were detected among *Pareuchaeta* species. Epi- to mesopelagic congeners produced high numbers (40 to >50) of relatively small eggs, while bathypelagic forms relied on larger, energy-rich eggs at the expense of reduced egg numbers (4 to 19). Thus, females of the bathypelagic *P. polaris* invested 4% of their own energy content per egg, whereas the energy content of single eggs of the other congeners accounted only for 0.8 to 1.6% of the females' energy. Conversely, the energetic investment per clutch was substantially higher in the epi- to mesopelagic *P. glacialis* (81.5%) and *P. norvegica* (37.4%) than in the deeper living *P. barbata* and *P. polaris*, which invested less than 25% of their body energy per clutch. The increase of egg size and energy content with depth is interpreted as an adaptation to the food-limited conditions of the deep-sea. A lecithotrophic

development based on the enhanced energy reserves within the eggs makes young stages of bathypelagic species less dependent on external food sources. In contrast, high offspring numbers may be important for epipelagic species to counter higher predation risks.

Differences in feeding behaviour and dietary composition among Euchaetidae and Aetideidae were studied by lipid biomarkers and feeding experiments. In general, Aetideidae fed omnivorously on phytoplankton as well as zooplankton. *Gaetanus* spp., however, preferred a carnivorous diet consisting of nauplii and small copepodids, whereas *Aetideopsis* spp. and *Chiridius obtusifrons* consumed a larger fraction of phytoplankton and/or phytodetritus. An analysis of trophic biomarkers supported these experimental results. The ratio between the fatty acid isomers 18:1(n-9) and 18:1(n-7), which has been proposed as a relative measure for carnivory, increased from 1.3 in *C. obtusifrons* via approximately 3 in *Aetideopsis spp.* and 4.9 in *G. tenuispinus* to 6.5 in *G. brevispinus*. Thus, carnivorous feeding was apparently more important in *Gaetanus* spp. than in the other aetideids. Highest ratios of 12 to 62 were detected in the predatory *Pareuchaeta* spp.

Based on the vertical distribution, dietary composition and reproduction strategies, the question is discussed as to which mechanisms act to minimise interspecific competition among closely-related sympatric species in the food-limited deep-sea environment. In general, congeneric species are restricted to distinct vertical ranges and partition the water column. Different feeding preferences reduce competition mainly between sympatric genera. However, the dominant *Pareuchaeta glacialis* and *P. norvegica* in the central Greenland Sea exhibit no apparent differences in vertical distribution, reproductive strategy or dietary composition. It is supposed that the complex current system and hydrographic-biological interactions are the keys to understanding their sympatric distribution.

Quantitative feeding experiments and respiration measurements were conducted to confirm ingestion rates and energy demands calculated by an allometric approach based on body mass. Predatory *Pareuchaeta glacialis* and *P. norvegica* took 0.25-2.3 *Calanus* copepodids per day, equivalent to an average food uptake of 4-6.7% of body mass per day.

The consumption of the total euchaetid and aetideid community ranged from less than 1 mg C m^{-2} d^{-1} on the East Greenland shelf to more than 13 mg C m^{-2} d^{-1} in oceanic regions of the central Greenland Sea, equivalent to 4-28% of primary production and 1-2% of mesozooplankton standing stock. Omnivorous aetideids consumed more than 40% of the vertical carbon flux. The potential ingestion of carnivorous *Pareuchaeta* species was one third to one half higher than the secondary production of their principal prey: *Calanus*. Thus, Aetideidae and Euchaetidae play an important role in the deep-sea ecosystem of the Greenland Sea. They contribute to the remineralisation of organic material in the pelagial and their feeding and faecal pellet production influences pelagic-benthic coupling processes. Moreover, carnivorous species, especially *Pareuchaeta* spp., may control prey populations by predation.

1 Introduction

1.1 The deep-sea challenge

The World Ocean covers 361 million square kilometres, equivalent to 70.8% of the Earth's surface. More than 74% of this area or 268 x 10^6 km^2 are represented by deep-sea basins. Thus, the waters of the World Ocean, from the surface to the deepest reaches of the bottom trenches, encompass a total volume of about 1.4 x 10^9 km^3, more than 99% of Earth's biosphere (Madin & Madin 1995).

Only about 150 years ago, biologists were convinced that the deep-sea was an azoic zone, where crushing pressure made life impossible. Early oceanographic expeditions in the late 19th and early 20th centuries, however, discovered a great variety of deep-ocean life, well adapted to pressure and cold. They proved that life existed even at greatest depths, refuting the earlier hypothesis of an azoic zone. Later studies demonstrated an exponential decline in zooplankton concentration with increasing depth and led to the conclusion that this decline reflected depressed growth rates at both the individual and population levels in the bathypelagic realm (Mauchline 1995 and references therein).

In recent decades, the employment of deep-diving submersibles and remotely-operated vehicles has increased our understanding of the midwater fauna, but the pelagic deep-sea still remains one of the least explored environments on Earth. Even today only five submersibles exist worldwide capable of diving deeper than 6000 m, and only once man has reached the bottom of Vitiaz Deep in the Marianas Trench, with 11022 m the deepest place on Earth.

Oceanic deep-sea ecosystems differ from all terrestrial and most marine shallow-water habitats in one decisive feature: the spatial separation of primary production and remineralisation processes. Phototrophic production is restricted to the thin epipelagic layer flooded by sunlight, whereas a large portion of consumption and secondary production takes place at greater depth and on the seafloor, often several kilometres from the surface. Organisms living below the euphotic zone depend on organic matter sedimenting from the surface layer as an energy source. In turn, phytoplankton growth requires inorganic nutrients released by the deep-sea community. The vertical differentiation of the water column in a thin "autotrophic" top layer and a wide "heterotrophic" bottom layer makes pelagic-benthic coupling processes the key to understanding carbon and energy flux in deep-sea ecosystems.

Recent studies in the central Arctic Ocean and the Greenland Sea revealed that, in spite of the obvious decrease in zooplankton concentration with depth, the major fraction of total zooplankton biomass was located in the meso- and bathypelagial (Richter 1994; Auel 1995). Thus, midwater and deep-sea communities probably play an important role in energy and carbon cycles, particularly in polar regions.

1.2 Why study deep-sea plankton in the Arctic?

The principal difficulty in studying deep-sea organisms under laboratory conditions is to obtain alive and fit specimens. Net hauls from great depths take a long time, so that captured individuals usually remain in the cod end of the net for several hours, before they are recovered and transferred into an aquarium. Increasing the hauling speed in order to shorten the sampling time cannot solve this problem, since the increasing drag would inevitably cause more harm to the animals and thus result in a poorer quality of the samples.

Moreover, deep-sea organisms are adapted to low and stable ambient temperatures. In most parts of the World Ocean, however, a permanent or temporary pygnocline separates the cold deep water from a warm surface layer. When deep-sea samples are retrieved, they must pass through the overlying stratum of warm water. The exposure to elevated temperatures causes severe stress and often the death of the stenothermic deep-sea organisms. Cold surface waters, which could effectively counter this problem, are restricted to Arctic and Antarctic regions, polewards of the respective polar fronts. Hence, only polar regions allow a careful live-capture of bathypelagic organisms and therefore offer an especially suitable investigation area for biological deep-sea studies.

1.3 Arctic zooplankton research

The Arctic Ocean has been a field of special interest in plankton research for the last 100 years. Scientific studies in the central basins started with Nansen's "Fram" expedition (1893-1896). These early investigations revealed a strong similarity between the Arctic zooplankton and the Atlantic fauna (Sars 1900). Long-term studies from drift ice stations elucidated seasonal trends in biomass and vertical distribution (Hopkins 1969a, b; Kosobokova 1982; Grainger 1989). Finally, the employment of powerful icebreakers opened the way for large-scale assessments in permanently ice-covered regions of the central Arctic Ocean (Mumm 1991; Mumm et al. 1998). Precisely planned sampling and the opportunity to cultivate plankton organisms under in-situ conditions on board allowed detailed behavioural studies and experimental approaches under controlled conditions. With these tools the life-cycles of several dominant zooplankton species could be revealed (e.g. Conover & Huntley 1991; Diel 1991; Hirche 1996a, b, 1997).

However, most studies were restricted to abundant epipelagic species, especially herbivorous calanoids. They ignored the fact that the majority of zooplankton biomass in the central Arctic Ocean and the Greenland Sea is located at meso- to bathypelagic depths (Richter 1994; Auel 1995). Therefore, our understanding of the life-cycle strategies, adaptations and the ecological role of abundant deep-sea plankton, such as euchaetid and aetideid copepods, is still fragmentary.

1.4 The copepod families Euchaetidae and Aetideidae

Copepods of the calanoid families Euchaetidae and Aetideidae are important components of pelagic communities throughout the World Ocean, especially in deep oceanic waters. Most species inhabit meso- and bathypelagic depths; some are epi- or benthopelagic (Park 1994b; Markhaseva 1996).

The global distribution of the genus *Pareuchaeta* has been reviewed by Park (1994b) and dominant species of both families are sometimes included in regional assessments of zooplankton abundance and biomass. In the central Arctic Basin *Pareuchaeta glacialis* is one of the five calanoid species most frequently encountered in net samples from surface waters (Grainger 1989) and comprises 1 to 6% of the total biomass of all copepods (Kosobokova 1982). Correspondingly, the congeneric *P. antarctica* contributes 3% to mesozooplankton biomass in the Antarctic Weddell Sea (Boysen-Ennen et al. 1991). In the Greenland Sea *Pareuchaeta* spp. belong to the ten most important taxa with respect to biomass (Richter 1994). Less abundant, but represented by a species-rich assemblage, Aetideidae are characteristic inhabitants of the Arctic deep-sea (Markhaseva 1984; Richter 1995).

In spite of their widespread distribution in polar waters, most studies on the feeding behaviour, biochemical composition and life-cycle strategies of Euchaetidae and Aetideidae were confined to boreal coastal areas, e.g. Loch Etive, Scotland, and Korsfjorden, Norway (Båmstedt 1975, 1978; Nemoto et al. 1976; Bakke 1977; Bakke & Valderhaug 1978; Båmstedt & Holt 1978; Skjoldal et al. 1984). Some results are also available from Pacific and tropical species (Yen 1985; Shuert & Hopkins 1987; Ikeda & Hirakawa 1996) and Antarctic regions (Yen 1991; Hopkins 1987; Øresland 1995). However, comparable data from the Arctic are still lacking.

Whenever the ecological role of Euchaetidae and Aetideidae has been assessed quantitatively, both taxa have proven to be important components of pelagic food webs (Båmstedt 1981; Øresland 1995). Aetideidae are generally referred to as omnivorous (Hopkins 1985a and references therein; Richter 1995). However, they comprise a very diverse group, so that significant variability in feeding behaviour and dietary composition is likely to occur. Their feeding and faecal pellet production result in a transformation and repackaging of organic material in the water column. Since the sedimentation speed of sinking particles strongly depends on their constitution, pelagic organisms may significantly affect the flux of organic material from the epipelagial to deeper layers and thus control the food supply to benthic communities (Ashjian et al. 1995).

Carnivorous *Pareuchaeta* are major predators on other mesozooplankton and fish larvae. They may even influence the recruitment of commercially important fish stocks, as has been demonstrated for Atlantic cod *Gadus morhua* and Pacific hake *Merluccius productus* (Bailey & Yen 1983; Yen 1987). In Kosterfjorden, Sweden, *Aetideopsis armata* and *Pareuchaeta norvegica* were responsible for 29 to 77% of the total energy flow through the carnivorous trophic level (Båmstedt 1981). More recent investigations have generally questioned the longstanding paradigm of food availability as the governing factor determining plankton distribution (Verity & Smetacek 1996; Tiselius et al. 1997). It is now believed that "top-down" control of zooplankton populations by predation may be equally important as the "bottom-up" concept in determining zooplankton biomass and the ranges of certain species. Based on these considerations, predatory Euchaetidae and Aetideidae may substantially affect the structure of pelagic communities.

1.5 Purpose of the present study

The major aim of the present study is to evaluate the ecological role of Euchaetidae and Aetideidae in Arctic deep-sea ecosystems. In order to quantify their carbon demands in the Greenland Sea, Fram Strait and the adjacent Arctic Ocean, field data on abundance and vertical distribution are combined with experimentally determined feeding and respiration rates, as well as calculated maximum ingestion rates. Additionally, distribution patterns of the different species in the Greenland Sea are discussed in relation to the hydrographic regime in this highly variable transitional zone between the Arctic Ocean and the North Atlantic.

Furthermore, Arctic Euchaetidae and Aetideidae are used in this study to exemplify and delineate principal ecological concepts of pelagic biodiversity and potential competition. A typical feature of many zooplankton communities is the sympatric co-occurrence of two or more closely-related calanoid species. This has been demonstrated both for herbivorous epipelagic Calanidae as well as for omnivorous Aetideidae and carnivorous Euchaetidae in different parts of the World Ocean (Markhaseva 1984; Geynrikh 1986; Park 1994b; Guglielmo & Ianora 1995). The most extreme examples of sympatric distribution are reported from *Pareuchaeta* communities in the Rockall Trough, NE Atlantic, and around South Georgia, Antarctica, where fourteen congeners share the same habitat (Ward & Wood 1988; Mauchline 1992, 1994a, b). How do such closely-related species avoid interspecific competition? Answering this question will contribute to a better understanding of the apparent paradox of a relatively high bathypelagic biodiversity in spite of the widely homogenous deep-sea environment.

In summary, the major aims of the present study are:
- to describe the regional and vertical distribution and abundance of Aetideidae and Euchaetidae in the Greenland Sea, Fram Strait and the adjacent Arctic Ocean;
- to provide data on individual dry mass and total lipid content for the different species and stages;
- to determine individual ingestion and respiration rates of euchaetid and aetideid species;
- to estimate the carbon demand of the total aetideid and euchaetid population in order to evaluate their impact on the carbon cycle in Arctic deep-sea ecosystems;
- to compare these carbon demands with primary and secondary production, as well as mesozooplankton standing stock and vertical fluxes of organic material;
- to assess different reproductive strategies among congeneric *Pareuchaeta* species;
- to reveal the fatty acid and alcohol composition of Aetideidae and Euchaetidae, in particular with respect to trophic biomarkers;
- to assess the feeding behaviour and dietary composition of Aetideidae and Euchaetidae;
- to identify mechanisms minimising potential interspecific competition among closely related sympatric species.

2 Study area

"Hinter Grönland liegt ein Reich von Eis und Finsternis
in einem dickflüssigen und von Ungeheuern bevölkerten Meer –
das Ende der Welt."
Adam von Bremen (um 1070)

2.1 The Arctic Ocean

2.1.1 Topography

The Arctic Ocean consists of a central deep-sea basin surrounded by extensive shallow shelf seas. The Eurasian Basin is subdivided by the Nansen Gakkel Ridge into the Nansen Basin (3800-4000 m depth) and the Amundsen Basin (>4000 m). The Lomonosov Ridge (sill depth 1300 m) separates the Amundsen Basin from the Makarov Basin, which belongs to the Canadian Basin.
As a mediterranean sea the Arctic Ocean is enclosed by land masses. The only deep water connection to the Atlantic Ocean is the Fram Strait between Greenland and Spitsbergen with a sill depth of 2600 m. Shallow connections to the northern Atlantic exist via Davis Strait west of Greenland and via the Barents Sea. The exchange to the Pacific Ocean is limited by the narrow and only 70 m deep Bering Strait (Aagård & Carmack 1989).

2.1.2 Hydrography

The water column of the Arctic Ocean consists of three major water masses: the Polar Surface Water (PSW), the Atlantic Intermediate Layer (AIL) and the Arctic Deep Water (ADW). The PSW occupies the upper 50 m of the Arctic Ocean and is characterised by very low temperatures (<-1.7°C) and a low salinity (<33.0) (Anderson et al. 1994), due to the enormous amounts of freshwater imported by the Siberian rivers (Aagård & Carmack 1989). Two major current systems in the Arctic determine the drift of the PSW and the transport of the sea ice. The Canadian sector is dominated by the Beaufort Gyre. In the Eurasian part the Transpolar Drift Current transports PSW and ice from the Siberian shelf towards Fram Strait, where they leave the Arctic Ocean into the Atlantic as the East Greenland Current.

Below a pronounced halocline a layer of warmer (0.5-1°C) and more saline (>34.5) water of Atlantic origin is found, the Atlantic Intermediate Layer (AIL). This Intermediate Water enters the Nansen Basin as the West Spitsbergen Current via Fram Strait. North of Spitsbergen the Atlantic inflow turns east and follows the Eurasian continental slope as a cyclonic boundary current (Fig. 1; Aagård 1989; Anderson et al. 1989; Rudels et al. 1994). The AIL can be detected throughout the Arctic Ocean at 200-600 m depth.

The deepest parts of the basins (>1000 m) are filled with Polar Deep Water (PDW), which is characterised by low temperatures (-0.5 to -1°C) and very high salinities (34.95 in 2000 m, Anderson et al. 1994). Since the exchange of PDW between the Eurasian and the Makarov Basins is limited by the Lomonosov Ridge, significant differences in temperature and salinity occur between both basins (Anderson et al. 1994).

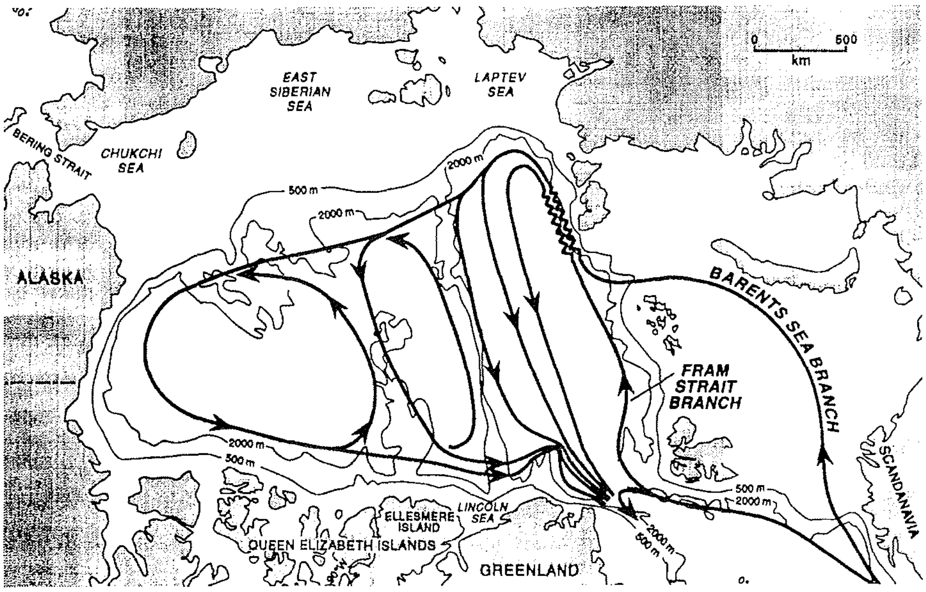

Fig. 1 Circulation within the Atlantic Intermediate Layer of the Arctic Ocean (Rudels et al. 1994)

2.2 The Greenland Sea and Fram Strait

2.2.1 Topography

Fram Strait and the Greenland Sea comprise the most important water connection between the Arctic Ocean and the North Atlantic. The Greenland Sea is bordered by the East Greenland coast to the West and by Spitsbergen to the Northeast. Topographic features, e.g. the Jan Mayen Ridge, Mohns Ridge and the Barents Sea slope, separate the Greenland Sea from the neighbouring Iceland, Norwegian and Barents Seas in the South and Southeast. Thus, the Greenland Sea is well defined by bathymetric features, but not isolated from other parts of the northern North Atlantic.

The Greenland Sea consists of a central deep-sea basin and a shallow shelf area stretching along the East Greenland coast. The width of the East Greenland shelf progressively broadens from less than 50 km in the South to a maximum extension of 280 km in the Fram Strait. Towards the East the shelf descends steeply into the deep-sea basin.

2.2.2 Hydrography

The circulation of surface water in the Greenland Sea is strongly governed by two meridional boundary currents (Fig. 2). On the East Greenland shelf Polar Surface Water originating from the Transpolar Drift Current is transported south by the East Greenland Current. One branch of the East Greenland Current is deflected at the Jan Mayen fracture zone extending eastward as the Jan Mayen Polar Current (Quadfasel et al. 1987; Quadfasel & Meincke 1987).

As an extension of the Norwegian Atlantic Current the West Spitsbergen Current transports warm and saline Atlantic water masses northward along the eastern periphery of the Greenland Sea. North-west of Spitsbergen the West Spitsbergen Current is divided into different branches. The eastern branch enters the Arctic Ocean via the Nansen Basin. It turns east, submerges beneath the Polar Surface Water and follows the Eurasian continental slope eastward as a cyclonic boundary current. A second branch, known as the Return Atlantic Current, is deflected to the West and entrained into the East Greenland Current in sub-surface layers. Perkin & Lewis (1984) assume that a third branch flows northward along the western slope of Yermak Plateau transporting Atlantic water masses directly towards high latitudes.

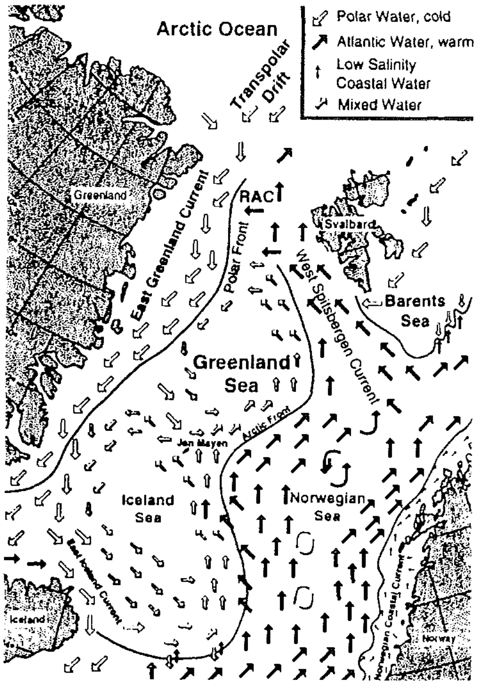

Fig. 2 Circulation in the Greenland Sea (modified after Blaume 1992)

Together with their deflections, the opposing meridional periphery currents form the cyclonic Greenland Sea Gyre, which is centred over the deep-sea basin. The Atlantic water at intermediate depth probably follows the same circulation pattern, although it is not fully understood whether this gyre is completely closed (Coachman & Aagård 1974). The hydrographic fronts, resulting from the close neighbourhood of different water masses, separate different hydrographic domains.

The area influenced by the East Greenland Current shows a water column structure similar to the Arctic Ocean and is therefore called the Polar Domain. Polar Surface Water with temperatures below 0°C occupies the upper 150 m. Below the halocline an Atlantic Layer originating from the Return Atlantic Current extends down to 800 m depth characterised by higher temperatures (0° to 2°C) and a high salinity of S = 35.0. Deep Water is found below 800 m depth (Coachman & Aagård 1974).

Bounded by the Polar Front to the West and by the Arctic Front to the East, the centre of the Greenland Sea Gyre is called the Arctic Domain. In contrast to the stratification of the Polar Domain, the cyclonic circulation within the Arctic Domain leads to a doming of the isopycnals and a reduced stratification stability in the centre of the Greenland Sea Gyre (Rudels 1993, 1995). The Arctic Surface Water is characterised by elevated, seasonally warmed temperatures of 2° to 4.5°C. Below the seasonal pycnocline Arctic Intermediate Water occupies the interval from 75 to >400 m depth. This layer can be further subdivided into upper and lower strata with considerable differences in temperature and salinity. The deepest parts of the basin are filled with Greenland Sea Deep Water comprising about 85% of the total volume of the Greenland Sea (Carmack & Aagård 1973).

2.3 Ice cover

Seven million square kilometres, equivalent to more than half of the Arctic Ocean, is permanently covered by sea ice, up to >6 m thick (Rey 1982). Most of the sea ice is formed over the Siberian shelf and transported across the Arctic Ocean by the Transpolar Drift Current. Thick multi-year ice floes form during their journey towards Fram Strait, which may last several years. In contrast to the permanent ice cover of the Arctic Ocean, the central Greenland Sea is only seasonally covered by ice. Areas of permanent ice cover are restricted to the Polar Domain, which is supplied with multi-year ice from the Arctic Ocean by the East Greenland Current (Parkinson & Cavalieri 1989; Parkinson 1991).

During the expedition ARK XIII/1 and 2 in May to July 1997 the ice cover in the Greenland Sea showed a pronounced regional and temporal variability. Due to the spring situation, most stations, even in the central Greenland Sea, were still covered by sea ice. As an exception St. 17 was located in the ice-free waters of the West Spitsbergen Current. The fast seasonal retreat of the ice could be observed at position 75°N 7°W, where the ice cover disappeared within three weeks (28 May – 18 June).

Strong variations in ice coverage were also evident in the northeastern part of the investigation area. In June all stations on the 81°N transect were ice-covered, while in July stations further north (81°35'N) were located within a large ice-free area.

3 Materials and methods

3.1 Sampling and sample processing

Stratified mesozooplankton samples were collected at 19 stations in the Greenland Sea and Fram Strait (Table 1; Fig. 3). Sampling concentrated on three latitudinal transects from the central deep-sea basin onto the East Greenland continental shelf at 75°, 81° and 81°35' N. A fourth transect was carried out from the southern Nansen Basin (82°39'N; 1°25'E) onto Yermak Plateau (81°54'N; 7°42'E). Sampling took place during the expeditions ARK XIII/1 and 2 of the German research vessel "Polarstern" between 27 May and 27 August 1997 (Spindler et al. 1998; Stein & Fahl 1997). Mesozooplankton was collected by stratified hauls conducted with a Multinet (Hydro Bios, Kiel), which allowed to discriminate between five discrete sampling layers within one haul (Weikert & John 1981). When the water depth exceeded 1000 m, two successive hauls were conducted to combine deep sampling with a higher resolution of the upper water layers. Usually, the entire water column was sampled down to the seafloor or to a maximum hauling depth of 2000 m. Sampled depth strata were 2000-1500-1000-500-200-100-50-0 m. In the southern Nansen Basin (St. 79) maximum hauling depth was 3000 m. The mouth opening of the net measured 0.25 m^2 and mesh size was 150 µm. Additional material for experiments and biochemical analyses was obtained from Bongo net hauls (mesh 100 to 330 µm) collected during the same expeditions to the Greenland Sea and during ARK XII (Arctic 1996) to the central Arctic Ocean (Augstein et al. 1997). All Multinet and Bongo samples were transferred into a cooling container (0-4°C) immediately after capture for further processing.

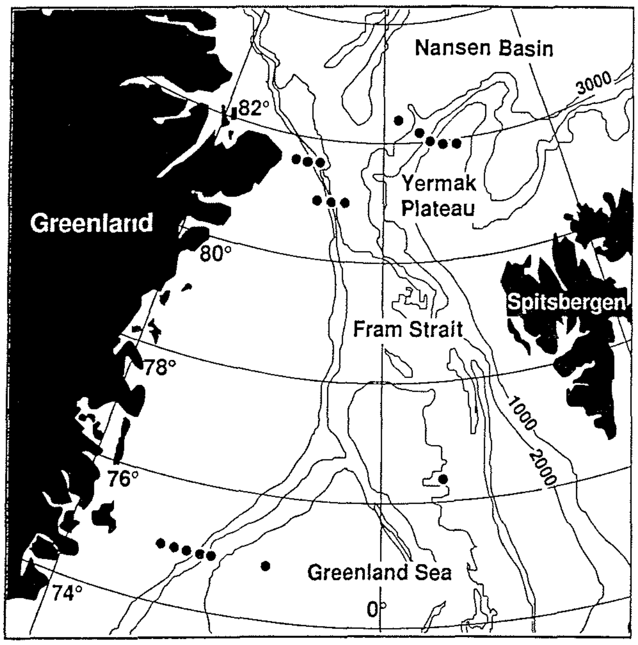

Fig. 3 Map of the investigation area showing the position of Multinet stations (after Diepenbroek et al. 1997). One position at 75°N 7°W was sampled twice as station 19 and 35.

Table 1 Station list of Multinet hauls

Station No.	Date d/m 1997	Position Latitude N	Longitude	Ice cover [%]	Sea surface temperature [°C]	Bottom depth [m]	Max. depth of haul [m]	Number of stratified samples
17	27/05	76°36′	4°39′ E	0	-0.2	3111	1000	5
19	28/05	74°57′	6°57′ W	80	-1.5	3461	2000	7
20	30/05	74°55′	11°15′ W	90	-1.6	2042	2000	7
21	31/05	74°42′	13°05′ W	10	-1.7	1483	1460	6
22	01/06	74°57′	12°48′ W	60	-1.5	675	650	5
23	01/06	74°57′	13°00′ W	90	-1.5	390	380	4
24	02/06	74°59′	13°50′ W	90	-1.6	195	170	3
30	10/06	80°54′	3°56′ W	90	-1.4	3359	2000	7
31	11/06	80°57′	5°54′ W	90	-1.5	1574	1500	6
32	13/06	81°00′	7°47′ W	90	-1.5	374	350	4
35	18/06	75°00′	7°00′ W	0	+0.4	3418	2000	7
72	17/07	81°35′	8°11′ W	5	-0.4	1976	1950	7
73	17/07	81°35′	9°49′ W	0	0.0	1085	1000	5
74	18/07	81°35′	10°01′ W	0	-0.1	507	500	4
79	21/07	82°39′	1°25′ E	90	-1.6	3233	3000	8
84	24/07	82°19′	3°40′ E	85	-1.6	2179	2000	7
87	25/07	82°03′	5°18′ E	85	-1.7	1409	1350	6
88	26/07	81°59′	5°45′ E	90	-1.7	928	900	5
89	27/07	81°54′	7°42′ E	90	-1.6	832	830	5

3.2 Abundance of Aetideidae and Euchaetidae

In order to describe the regional and vertical distribution of Euchaetidae and Aetideidae in the Greenland Sea and to measure their abundance, all individuals of these copepod families were sorted alive, staged and counted under a dissecting microscope (Wild M3B). The following literature was used for identification:

Brodskii (1950)
Markasheva (1984, 1996)
Park (1978, 1994a)
Sars (1900, 1903)
Vervoort (1952a to i)

Specimens were frozen at –80°C for later laboratory analysis and the remains of each sample were preserved in a 4% formaldehyde-seawater solution. Abundance data were calculated assuming 100% filtering efficiency of the Multinet according to the equation:

$$A = \frac{n}{(d_{opened} - d_{closed}) \times a} \quad \text{, where}$$

A = abundance (ind. m^{-3})
n = number of individuals in a sample
d_{opened} = depth, where the net was opened (m)
d_{closed} = depth, where the net was closed (m)
a = mouth opening of net; $a = 0.25\ m^2$

3.3 Scientific names and taxonomic difficulties

> *"There was no end to Nature's extravagant inventions in the plankton world; a surrealist artist might well own himself beaten here."*
>
> Thor Heyerdahl (1948) The Kon-Tiki expedition.

With respect to taxonomy, Calanoida are probably the best-studied zooplankton group. However, many species were already discovered at the end of the last century and descriptions of type specimens are sometimes incomplete or inexact (Markhaseva 1996). Especially among little known bathypelagic forms, individuals retrieved from distinct parts of the World Ocean were often attributed to already established species, ignoring minor, but decisive morphological differences. During a careful revision of the genus *Pareuchaeta*, for instance, Park (1994a) discovered that the number of species with a worldwide distribution was surprisingly small. Contrary to earlier concepts, the genus does not consist of a few cosmopolitan species, but of many morphologically similar species, endemic to more or less closely confined ranges.

In some genera, e.g. *Euchaeta*, *Pareuchaeta* and some Aetideidae, identification to species level is principally made on morphological features of the secondary sex characteristics (Hopkins 1978; Mauchline 1998). Thus, many species are only known from adult females, a few from males. This problem complicates the matching of the respective female and male of a species and sometimes leads to confusion when females and males are described as separate species. Moreover, recurring revisions, during which scientific names were often changed and species regrouped within and between genera, resulted in a number of synonyms for many species.

Fortunately, the families Aetideidae and Euchaetidae, investigated here, were the target of recent detailed revisions (Park 1994a, Markhaseva 1996). Park (1994a) recounted the history of the genera *Euchaeta* and *Pareuchaeta*, often used synonymously, and re-examined their validity. He redefined both genera and renamed *Pareuchaeta* as *Paraeuchaeta*. The species were divided into *Euchaeta* and *Paraeuchaeta* and both taxa were further subdivided by creating distinct species groups. Correspondingly, the family Aetideidae was revised in detail by Markhaseva (1996).

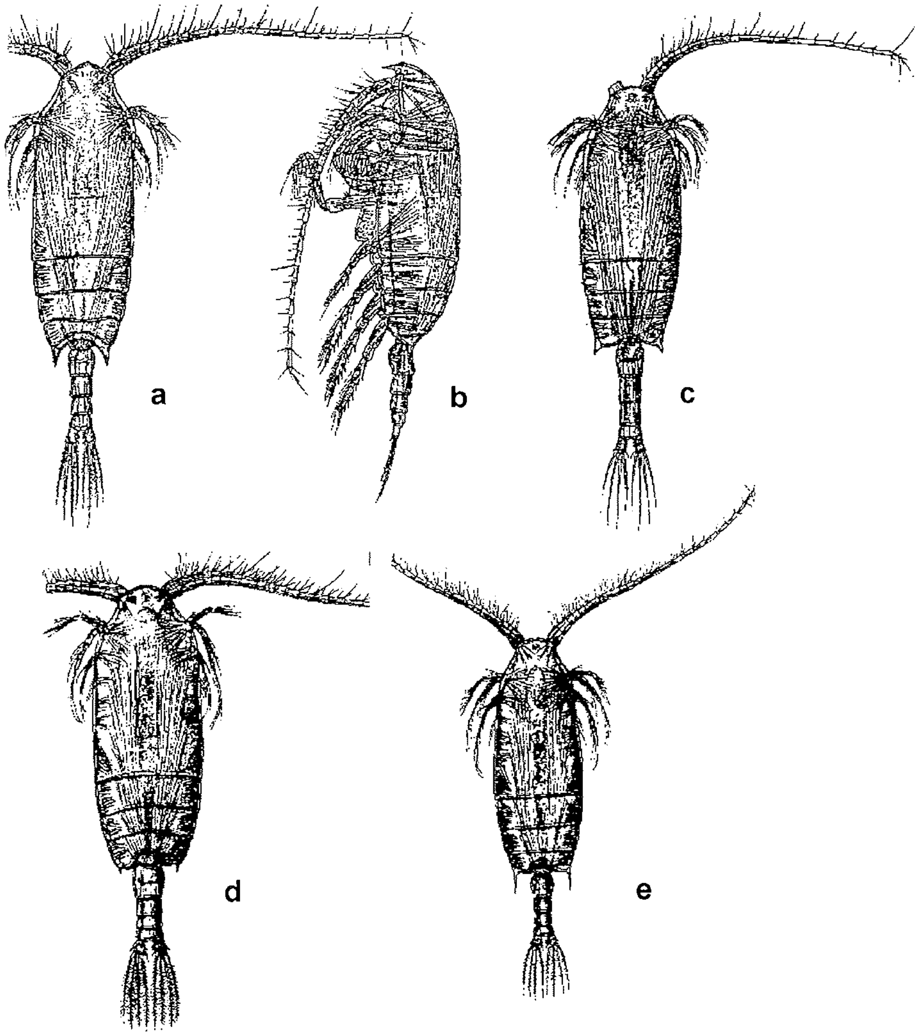

Fig. 4 Some Aetideidae of the Greenland Sea. Dorsal views of *Aetideopsis rostrata* (a), *Chiridius obtusifrons* (c), *Gaetanus brevispinus* (d), *G. tenuispinus* (e) and lateral view of *A. rostrata* (b). Drawings by Sars (1900)

Table 2 Species names of the Euchaetidae and Aetideidae considered in the present study and frequently used synonyms

Valid species name	Frequently used synonyms
Euchaetidae	
Pareuchaeta barbata (Brady)	*Euchaeta barbata* Mauchline 1994a, b, 1995
	Paraeuchaeta barbata Park 1994a, b, Kosobokova et al. 1998
Pareuchaeta glacialis (Hansen)	*Euchaeta glacialis*
	Paraeuchaeta glacialis Park 1994a, b, Kosobokova et al. 1998
Pareuchaeta norvegica (Boeck)	*Euchaeta norvegica* Mauchline 1992, 1994a, b, 1995
	Paraeuchaeta norvegica Park 1994a, b, Kosobokova et al. 1998
Pareuchaeta polaris Brodskii	*Euchaeta polaris*
	Paraeuchaeta polaris Park 1994a, b, Kosobokova et al. 1998
Aetideidae	
Aetideopsis minor (Wolfenden)	*Aetideopsis multiserrata* (non Wolfenden 1904): Brodskii 1950, Markhaseva 1984
	Faroella minor Wolfenden 1911
	Chiridius minor Farran 1929
	Chiridius modestus With 1915
	Aetideopsis modestus Bradford 1969, Bradford & Jillett 1980, Park 1978, Shih & Maclellan 1981
Aetideopsis rostrata Sars	*Aetideopsis divaricata* Esterly 1911
	Aetideopsis trichecus Vervoort 1949
	Aetideopsis divergens Tanaka 1957a, b
	Aetideopsis inflata Park 1978
Chiridiella abyssalis Brodskii	*Chiridiella reducta* Brodskii 1950
Chiridius obtusifrons Sars	*Gaidius obtusifrons* Seiler & Brandt 1997
Gaetanus brevispinus (Sars)	*Chiridius brevispinus* Sars 1900
	Gaidius brevispinus Sars 1903, Brodskii 1950, Tanaka 1957a, b, Tanaka & Omori 1970a, b
	Gaidius affinis Sars 1905, Vervoort 1957, Bradfort & Jillett 1980
	Gaetanus affinis Park 1975a, b
	Gaidius intermedius Farran 1929, Hardy & Gunther 1935 Davis 1949, Vervoort 1951, Park 1978
	Gaetanus intermedius Park 1975a, b
	Mesogaidius intermedius Wolfenden 1911
	Gaidius major Wolfenden 1904
	Gaidius robustus (non Sars 1905) Vervoort 1949
Gaetanus tenuispinus (Sars)	*Chiridius tenuispinus* Sars 1900
	Gaidius tenuispinus Brodskii 1950, Vervoort 1957, Tanaka 1957a, b, Owre & Foyo 1967, Tanaka & Omori 1970a, b, Wheeler 1970, Bjornberg 1973, Park 1978, Bradford & Jillett 1980
	Gaidius boreale
	Gaidius similis Scott 1909
	Gaidius gracilis Brady 1918
Pseudochirella spectabilis Sars	*Undeuchaeta spectabilis* Sars 1900
	Euchirella elongata Wolfenden 1911
	Pseudochirella elongata Vervoort 1957, Park 1978, Markhaseva 1984, 1989

Apart from one exception, this study uses the species names proposed by Markhaseva (1996) for Aetideidae and Park (1994a) for Euchaetidae. The exception concerns the proposed genus name *Paraeuchaeta*, which failed to replace the more familiar term *Pareuchaeta* in many recent publications, e.g.

Mauchline (1998). The discussion section also follows the valid names, even where the references originally used older synonyms. A compilation of the valid species names and frequently used synonyms is given in Table 2.

3.4 Identification of *Pareuchaeta* species

Encompassing 102 recognised species, *Euchaeta*/*Pareuchaeta* is the largest calanoid genus (Mauchline 1998). Identification of *Pareuchaeta* to species level is principally based on morphological differences of secondary sex characteristics (Fig. 5). Females are identified by the shape of the genital somite and the morphology of the genital field (Zvereva 1976; Tanaka & Omori 1968), while in males the morphology of the modified fifth pair of legs is species-specific. Evidently, this considerably complicates the identification of juveniles to species level.

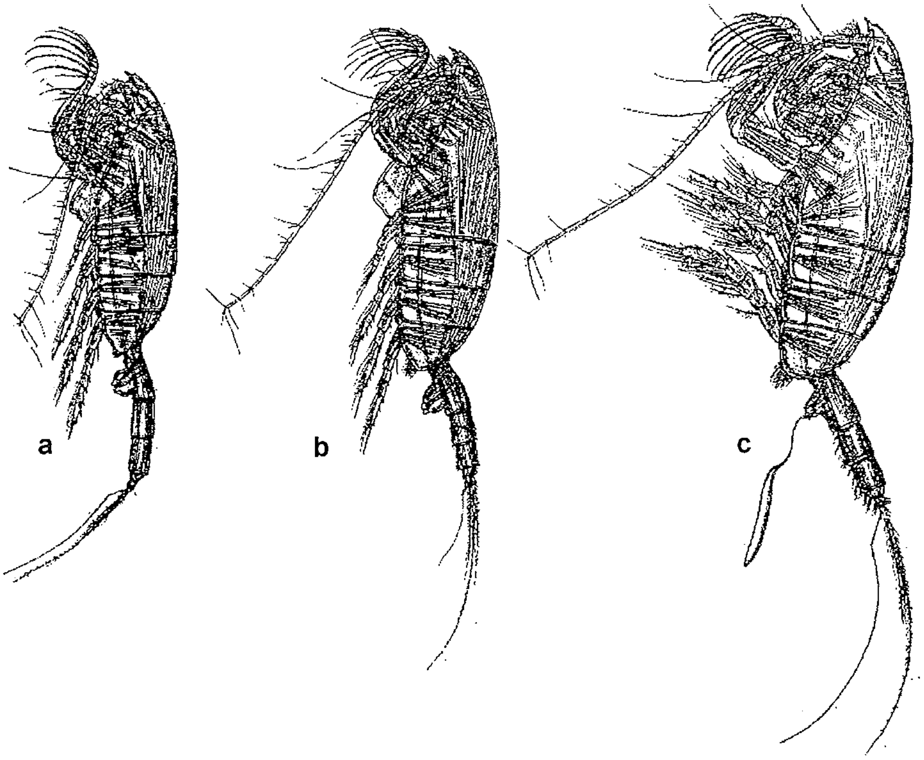

Fig. 5 Some Euchaetidae of the Greenland Sea. Females of *Pareuchaeta norvegica* (a), *P. glacialis* (b) and *P. barbata* (c) with spermatophore attached to genital segment. Note species-specific differences in the shape of the genital somite. Drawings by Sars (1900)

Copepodite stages of *Pareuchaeta barbata* and *P. polaris* can usually be identified by size, habitus and coloration. Specimens of *P. barbata* are at all stages considerably larger and more heavily built than the respective copepodids of the other species. Moreover, they are coloured bright red and often carry a typical armoury of bristles. In contrast, *P. polaris* combines a compact cephalothorax with a relatively long abdomen and is coloured orange.

Distinguishing young copepodids of the co-occurring *P. glacialis* and *P. norvegica* is a more difficult task. During the field work it was discovered that in live individuals the colour pattern may be species-specific. Adults, CV and often CIV of *P. glacialis* showed a characteristic distribution of red and transparent body areas. When seen ventrally, a red band extended like a median from the anterior to the posterior end of the cephalothorax, while the body flanks were colourless. In addition, the abdomen often had an orange to reddish tone. In contrast, *P. norvegica* adults and older copepodids were characterised by a bright red anterior part of the cephalothorax, including the mouthparts, and sharply contrasting to the rest of the body and abdomen, which were colourless and transparent.

However, no differences in the coloration of younger copepodids of both species were detected, limiting the use of this method for species identification. Moreover, animals preserved in formaldehyde soon lost their characteristic coloration, making it impracticable to apply the method on preserved samples. Therefore, copepodite stages of *Pareuchaeta glacialis* and *P. norvegica* had to be combined into common categories during this study.

3.5 Individual dry mass of euchaetid and aetideid copepods

To measure the individual dry mass of euchaetid and aetideid species and stages, frozen individuals were dried by lyophilisation for 48 h and subsequently weighed on a Sartorius micro-balance with a precision of 10 µg (Hagen 1988). In the case of rare and/or small stages, samples from neighbouring stations had to be pooled. Thus, the data presented are mean values and the standard deviation SD describes variations between samples and not between individuals.

3.6 Distribution of total mesozooplankton biomass

The determination of total mesozooplankton biomass required a complex procedure consisting of three major steps.

Dry mass of the formaldehyde preserved samples

First, the preserved remains of the Multinet samples were dried at 60°C for 48 h (modified after Båmstedt 1974) and sample dry mass was determined on a micro-balance. If sufficient material was available, samples were split using a Folsom splitter and only one half was used for the biomass determination.

Correction of preservation-induced dry mass loss

Considerable losses in dry mass may occur due to formaldehyde preservation (Giguère et al. 1989). Therefore, in a second step measured dry mass values had to be corrected applying a correction factor determined during the same expedition. Bongo net samples (1500 to 0 m depth) were collected at eight stations and split onboard immediately after capture using a Folsom splitter. One half was preserved in a 4% formaldehyde-seawater solution applying the same procedure as for the Multinet samples. The other half was carefully rinsed with freshwater to remove salt remains and deep-frozen at –80°C. Formaldehyde-preserved samples were treated in the same way as the Multinet samples and measured after drying at 60°C (Båmstedt 1974), whereas the frozen samples were carefully dried by lyophilisation. In all eight experiments formaldehyde preservation reduced dry mass considerably. Losses ranged from 19.3 to

40.2% when compared to the dry mass of the respective frozen subsamples. On average, the formaldehyde-preserved subsamples weighed 72.3% of the frozen subsample.

These results are in good accordance with Giguère et al. (1989), who reported a reduction of dry mass by 37 to 43% during 66 weeks of chemical preservation. Our slightly lower losses may be due to shorter storage time and the dominance of large calanoid copepods in Arctic zooplankton samples, since dry mass losses seem to be size-dependent with a stronger effect on smaller individuals (Giguère et al. 1989). To compensate for the loss due to preservation, measured dry mass values of the Multinet samples were multiplied with a correction factor f = 100/72.3 = 1.38.

Euchaetid and aetideid dry mass

In a third step the mass of euchaetid and aetideid copepods sorted from each sample was calculated by multiplying measured stage-specific individual dry masses with abundance data for each sample. These values were added to the measured mass of the remaining sample. To provide total mesozooplankton dry mass concentrations per m^{-3}, the calculated total dry mass of each sample was divided by the volume filtered, assuming a fishing efficiency of 100%.

Thus, the determination of total mesozooplankton dry mass concentration can be described mathematically by

$$M_{total} = \frac{f \times M_{measured} + \sum_{j}\sum_{i} m_{ij} \times n_{ij}}{a \times (d_{opened} - d_{closed})} \quad \text{,where}$$

M_{total} = total mesozooplankton dry mass; (M_{total}) = mg DM m^{-3}
$M_{measured}$ = measured dry mass of the formaldehyde preserved sample (mg DM)
f = correction factor for preservation-induced dry mass loss; f = 1.38
m_{ij} = individual dry mass of stage i of species j
n_{ij} = number of stage i of species j sorted from the sample
i : stage index (CI, CII, CIII, CIV, CV, CVI-male, CVI-female)
j : species index
a = mouth opening of net; a = 0.25 m^2
d_{opened} = depth, where the net was opened; (d_{opened}) = m
d_{closed} = depth, where the net was closed; (d_{closed}) = m

3.7 Lipid content

Lipids function as major energy reserves in zooplankton organisms. Efficient energy storage is particularly important for organisms living at high latitudes, where a strong seasonality in environmental parameters controls food availability. Due to their low density, lipids may also provide buoyancy for pelagic organisms (e.g. Morris 1972; Hagen 1988). Seasonal trends in lipid content can elucidate life cycle characteristics, e.g. whether organisms overwinter actively or in a dormant state, and when reproduction takes place (Kattner & Hagen 1995; Schnack-Schiel & Hagen 1995; Hirche 1996a). The present study mainly focuses on the ontogenetic changes in total lipid content and on interspecific comparisons.

Lipids were extracted and determined gravimetrically essentially according to Folch et al. (1957) and Bligh & Dyer (1959). The method efficiently removes 95 to 99% of all lipids from the samples (Christie 1982). Generally it was necessary to pool samples from neighbouring stations in order to obtain a sufficient quantity of lipids. In the case of rare species and/or small stages, samples from the entire expedition had to be combined.

Copepod samples were transferred into an organic solvent (dichloromethane : methanol = 2:1 by volume) and homogenised mechanically (Potter) and by ultrasonic. To clean the extract a 0.88% KCl/Aqua bidest. solution was added. The mixture was shaken and centrifuged, before the organic phase was removed by Pasteur pipette. After the evaporation of the solvent under a stream of nitrogen to avoid oxidation processes, the remaining extracts were weighed on a micro-balance (precision 10 µg). For details of the method see Hagen (1988) and Fahl (1995).

3.8 Fatty acid and alcohol composition

In 1971 Lee et al. (1971) discovered that the fatty acids of calanoid body lipids resembled the fatty acid composition of their principal food. The authors concluded that copepods incorporated dietary fatty acids largely unchanged into their wax esters. Therefore, fatty acids can be used as trophic biomarkers to elucidate predator-prey relationships within pelagic food webs.

In laboratory experiments the fatty acid composition of herbivorous copepods changed with dietary compositions (Graeve et al. 1994). Lipid biomarkers were traceable even at higher trophic levels (Hopkins et al. 1993) and enabled St. John & Lund (1996) to link the enhanced condition of juvenile cod to frontal phytoplankton blooms. In the Antarctic calanoids, *Pareuchaeta antarctica* and *Euchirella rostromagna*, however, the potential of fatty acids and alcohols as trophic markers was rendered largely insignificant due to catabolic processes (Hagen et al. 1995).

Among the specific lipid components suitable for use as trophic biomarkers, the fatty acids 16:1(n-7) and 18:1(n-7) are considered to be indicators for a herbivorous diet consisting mainly of diatoms (Graeve et al. 1994, 1997). In contrast, 18:1(n-9) is indicative of carnivorous feeding (Graeve at al. 1997). The monounsaturated fatty acids 20:1(n-9) and 22:1(n-11) are typical components of wax esters synthesised by herbivorous calanoids (Hopkins et al. 1993 and references therein). High amounts of these fatty acids in carnivores might, therefore, indicate feeding on *Calanus*.

Recently, Graeve et al. (1997) evaluated the potential of lipid analyses for deducing the principal food sources of benthic invertebrates. The ratio of the two fatty acid isomers 18:1(n-9) and 18:1(n-7) was found to reflect different feeding behaviours and trophic levels. This ratio can thus be used as a relative index for carnivory. High values are typical of carnivores, whereas low ratios indicate herbivorous feeding.

For the analysis of lipid composition, fatty acids were converted into methyl esters and analysed by gas-liquid chromatography according to Kattner & Fricke (1986). Fatty acid methyl esters were prepared by transmethylation in methanol-sulphuric acid and analyses were performed using a Packard gas chromatograph according to the specifications listed below (for details see Fahl 1995).

	GC United Technologies Packard 438A	
Column:	30 m x 0.25 mm	
Liquid phase:	DB-FFAP	
Temperature programme:	Initial:	165°C
	Rise:	4°C min^{-1}
	Final:	240°C for 15 min
Carrier gas:	Helium, pressure 115 kPa	
Carrier gas stream:	1.25 ml min^{-1} at 28°C	
Flame ionisation detector:	Operating temperature: 280°C	
	Hydrogen	100 kPa
	Nitrogen	100 kPa
	Synthetic air	100 kPa
Injector in split mode:	Operating temperature 280°C	
	Split rate	1:60
	Split stream	75 ml min^{-1}, both measured at 28°C

Chromatograms were recorded on an integrator connected to a PC. Peaks were identified according to retention times by comparison with a fish triacylglycerol standard (Marinol) and a copepod standard of known composition. Since the lipid compositions were analysed to determine trophic relationships in the present study, focus was given to those fatty acids known as trophic biomarkers.

3.9 Reproductive strategies

Females of all *Pareuchaeta* species as well as *Chiridius obtusifrons* produce egg sacs and carry their brood attached to the genital opening until the offspring hatches. The fraction of these females carrying egg sacs, egg diameter and mean number of eggs per clutch were measured.

Additionally, dry mass and total lipid content of egg sacs were measured according to the procedure described for copepodids. Based on dry mass and lipid content, a two-compartment model was applied to calculate the caloric value of eggs and to estimate the energetic investment of females into egg production. Assuming a caloric value of 39.6 kJ g^{-1} for lipids and that the remaining fraction of dry mass consisted of proteins and carbohydrates with an average caloric value of 20.5 kJ g^{-1} (Sommer 1998), the total energy content of eggs, clutches and females can be determined according to:

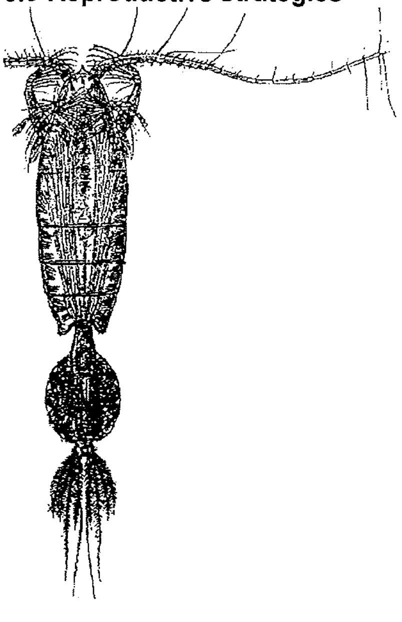

Fig. 6 *Pareuchaeta norvegica* female with egg sac attached to the genital somite. Drawing by Sars (1900).

$$E = (L \times 39.6\ J\ mg^{-1} + (1-L) \times 20.5\ J\ mg^{-1}) * M$$,where

E = energy content (J)
L = lipid content as fraction of total dry mass
M = total dry mass (mg).

Ratios between the energy content of eggs and females and between clutches and females, respectively, were calculated to assess the energetic investment of females in reproduction. This approach was necessary since the total lipid content of the eggs was considerably higher than that of the females, so that a simple ratio between dry mass values would have been inappropriate.

3.10 Respiration measurements

Respiration is often used as an easily measurable parameter to approximate the metabolic rate of organisms, when anaerobic processes may be neglected (Clarke 1983). The respiration rates of euchaetid and aetideid copepods were measured by couloximetry. This method was originally developed by Hersch (1973) to quantify trace amounts of oxygen in gas streams. Peck & Uglow (1990) and Schmid (1996) adapted this technique to measure the respiration of marine benthic invertebrates. Compared to oxygen electrodes, this method offers the higher resolution necessary to measure the low oxygen consumption of single copepods.

The system is based on a fuel cell consisting of a cadmium coated nickel core separated from an outer carbonaceous layer by an inert fabric impregnated with an aqueous KOH solution. Oxygen passing through the fuel cell is converted into hydroxyl ions and oxidises the cadmium to cadmium hydroxide.

$$O_2 + 2\,H_2O + 4\,e^- \longrightarrow 4\,OH^-$$
$$2\,Cd + 4\,OH^- \longrightarrow 2\,Cd(OH)_2 + 4\,e^-$$

Hence, each oxygen molecule releases four electrons measurable as an electric current, which is directly proportional to the oxygen content within the probe. Therefore, couloximetry is an absolute method, requiring no calibration (Peck & Uglow 1990).

To analyse the oxygen content of a water sample, the oxygen has to be transferred from the liquid into a carrier gas stream. In this system nitrogen is used as an inert carrier gas. Contamination of the carrier gas with air is avoided by gas-tight installations and two oxygen traps inserted into the carrier gas stream. A small probe (100 µl) of the water sample is injected through a teflon/rubber seal into a desorber filled with an aqueous KOH solution. The carrier gas passes through the solution, expels the oxygen and transports it into the fuel cell, where the electric signal is recorded by an integrator.

Respiration measurements were conducted as closed-bottle experiments (Steffensen 1989). Single individuals were kept in glass bottles of 33 or 50 ml volume filled with filtered seawater and sealed gas-tightly with rubber septa. Experiments were run in darkness at an in situ temperature of 0° ± 1°C for up to 72 h. Control experiments were conducted simultaneously without animals under the same conditions. At the end of the experiments water samples of 100 µl were taken with a gas-tight syringe through the rubber seal of each bottle and injected into the desorber of the couloximeter system. Respiration rates were calculated from the differences in oxygen concentration between experimental bottles and controls without animals. This procedure has several advantages in comparison to start and stop measurements for each bottle. It minimises the risk of leakage of the rubber seals and air intrusion into the experimental bottles, since it is not necessary to penetrate the rubber seals at the beginning of the experiments. In addition, potential bias of respiration rates by microbial activity is inherently corrected for, since it would also occur in the control bottles (Steffensen 1989). Also temperature changes during the experiments could be neglected, since control values were measured together with the replicates.

3.11 Feeding experiments

Ingestion rates of *Pareuchaeta norvegica* and *P. glacialis* were determined during feeding experiments according to Yen (1982, 1983, 1985). Single individuals of these predators were sorted from Bongo net samples immediately after capture and kept in beakers filled with 2 l of filtered seawater. Experiments were started with the addition of ten *Calanus* CV or females as prey and run for three days in darkness at an in situ temperature of 0°±1°C. After termination remaining prey individuals were counted and predators and prey samples were deep-frozen.

Body dry mass of predators and prey was determined after lyophilisation as described under 3.5. Daily consumption rates were calculated as ingestion of ind. prey d^{-1} or mg DM d^{-1} and converted into mass-specific ingestion rates (d^{-1}).

In addition, qualitative feeding experiments were conducted with several aetideid and euchaetid species to elucidate their dietary preferences. Therefore, different food items, including a phytoplankton suspension, nauplii of *Calanus glacialis* and *Pareuchaeta barbata*, and copepodids of different sizes were offered. The prey selection included *Microcalanus pygmaeus*, *Pseudocalanus minutus*, *Metridia longa*, *Scaphocalanus magnus*, *Spinocalanus antarcticus* and *Calanus* spp. The reaction to the different prey items and the production of faecal pellets were recorded.

3.12 Maximum ingestion rates of Aetideidae and Euchaetidae

To evaluate the effect of euchaetid and aetideid communities on the carbon flux in Arctic pelagic ecosystems, the potential maximum ingestion of these communities (mg C m^{-2} d^{-1}) was estimated by combining field data on abundance and stage composition with mass-specific individual respiration rates (d^{-1}) and mean individual mass (mg C). Potential ingestion rates were calculated separately for each copepodite stage and species by an allometric equation relating mass-specific maximum ingestion I_{max} to body mass M ($I_{max} = 63 \times M^{-0.25}$) proposed by Moloney & Field (1989) for particle-feeding heterotrophs living at a temperature of 20°C.

Values were converted to an ambient temperature of 0°C applying a coefficient of $Q_{10} = 3$ (Paffenhöfer 1971; Ross 1982; Hirche 1987). Similar approaches were used by Mahaut et al. (1995) to estimate the respiration of a benthic deep-sea community in the NW Atlantic, by Piepenburg & Schmid (1997) for brittle star populations in the Laptev Sea and by Gradinger et al. (in press) for the maximum ingestion rate of Arctic sea-ice communities.

Additionally, daily ingestion rates were estimated based on the results of the respiration measurements and an energy budget approach. Generally, net conversion efficiency k_2 and the assimilation coefficient U are defined according to the equations:

$k_2 = P/(P+R)$
$U = (P+R)/C$ (Vinberg 1956), where
P = production
R = metabolic energy demands
C = consumption

The first equation leads to $P = R \times k_2/(1-k_2)$ and the subsequent elimination of P from the second equation yields

$$C = (P+R)/U = R/((1-k_2) \times U)$$

For net conversion efficiency a value of $k_2 \sim 0.3$ has been proposed as a grand average for wild poikilothermic populations from boreal regions (Wieser 1986). In zooplankton k_2 ranges from 0.2 to 0.5 and usually equals ~ 0.3 for adults (Vinogradov & Shushkina 1987).

Assuming an assimilation coefficient of $U \sim 0.8$ for the omnivorous and carnivorous species considered here (Vinberg 1956; Vinogradov & Shushkina 1987), consumption can be described as a function of metabolic energy demands according to:

$$C \sim 1.79 \times R$$

However, it must be taken into account that under natural conditions metabolic rates are considerably higher than the standard oxygen consumption of resting animals (Dorrien 1993). Pakhomov & Perissinotto (1996) estimated that the natural metabolic demands of active carnivorous zooplankton (*Themisto gaudichaudi*) are double that of their basic metabolic needs.

During the present study copepods often rested on the bottom of the vials and highly energetic predatory behaviour was not observed during the respiration measurements. Thus, the respiration rates measured here generally approximated standard oxygen consumption. According to Pakhomov & Perissinotto (1996), the relationship between consumption and measured respiration, therefore, has to be modified to:

$$C \sim 1.79 \times R = 2 \times 1.79 \times R_b = 3.58 \times R_b \quad \text{, where}$$

R_b = measured basic metabolic rate

To evaluate whether the I_{max} values derived from the allometric function appropriately approximated real carbon demands, they were compared to the measured results available for some species and stages from respirometry and feeding experiments. However, direct measurements covered only a fraction of the size and species spectra recorded in the field. Therefore, it was necessary to apply the allometric approach taking into account the size dependence of individual ingestion and respiration rates.

4 Results

4.1 Arrangement of transects

For the presentation of the results the stations are grouped along four transects: Transect A includes the eight southernmost stations, starting at 13°50' W on the East Greenland shelf and following latitude 75°N eastward, down the continental slope into the deep-sea basin of the central Greenland Sea. In addition, St. 17 at 76°36'N 4°39'E is included as the most easterly position on this transect. All stations were sampled between May 27 and June 18, 1997.

Transect B comprises three stations with bottom depths of 3359, 1574 and 374 m respectively, located at 81°N across the East Greenland continental rise. Similarly, three stations between 1976 m and 507 m water depth were sampled at 81°35'N during ARK XIII/2 and combined to transect C.

The northernmost transect D starts in the southern Nansen Basin (82°39'N 1°25'E; 3233 m bottom depth) and extends via five stations in a south-easterly direction onto Yermak Plateau (81°54'N 7°42'E; 832 m).

4.2 Distribution of total mesozooplankton biomass

The distribution of total mesozooplankton biomass showed strong vertical and meridional gradients. Highest biomass concentrations were observed close to the surface. On the southern transect A dry mass decreased from 37-132 mg DM m^{-3} in the upper 50 m to less than 10 mg DM m^{-3} below 100 m. Below 500 m biomass never exceeded 4 mg DM m^{-3}. Along the northern transects across the East Greenland continental rise and onto the Yermak Plateau mesozooplankton biomass declined from 7-46 mg DM m^{-3} at the surface to less than 4 mg DM m^{-3} below 100 m (Fig. 7).

This depth-dependent decrease in biomass was more pronounced over the deep-sea basins, whereas on shallow stations biomass was distributed more evenly throughout the water column. This was in particular the case on the East Greenland shelf (Sts. 23, 24 and 32), where lower biomass in the upper 50 m coincided with relatively high values in deeper layers, as compared to oceanic areas. A similar tendency was apparent on the Yermak Plateau with a relatively stable biomass from 50 m depth down to the seafloor.

A weakly expressed mesopelagic biomass maximum was detected in the central Greenland Sea. At Sts. 17 and 35 concentrations in 200-500 m depth ranged from 6 to 10 mg DM m^{-3}, two to four times higher levels than in the adjacent water layers above and below.

Another emerging feature was a decline in epipelagic mesozooplankton from the southern transect towards the north. Maximum biomass values between 37 and 132 mg DM m^{-3} occurred in surface waters at 75°N, whereas epipelagic biomass was limited to less than 18 mg DM m^{-3} in the northwestern part of the investigation area (Fig. 7).

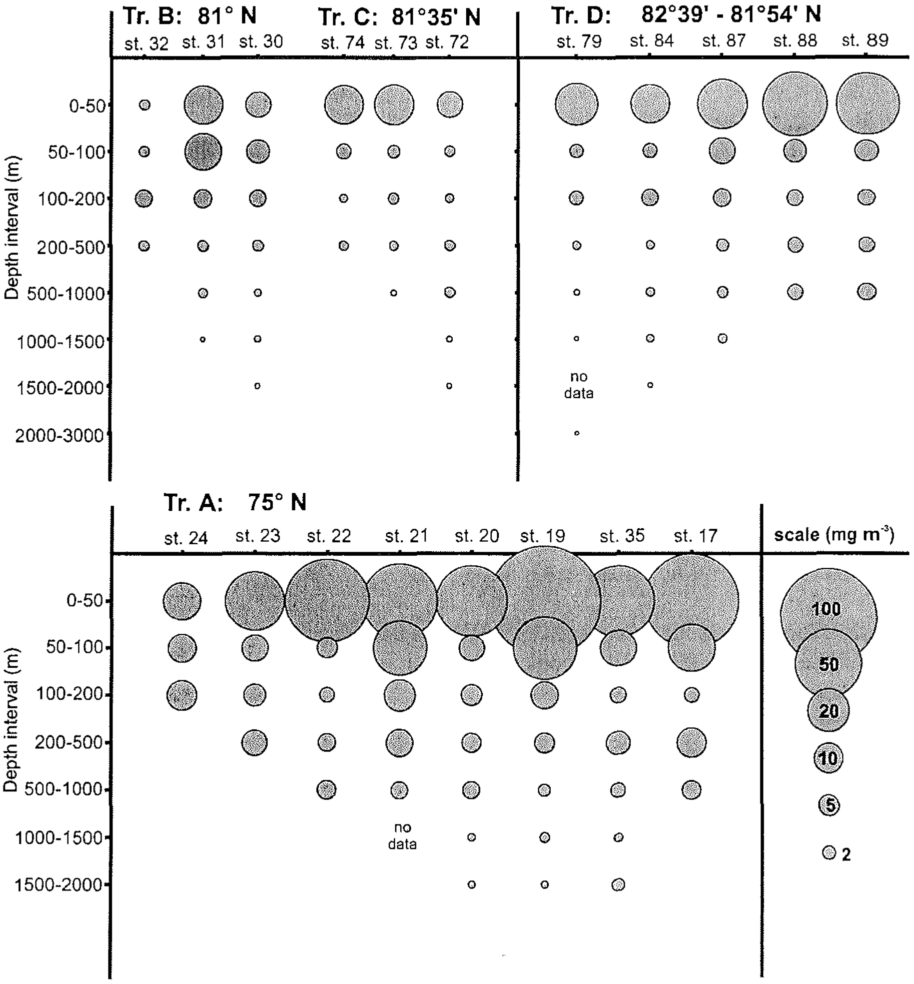

Fig. 7 Vertical distribution of total mesozooplankton dry mass (mg m^{-3}) in the Greenland Sea. Circle areas are proportional to mesozooplankton dry mass. The scale exemplifies certain values for easier interpretation.

This meridional decline was overlaid by an eastward increase in biomass across the northern part of Fram Strait. While epipelagic biomass ranged below 20 mg DM m^{-3} on the East Greenland side and in the Nansen Basin, considerably higher values of 40-45 mg DM m^{-3} were detected over the Yermak Plateau.

In spite of the obvious decrease in biomass concentration from the surface to greater depths, the major fraction of total mesozooplankton biomass was situated below 100 m depth. With regard to absolute values, it has to be considered that the sampling intervals progressively widened with increasing depth. Fig. 8

illustrates the vertical distribution of mesozooplankton dry mass along a depth axis with linear scale, so that the depicted areas are directly proportional to the absolute mesozooplankton biomass. More than half of the total mesozooplankton biomass was located below 100 m depth. In high-Arctic regions of the northern East Greenland continental rise (transects B and C) even two thirds of the total biomass (0-2000 m) occurred below 100 m, and these figures are still under-estimates, since the Greenland Sea and the Arctic Ocean are deep-sea ecosystems with water depths exceeding 4000 m.

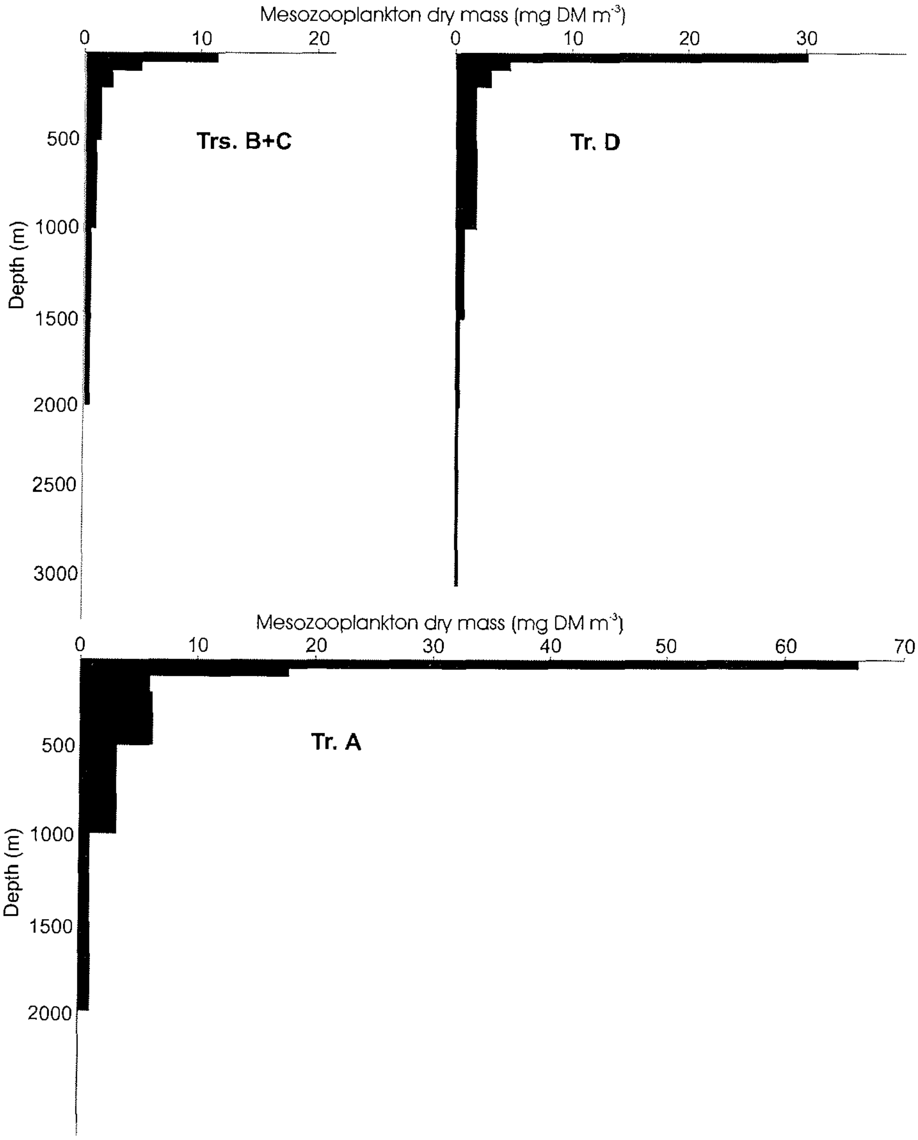

Fig. 8 Vertical distribution of mean total mesozooplankton biomass (mg DM m^{-3}) along a linearly scaled depth axis.

4.3 Distribution of Aetideidae and Euchaetidae

The calanoid families Euchaetidae and Aetideidae comprise medium-sized to large copepods, which mainly inhabit deeper water layers. For the Arctic Ocean four *Pareuchaeta* species and at least nine species of the family Aetideidae have been reported (Park 1994b; Markhaseva 1984, 1996). During the field work of the present study all four Arctic species of the genus *Pareuchaeta* and eight aetideid species were recorded:

Euchaetidae
Pareuchaeta barbata
Pareuchaeta glacialis
Pareuchaeta norvegica
Pareuchaeta polaris

Aetideidae
Aetideopsis minor
Aetideopsis rostrata
Chiridiella abyssalis
Chiridiella sp.
Chiridius obtusifrons
Gaetanus brevispinus
Gaetanus tenuispinus
Pseudochirella spectabilis

4.3.1 Distribution of *Pareuchaeta barbata*

Pareuchaeta barbata occurred abundantly in the meso- to bathypelagial of the central Greenland Sea. Up to 200 ind. 1000^{-1} m^{-3} were reported between 500 and 1500 m depth at oceanic station along transect A and comparable numbers were present at 82°N over the Yermak Plateau (Fig. 9). However, the species was not found at shallow shelf stations and only one single individual was collected in polar waters of the northern East Greenland continental rise. Thus, *Pareuchaeta barbata* can be described as a boreal-Atlantic deep-sea species, whose distribution in the Greenland Sea is related to the Atlantic inflow.

4.3.2 Distribution of *Pareuchaeta glacialis* females

Pareuchaeta glacialis females occurred throughout the investigation area. Highest abundances of 300 to 600 ind. 1000^{-1} m^{-3} were determined in the Polar Surface Water at the northernmost stations (Fig. 10).

Along the northern transects the species was confined to the upper 500 m, being restricted to epipelagic and upper mesopelagic depths. In the central Greenland Sea (transect A), however, *P. glacialis* had a wider vertical range, also inhabiting deeper layers down to 1000 m depth. Abundance was distributed more evenly throughout the water column with 80 to 100 ind. 1000^{-1} m^{-3} from the surface to 500 m depth. Thus, *P. glacialis* is characterised as a polar epipelagic species, submerging to greater depths in lower latitudes.

4.3.3 Distribution of *Pareuchaeta norvegica* females

Pareuchaeta norvegica females were encountered in high numbers at all stations on 75°N (transect A). In oceanic regions of the central Greenland Sea the species inhabited the epipelagial and upper mesopelagial from the surface down to 500 m depth with a maximum abundance of 80 ind. 1000^{-1} m^{-3}. In contrast, *P. norvegica* apparently avoided the Polar Surface Water of the East Greenland Current and populations on the East Greenland Shelf were therefore restricted to the bottom layer, reaching >100 ind. 1000^{-1} m^{-3} (Fig. 11).

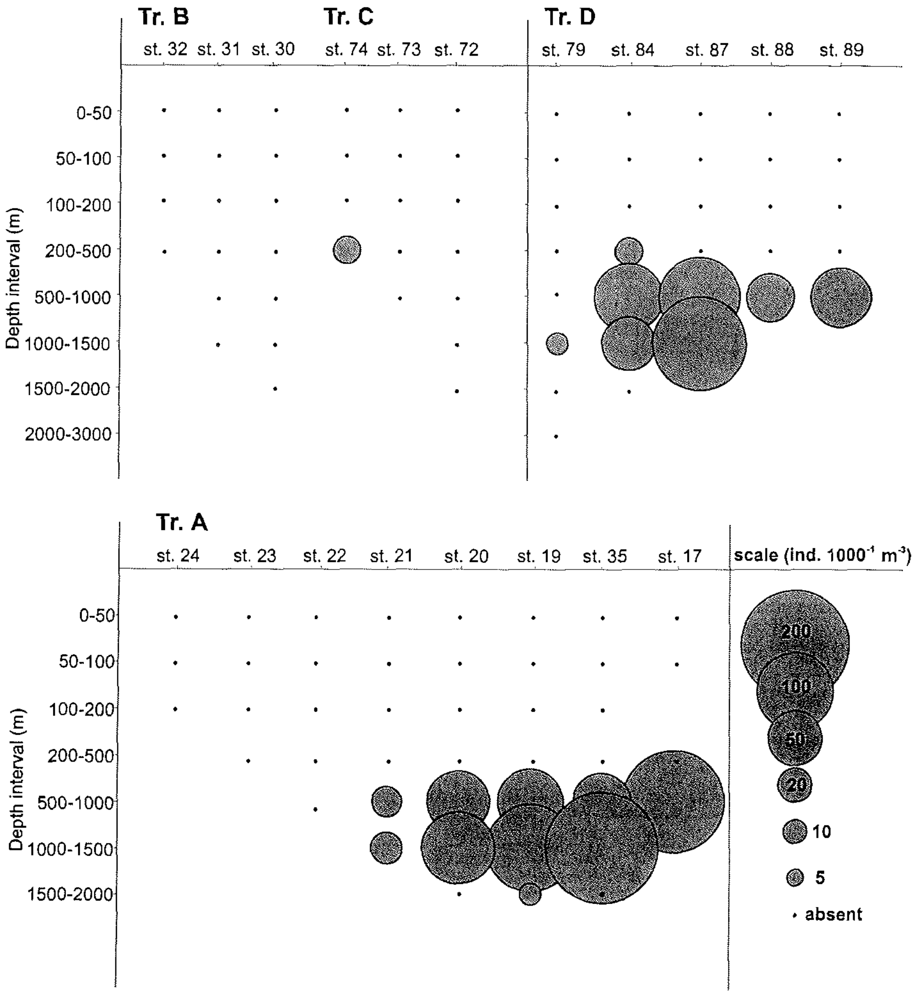

Fig. 9 Vertical distribution and abundance of *Pareuchaeta barbata* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Pareuchaeta norvegica was absent from high-Arctic regions of the northern East Greenland continental rise (transects B and C) and from the Nansen Basin. However, it occurred as far north as 82°N over the Yermak Plateau, inhabiting the whole water column with up to 120 ind. 1000^{-1} m^{-3} (Sts. 88 and 89).

Thus, *Pareuchaeta norvegica* showed the typical distribution of a boreal-Atlantic species. Its abundance was closely coupled to the inflow of Atlantic water masses into the Greenland Sea. It was present in the eastern and central part of the Greenland Sea influenced by the Atlantic West Spitsbergen Current. On the East Greenland shelf the species was an indicator for the Return Atlantic Current entraining close to the seafloor beneath the Polar Surface Water of the East Greenland Current. Correspondingly, it did not occur in high-Arctic areas north-east of Greenland and in the Nansen Basin. However, the presence of *P.*

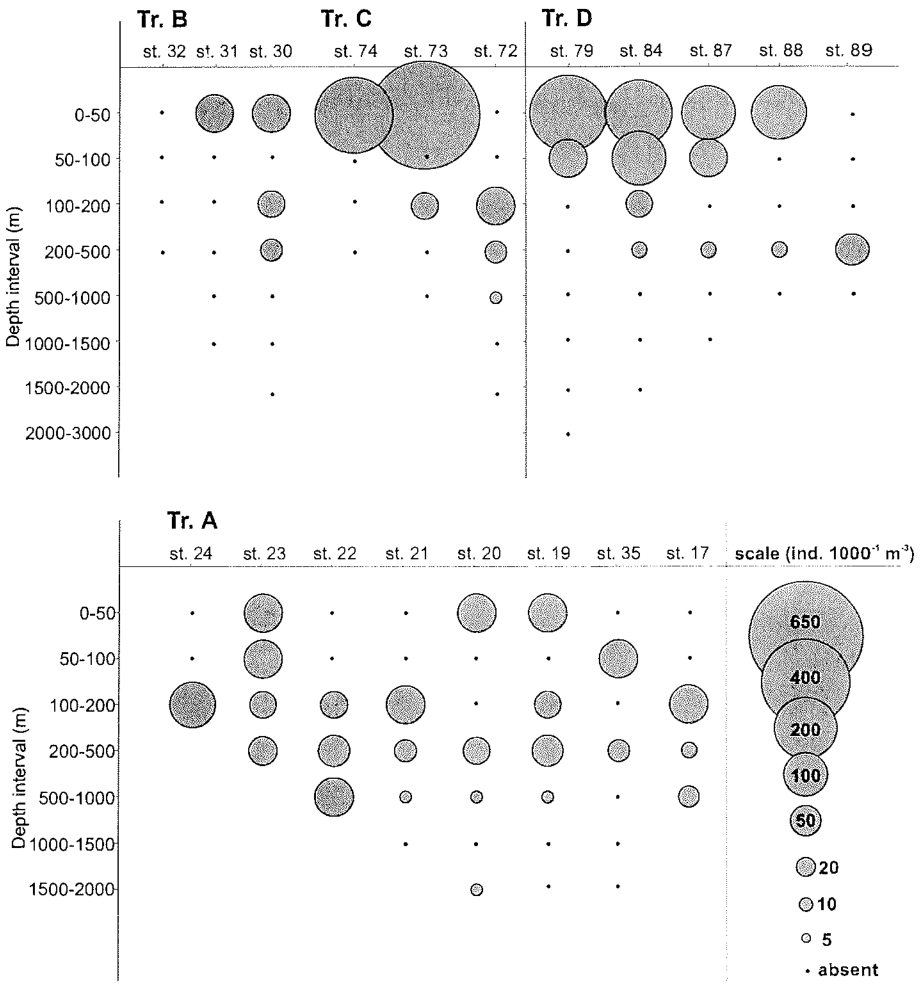

Fig. 10 Vertical distribution and abundance of *Pareuchaeta glacialis* females in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

norvegica over the Yermak Plateau indicated that a branch of the West Spitsbergen Current transports Atlantic water masses northward along the western slope of this plateau.

4.3.4 Distribution of *Pareuchaeta glacialis* and *P. norvegica* copepodids

Since it was impossible to reliably distinguish young copepodite stages of the two closely related species *Pareuchaeta glacialis* and *P. norvegica* (c.f. paragraph 3.4), they had to be combined to one category.

Copepodite stages CI to CV were abundant throughout the investigation area. At the northern transects high epipelagic (0 to 200 m) abundances of 200 to 700 ind. 1000^{-1} m^{-3} strongly decreased towards greater depths (<50 ind. 1000^{-1} m^{-3}). In contrast, on the southern transect A young stages were less abundant in the surface layer, but more evenly distributed down to 1500 m (Fig. 12).

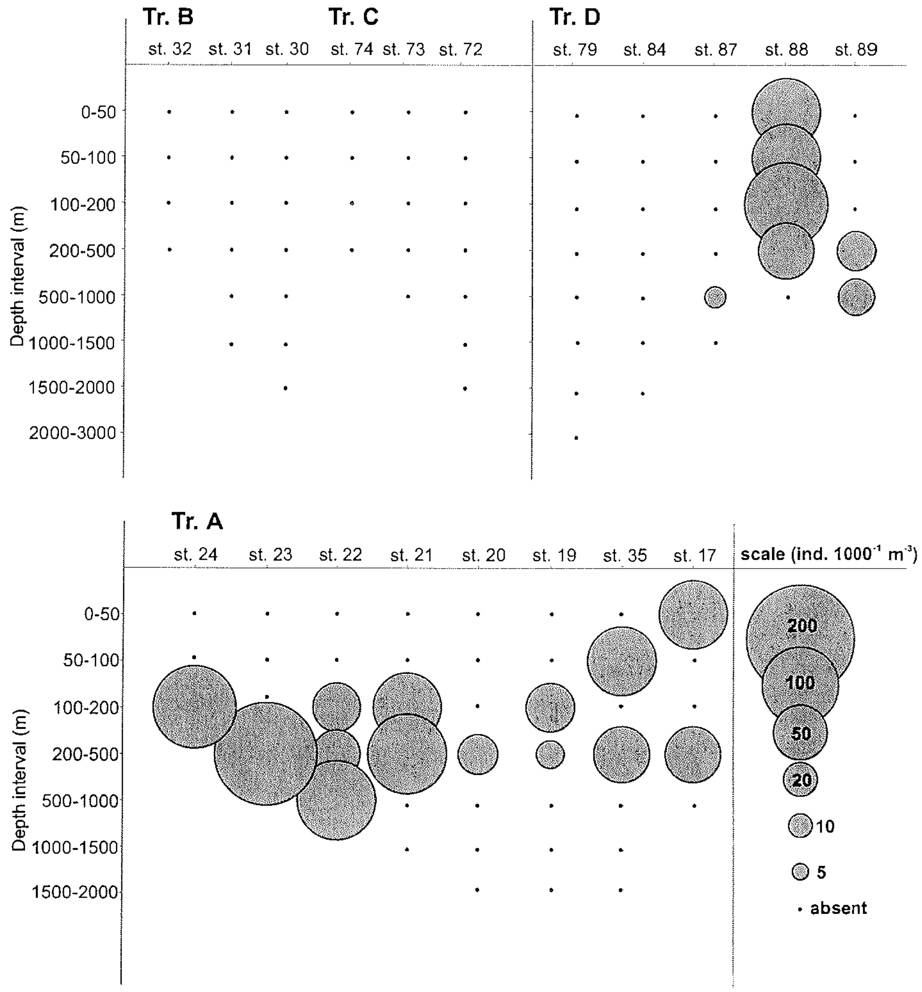

Fig. 11 Vertical distribution and abundance of *Pareuchaeta norvegica* females in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Apart from this general impression, three distinct areas with higher concentrations of young copepodids could be identified. In 50 to 100 m depth over the southern East Greenland continental rise (Sts. 23, 24) more than 1000 ind. 1000^{-1} m^{-3} were detected, comprising the maximum for the southern transect. Elevated numbers of 400 to 800 ind. 1000^{-1} m^{-3} were also measured in 200 to 1000 m depth in the central Greenland Sea (Sts. 19, 35). Concentrations of more than 3000 ind. 1000^{-1} m^{-3} in 50 to 200 m depth over the Yermak Plateau were the absolute highest abundance throughout the investigation area.

The absence of adult *Pareuchaeta norvegica* from the north-western part of the investigation area and from the Nansen Basin suggests that copepodids in this region belong to *P. glacialis*. Similarly, the concentration of copepodids between 50 and 100 m depth on the southern East Greenland shelf probably consisted of *P. glacialis*, since *P. norvegica* adults were restricted to the bottom layer at these stations. Conversely, the extremely high abundances of young *Pareuchaeta* over the Yermak Plateau coincided with high numbers of adult *P. norvegica* indicating that the copepodids also belonged to this species.

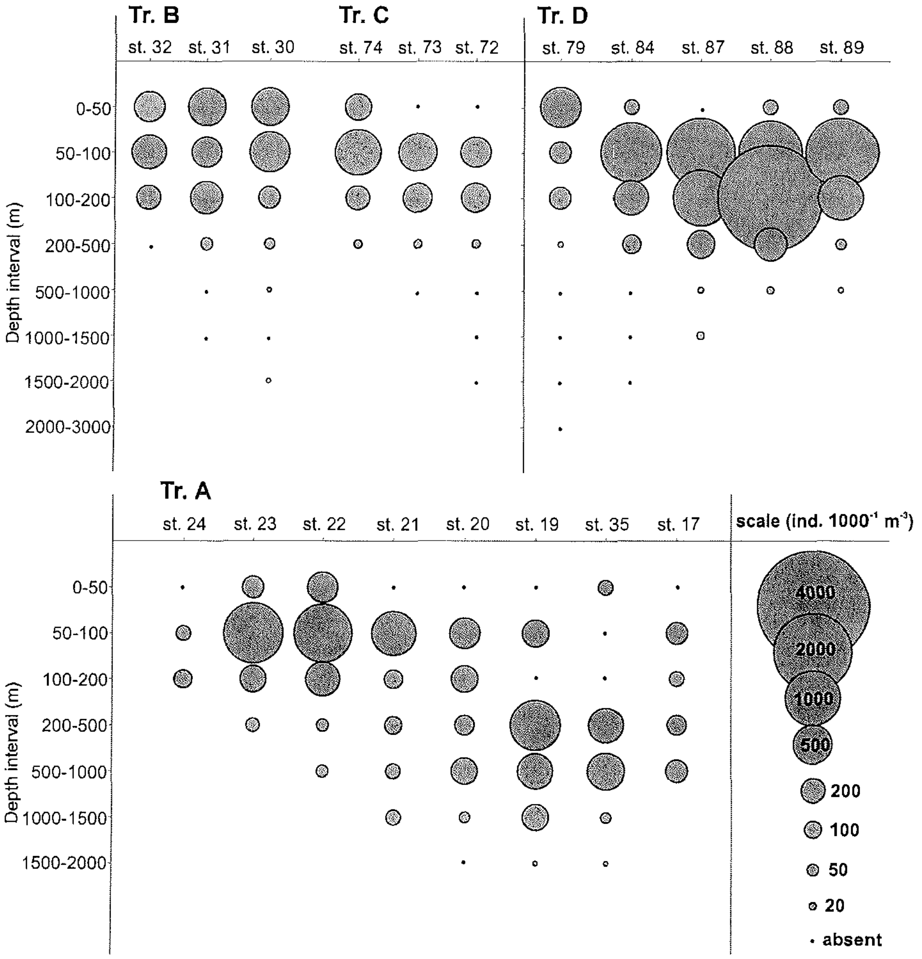

Fig. 12 Vertical distribution and abundance of *Pareuchaeta glacialis* and *P. norvegica* copepodite stages CI to CV in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

4.3.5 Distribution of *Pareuchaeta polaris*

Pareuchaeta polaris occurred on all transects. Strong variations in the vertical range of the species, however, appeared between the northern and southern transects. In polar regions of the northern East Greenland continental rise (transect B and C) and in the Nansen Basin *P. polaris* regularly occurred in the mesopelagial (200 to 1000 m) with 60 to 80 ind. 1000^{-1} m^{-3} (Fig. 13). In the central Greenland Sea comparable numbers were found in bathypelagic depths below 1000 m. In contrast, *P. polaris* was absent from shallow shelf stations and from the Atlantic-influenced Yermak Plateau. Thus, *P. polaris* is characterised as an Arctic mesopelagic species, occurring at bathypelagic depths in the southern part of its range.

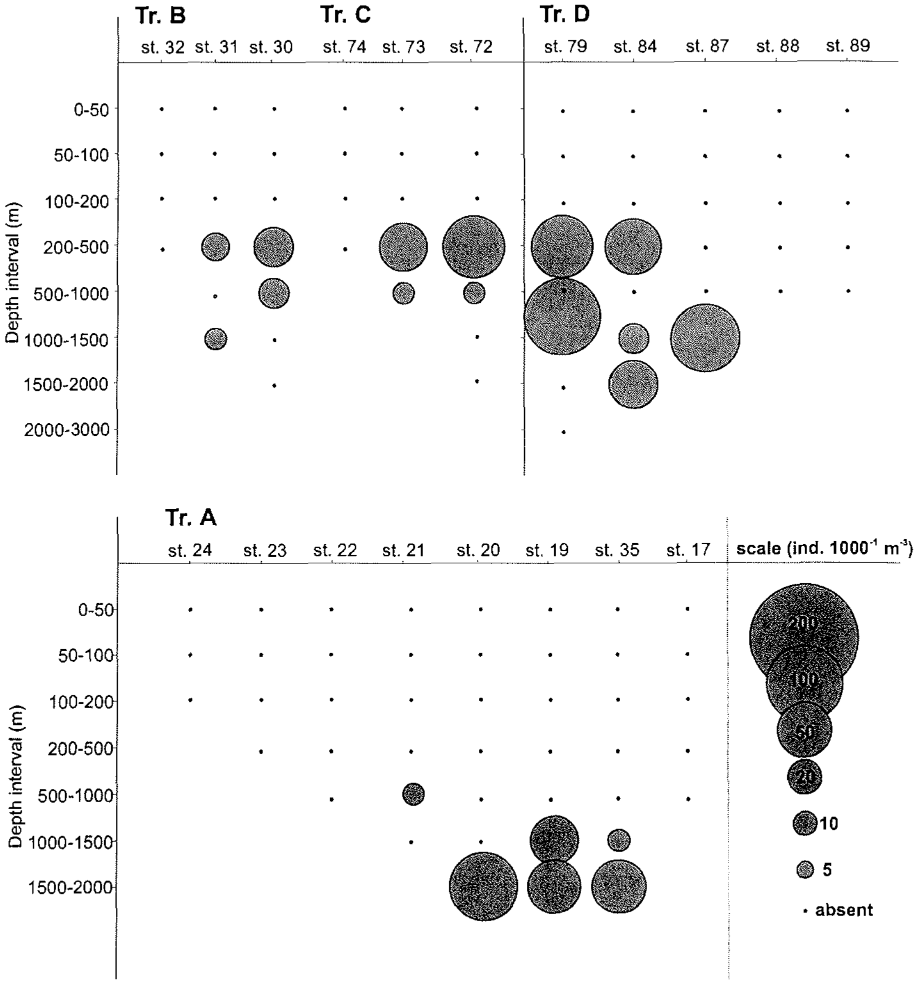

Fig. 13 Vertical distribution and abundance of *Pareuchaeta polaris* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

4.3.6 Distribution of *Aetideopsis minor*

Aetideopsis minor occurred at all but one station throughout the investigation area (Fig. 14). Along the southern transect the species inhabited meso- and bathypelagic layers from 200 to 1500 m depth. Highest concentrations of more than 150 ind. 1000^{-1} m^{-3} were detected in a relatively narrow depth range between 500 and 1000 m in the central Greenland Sea. Along the northern transects abundance was generally lower (<80 ind. 1000^{-1} m^{-3}) and confined to the upper mesopelagial (200 to 500 m). However, an exceptionally wide vertical range was observed at St. 74. The distribution of *Aetideopsis minor* is a typical example of polar emergence, which was apparent in a northward ascent between 75°N (500 to 1000 m) and 81°N (200 to 500 m) and also, on a smaller scale, between Atlantic and polar domains along transect D. Over the Atlantic-influenced Yermak Plateau the species inhabited 500 to 1000 m depth, comparable to the central Greenland Sea, whereas populations in the polar Nansen Basin occurred closer to the surface (200 to 500 m). In general, *A. minor* is a mesopelagic species, prevailing in the Arctic domain of the central Greenland Sea.

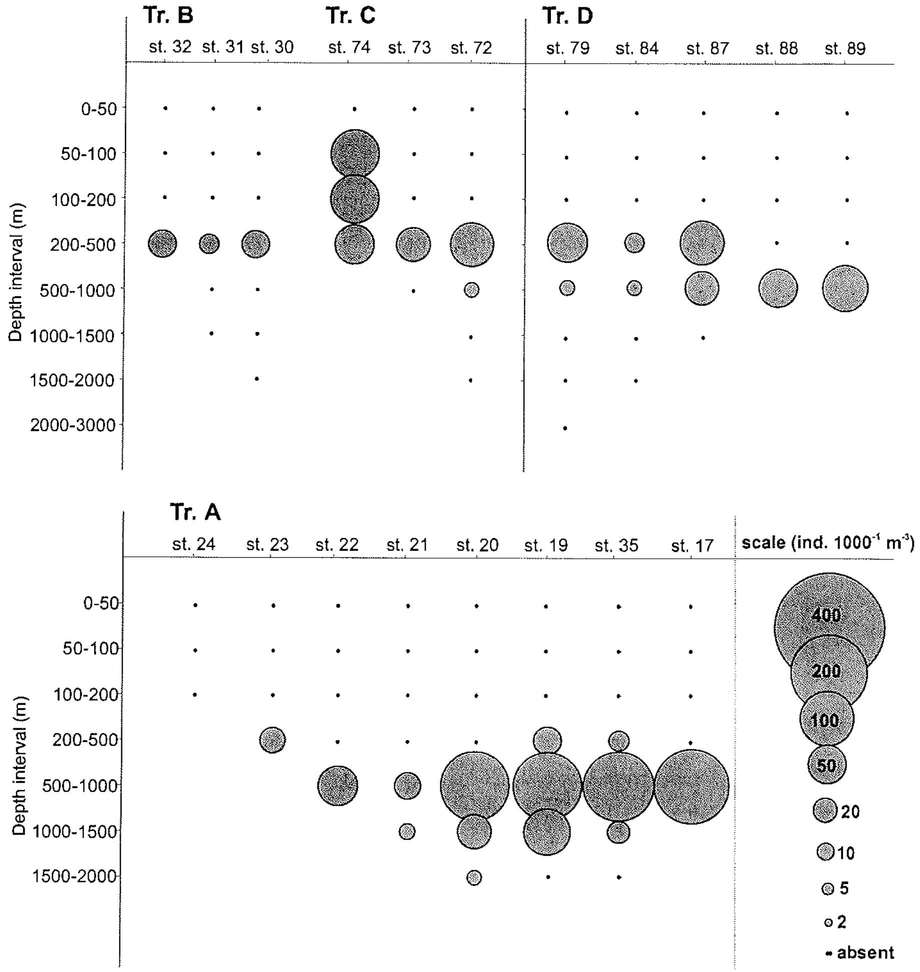

Fig. 14 Vertical distribution and abundance of *Aetideopsis minor* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

4.3.7 Distribution of *Aetideopsis rostrata*

In contrast to its congener *Aetideopsis minor*, *A. rostrata* was restricted to bathypelagic depths throughout the investigation area. Abundances of more than 100 ind. 1000^{-1} m^{-3} were determined below 1000 m depth in the central Greenland Sea and over the western flank of Yermak Plateau (Fig. 15). It also occurred in high-Arctic regions, but with lower numbers of 20 to 30 ind.

1000^{-1} m^{-3}. Thus, *Aetideopsis rostrata* belongs to the bathypelagic fauna of Arctic deep-sea basins.

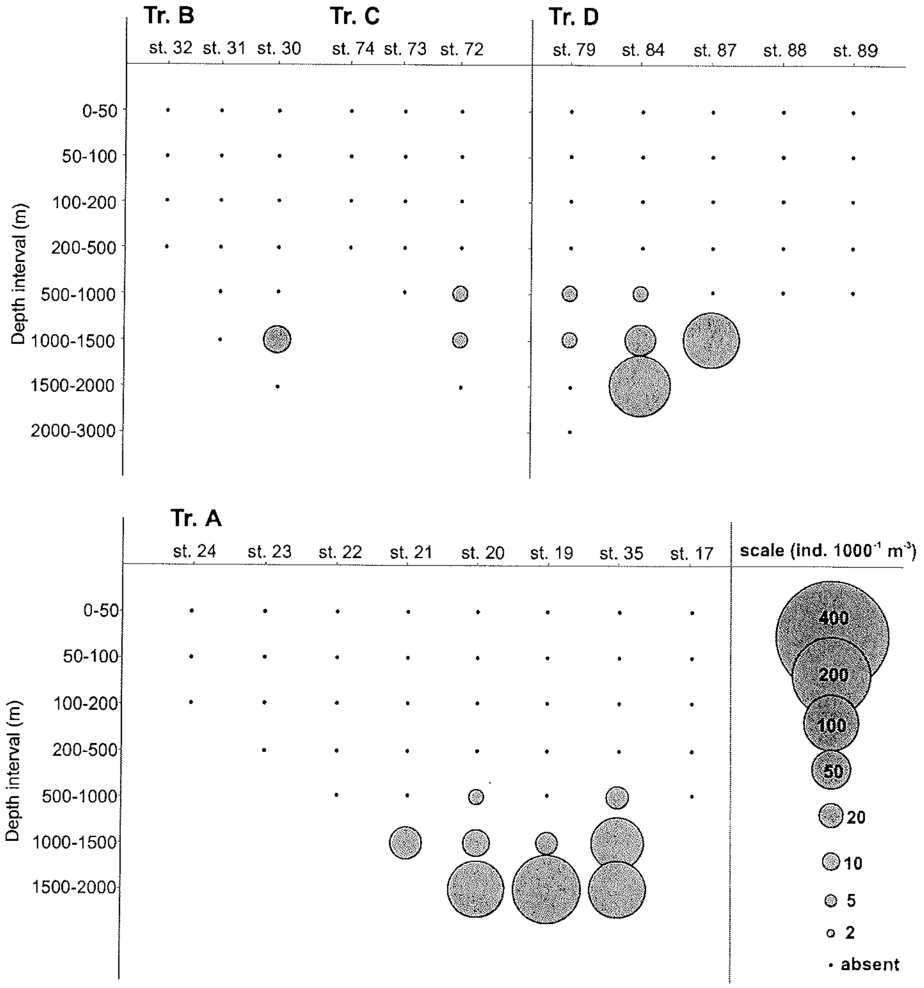

Fig. 15 Vertical distribution and abundance of *Aetideopsis rostrata* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Aetideid males are generally rare and several species are known only from females. Nevertheless, 24 *Aetideopsis rostrata* males were recovered from the suprabenthic net of an epibenthic sledge trawled over the seafloor in 1090 m depth on the continental rise of the Yermak Plateau (St. 90). This unusual phenomenon may indicate a benthopelagic distribution of *A. rostrata* males, which would explain their poor representation in pelagic hauls. However, local hydrographic features resulting in an enrichment of bathypelagic zooplankton in the bottom layer cannot be excluded as a potential cause.

4.3.8 Distribution of *Chiridius obtusifrons*

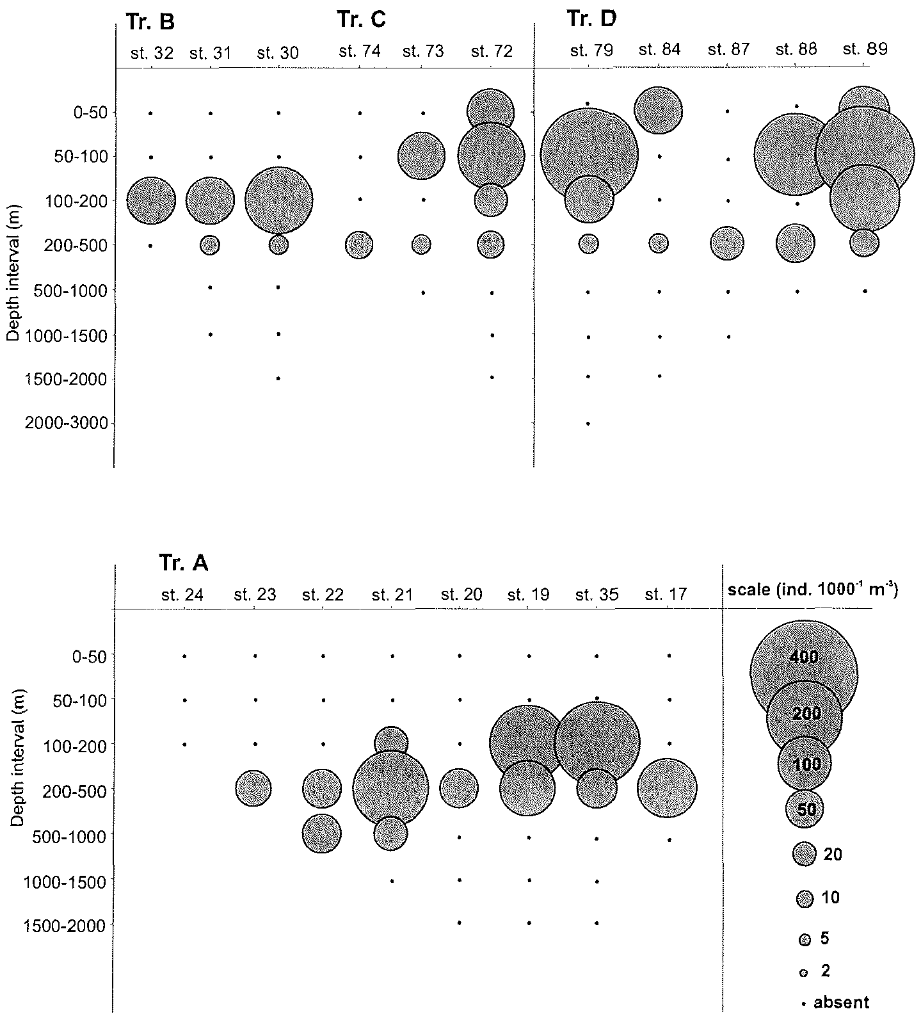

Fig. 16 Vertical distribution and abundance of *Chiridius obtusifrons* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Closely resembling *Aetideopsis minor* in size and habitus, *Chiridius obtusifrons* was one of the most abundant aetideid species in the investigation area. In the central Greenland Sea *C. obtusifrons* was concentrated between 100 and 500 m with more than 200 ind. 1000^{-1} m^{-3} (Fig. 16). Along the northern transects the species appeared also in the epipelagic layer. Maximum abundances of 320 ind. 1000^{-1} m^{-3} were recorded between 50 and 100 m of the Nansen Basin and over the Yermak Plateau. Thus, *Chiridius obtusifrons* represents another example of polar emergence and can be specified as an Arctic epipelagic species, descending to the mesopelagial in the central Greenland Sea.

4.3.9 Distribution of *Gaetanus brevispinus*

Gaetanus brevispinus was an abundant inhabitant of meso- and bathypelagic waters throughout the investigation area. In the central Greenland Sea it was restricted to waters below 200 m with highest abundances of more than 200 ind. 1000^{-1} m^{-3} between 500 and 1500 m (Fig. 17).

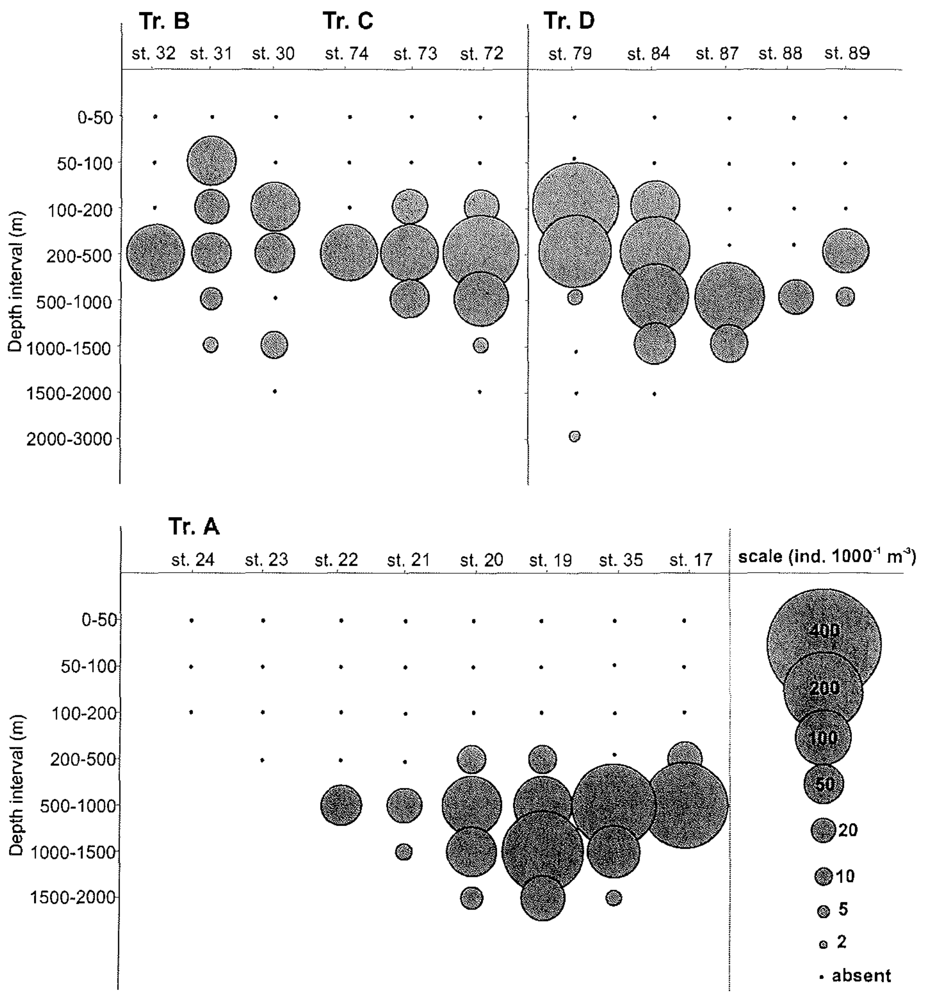

Fig. 17 Vertical distribution and abundance of *Gaetanus brevispinus* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Along the northern transects the species was distributed more evenly throughout the water column between 100 and 1500 m depth with maxima in 200 to 500 m depth. At St. 31 it also appeared in 50 to 100 m depth and in the Nansen Basin individuals were collected from the deepest sample down to 3000 m.

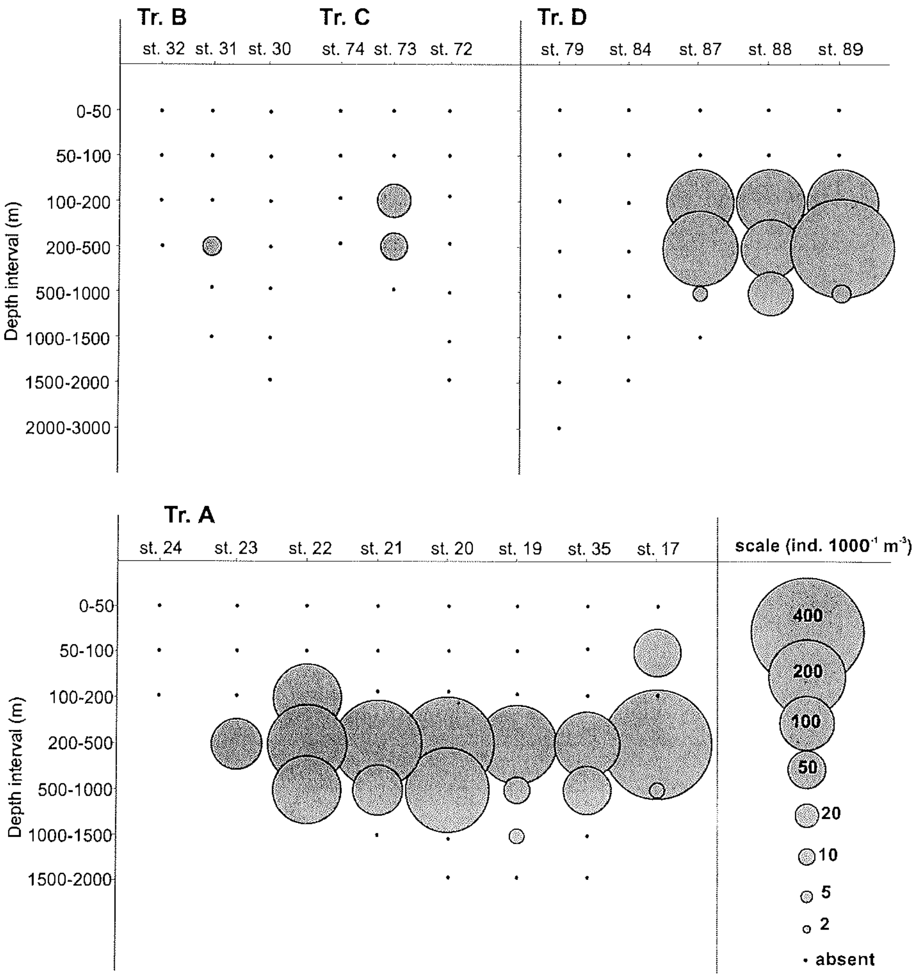

Fig. 18 Vertical distribution and abundance of *Gaetanus tenuispinus* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

Generally, the vertical distribution of *Gaetanus brevispinus* was characterised by polar emergence combining a mainly mesopelagic range in polar waters with a more bathypelagic distribution along the southern transect. A shift in the vertical distribution was also apparent along transect D between the polar Nansen Basin (St. 79: 100 to 200 m) and the Atlantic-influenced western slope of Yermak Plateau (St. 87: 500 to 1000 m). Since the absolute abundance of *G. brevispinus* was rather stable throughout the investigation area, no clear preference for either polar or Atlantic domains could be identified.

4.3.10 Distribution of *Gaetanus tenuispinus*

Gaetanus tenuispinus was the most abundant aetideid species along the southern transect. The species was concentrated between 200 and 1000 m depth with 300 to 400 ind. 1000^{-1} m^{-3} (Fig. 18). Only single individuals were found in high-Arctic areas of the northern East Greenland continental rise, and the species was absent from the polar Nansen Basin. However, high abundances occurred over the Yermak Plateau, similar to the central Greenland Sea. These individuals probably originated from an extension of the West Spitsbergen Current. Thus, the distribution of *G. tenuispinus* is typical of a boreal-Atlantic species and directly related to the inflow of Atlantic water masses into the Arctic.

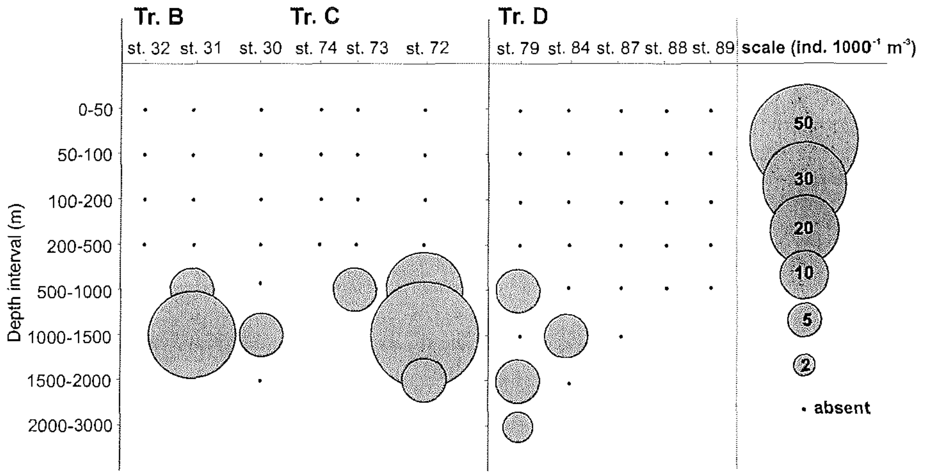

Fig. 19 Vertical distribution and abundance of *Chiridiella abyssalis* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation. Transect A is not shown, since the species was restricted to the northern part of the investigation area. For details see text.

4.3.11 Distribution of *Chiridiella abyssalis*

Chiridiella abyssalis was a rare inhabitant of the bathypelagic Arctic Ocean. The species occurred regularly with 10 to 50 ind. 1000^{-1} m^{-3} in 500 to 2000 m depth at high-Arctic stations in the northern Fram Strait (Fig. 19). In the Nansen Basin it was even found in the deepest sample between 2000 and 3000 m. In contrast, the species was absent from all stations in the central Greenland Sea (transect A) and from the Yermak Plateau. Thus, *Chiridiella abyssalis* is an exclusive representative of the Arctic bathypelagic fauna.

Only one *Chiridiella* specimen was collected on the 75°N transect and this individual apparently belonged to a different species, since its size and dry mass exceeded substantially the respective values of *Chiridiella abyssalis* specimens.

4.3.12 Distribution of *Pseudochirella spectabilis*

Similar to *Chiridiella abyssalis, Pseudochirella spectabilis* was a rare but regular inhabitant of the deep Arctic Ocean (Fig. 20). It occurred with 10 to 20 ind. 1000^{-1} m^{-3} in 500 to 2000 m depth off northeastern Greenland (transects B and C) and in the Nansen Basin (Sts. 79, 84). In the central Greenland Sea only single individuals were collected between 500 and 1500 m depth. Therefore, *Pseudochirella spectabilis* is considered an Arctic bathypelagic species.

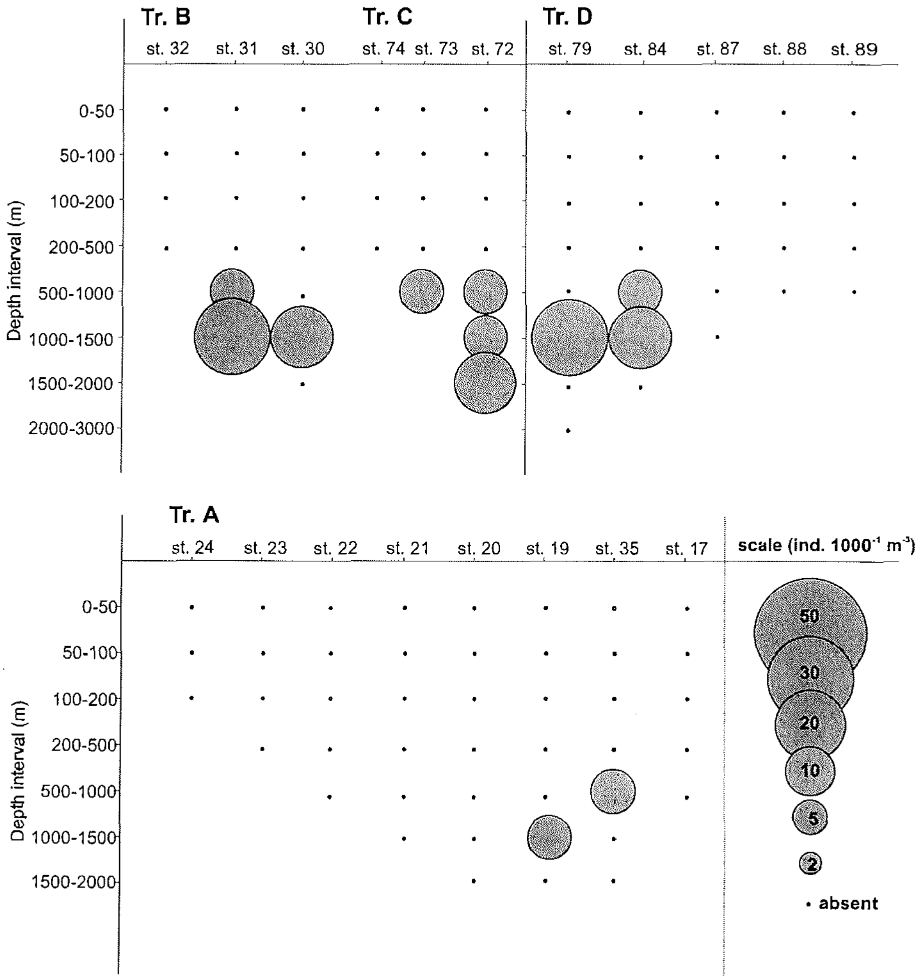

Fig. 20 Vertical distribution and abundance of *Pseudochirella spectabilis* in the Greenland Sea. Circle areas are proportional to abundance. The scale exemplifies certain values for easier interpretation.

4.4 Stage composition

The stage composition of most euchaetids and aetideids did not show clear regional differences. Especially, *Aetideopsis rostrata* (Fig. 21) and the two *Gaetanus* species (Fig. 22, 23) were represented by a constant mixture of all copepodite stages from CI to adults throughout their distribution ranges. *Pareuchaeta polaris*, *Chiridiella abyssalis* and *Pseudochirella spectabilis* were also present with most copepodite stages in the investigation area. The rarity of these species, however, did not allow reliable regional comparisons of stage composition (Figs. 24, 25, 26).

Apart from this general impression, some regional peculiarities in stage composition were detected:

- Adult females and CV dominated the population of *Aetideopsis minor* in the central Greenland Sea by 70 to 100%, whereas younger stages, e.g. CIV on transect B and CIII on transects C and D, were more important on the northern transects (Fig. 27).
- High numbers of young *Chiridius obtusifrons* CIII contributed 50% of the species' abundance over the northern East Greenland shelf (Sts. 73 and 74) (Fig. 28).
- Adult *Pareuchaeta barbata*, both males and females, were more important along the southern transect, e.g. in the central Greenland Sea, than over the Yermak Plateau (Fig. 29).
- Extremely high numbers of young copepodids CI and CII of *Pareuchaeta glacialis* and *P. norvegica* occurred over the Yermak Plateau. At the Sts. 87 and 88 CI and CII stages comprised over 80% of the total population (Fig. 30).

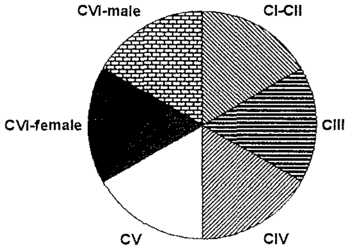

Figure legend for Figs. 21 to 30

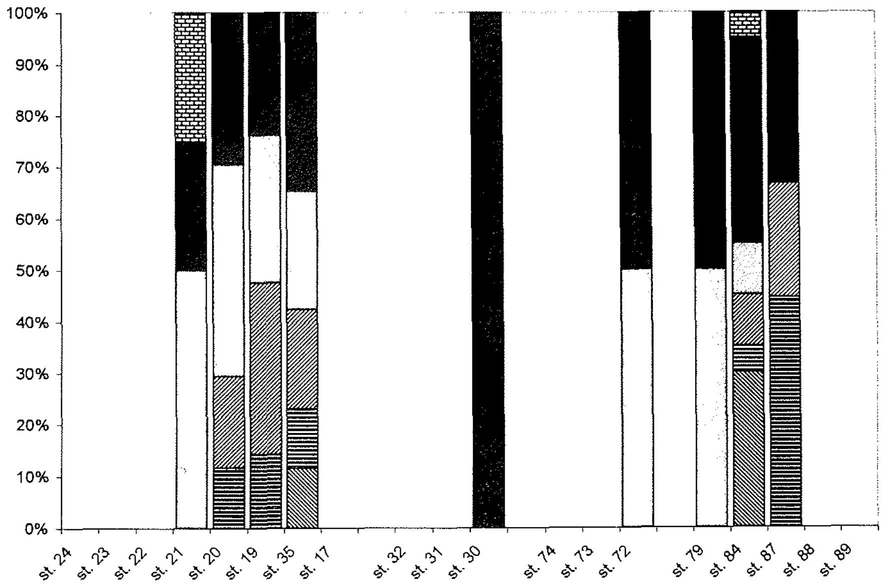

Fig. 21 Stage composition of *Aetideopsis rostrata*

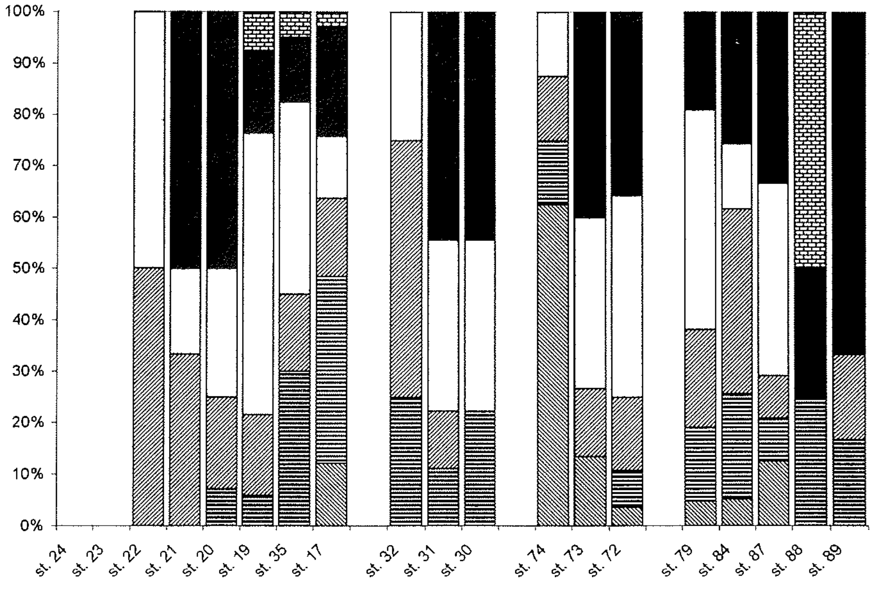

Fig. 22 Stage composition of *Gaetanus brevispinus*

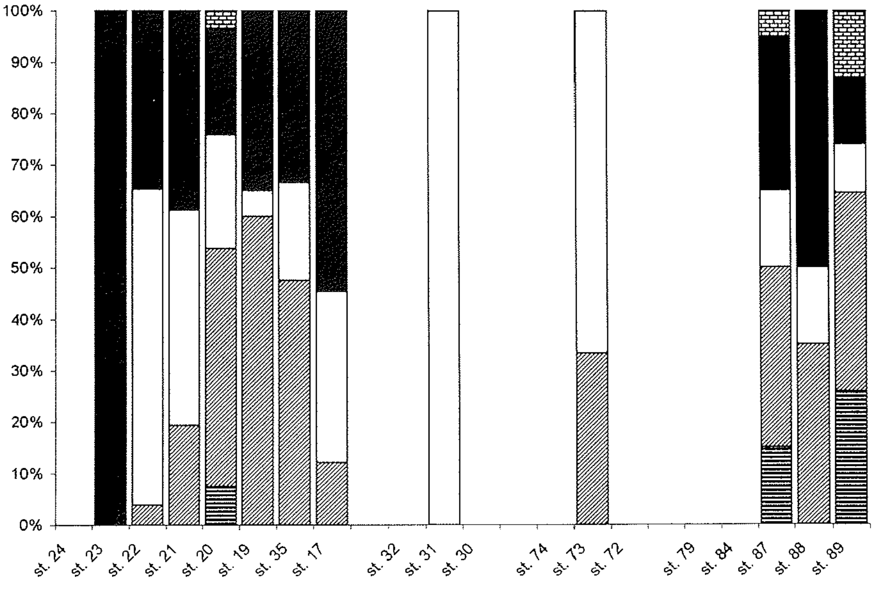

Fig. 23 Stage composition of *Gaetanus tenuispinus*

The interpretation of these data is difficult, since seasonal changes in stage composition cannot be excluded during the two month period of the expedition. The presence of young copepodids throughout the investigation area indicates that all species are able to reproduce under high-Arctic conditions. Reproduc-

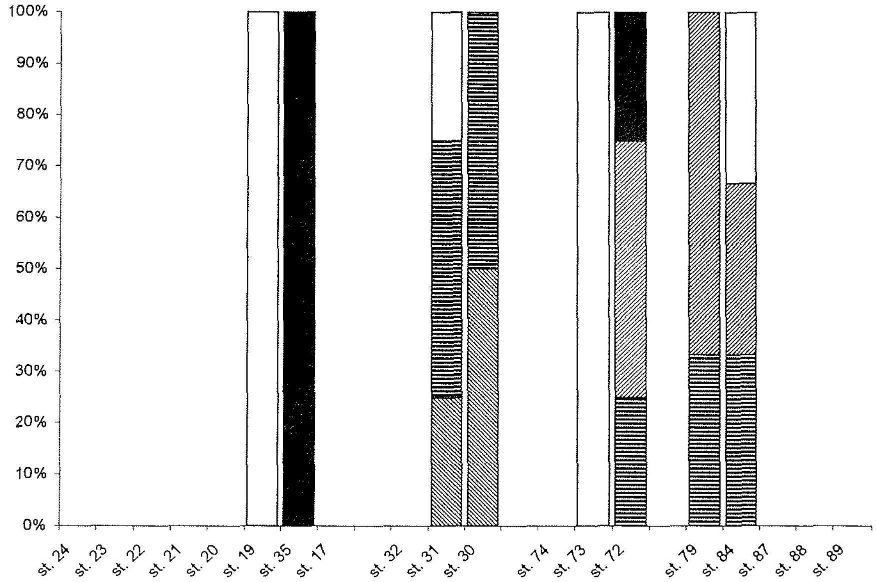

Fig. 24 Stage composition of *Pseudochirella spectabilis*

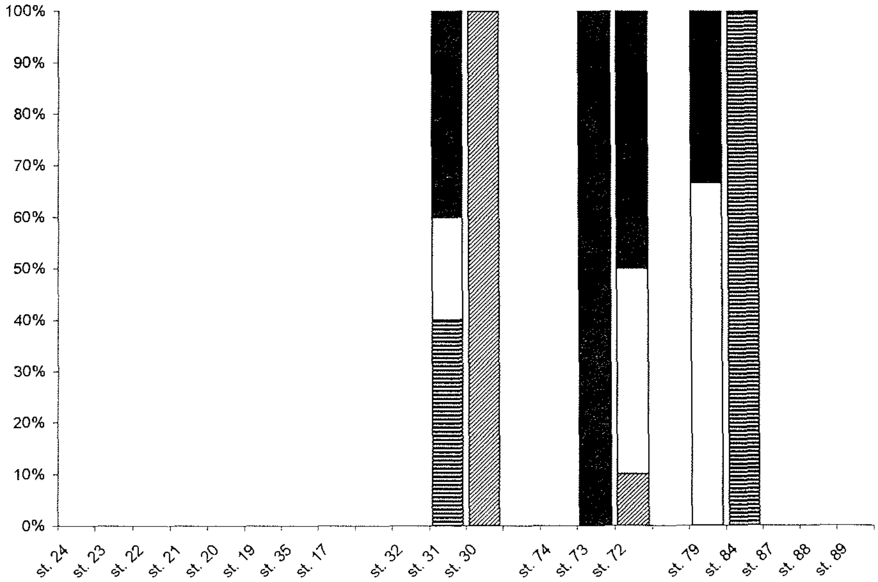

Fig. 25 Stage composition of *Chiridiella abyssalis*

tion of *Aetideopsis minor* and *Chiridius obtusifrons* appears to be even more intense in the northern part than in the central Greenland Sea and for *Pareuchaeta glacialis*/ *P. norvegica* the Yermak Plateau seems to provide an important breeding area.

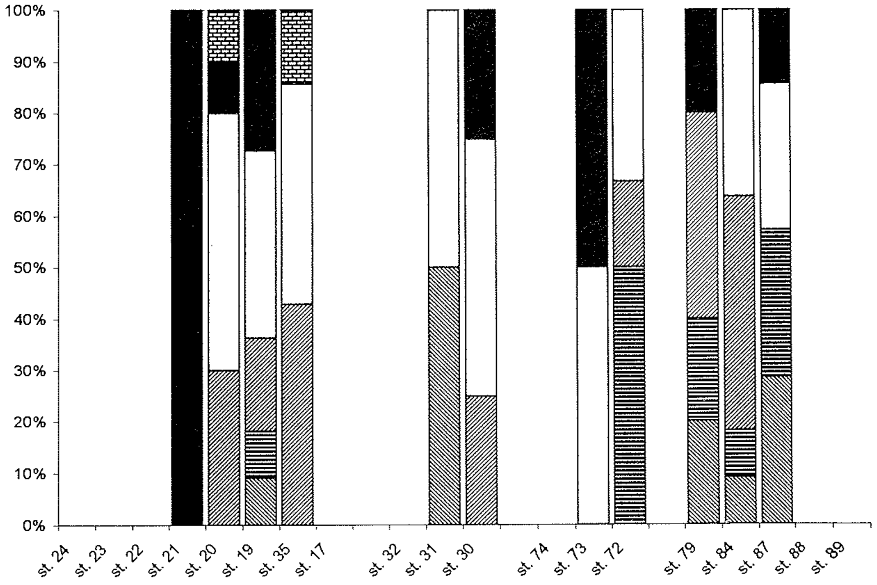

Fig. 26 Stage composition of *Pareuchaeta polaris*

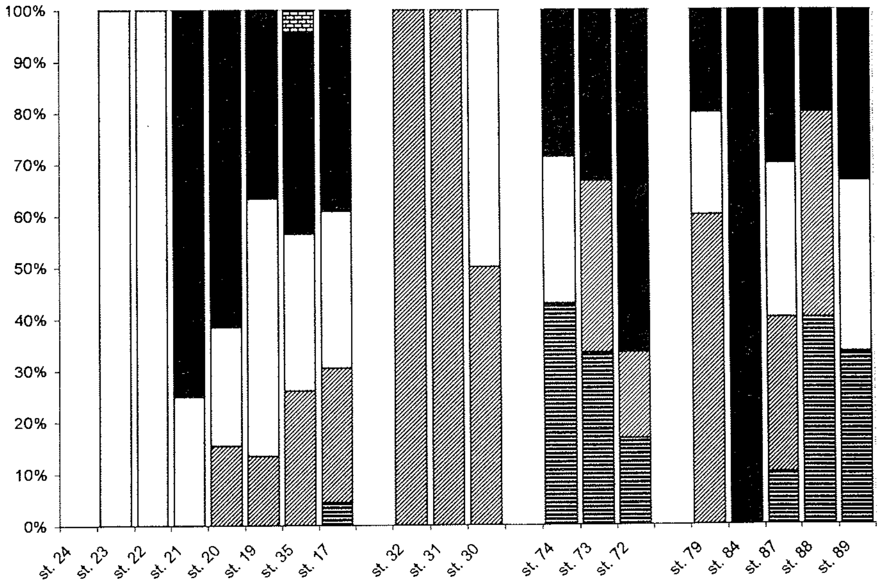

Fig. 27 Stage composition of *Aetideopsis minor*

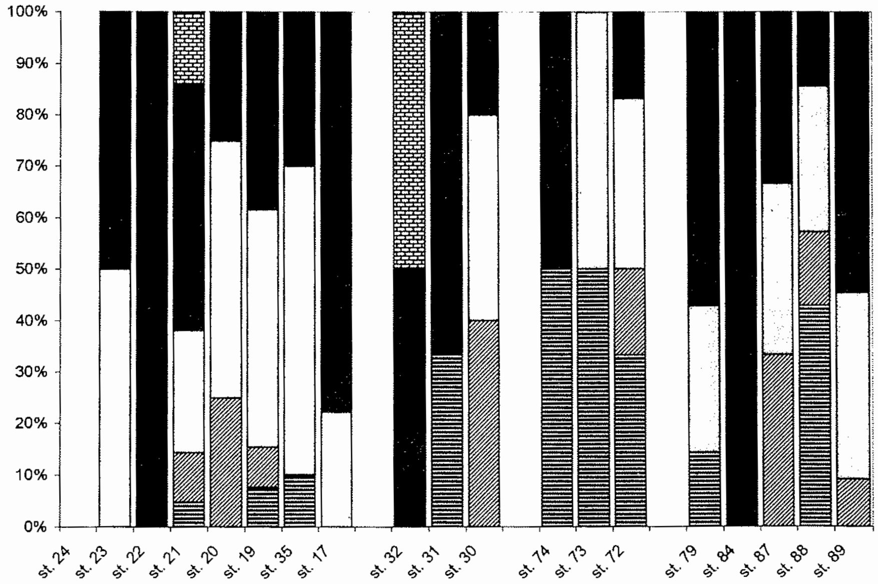

Fig. 28 Stage composition of *Chiridius obtusifrons*

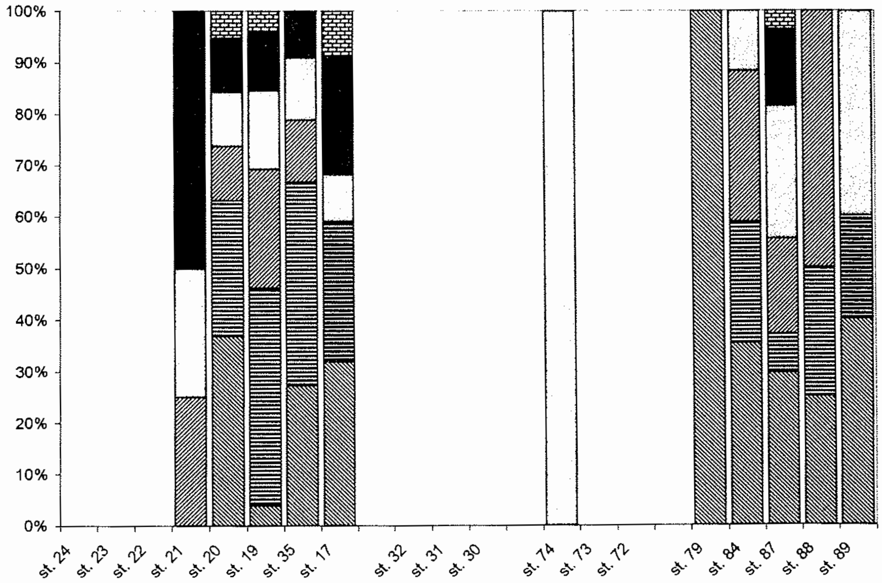

Fig. 29 Stage composition of *Pareuchaeta barbata*

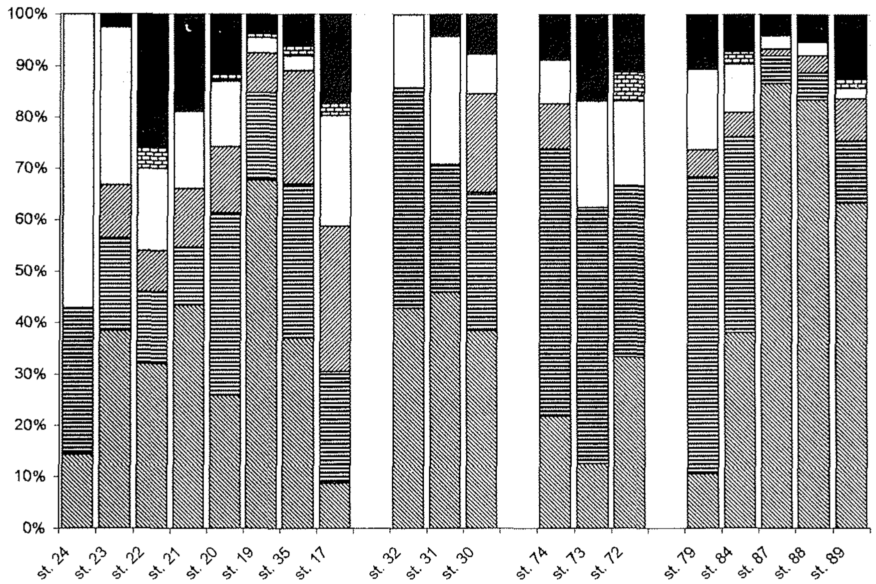

Fig. 30 Stage composition of *Pareuchaeta glacialis* / *P. norvegica*

4.5 Individual dry mass and growth

Individual dry mass values were determined after lyophilisation for all available aetideid and euchaetid species and stages (Tables 3 and 4). The increase of individual dry mass between successive ontogenetic stages ("growth") is illustrated in Figs. 31, 32 and 33.

Pareuchaeta glacialis and *P. norvegica* showed a steady biomass increase throughout the copepodite stages CI to CV (Table 3; Fig. 31). On average, their mass tripled with every moult. The strongest increase occurred from 0.45 mg DM in stage CIV to 1.61 mg DM in CV. Males lost mass compared to copepodids CV, since they have reduced mouthparts and do not feed (c.f. Båmstedt 1975; Mauchline 1998; Shuert & Hopkins 1987; Yen 1991). In contrast, females tripled their mass to a mean dry mass of 3.99 mg in *P. norvegica* and 4.9 mg in *P. glacialis* (Table 3). However, *P. glacialis* females varied considerably in individual dry mass with the largest individuals (>10 mg) weighing four times as much as the smallest specimen (<2.5 mg). Substantial variation between 1.9 mg and 6.2 mg DM also occurred among *P. norvegica* females (Fig. 31).

In *Pareuchaeta barbata* first moults were not associated with an increase in body mass. Nauplii and copepodids CI and CII had similar dry mass values (Table 3). Dry mass started to increase with stage CIII and continued exponentially throughout the following stages (Fig. 31). During the moults towards CIV and CV body mass increased 3.5 times. Like *P. glacialis* and *P. norvegica*, males did not substantially gain body mass in comparison to the CV stage, whereas females grew to a mean dry mass of 9.2 mg (Table 3). The largest specimens of this species exceeded 11 mg DM (Fig. 31).

Table 3: Individual dry mass data of *Pareuchaeta* species and stages in the Greenland Sea

Species	Stage	Individual dry mass (mg)		No. of samples	Total no. of individuals analysed
		Mean	SD		
Pareuchaeta barbata	Egg sac	2.04	0.05	2	32
	Nauplius	0.12	-	1	32
	CI	0.09	-	1	28
	CII	0.13	0.01	2	48
	CIII	0.28	0.03	2	67
	CIV	1.01	0.24	6	89
	CV	3.51	0.96	12	74
	Male	4.02	0.49	2	15
	Female	9.22	1.49	14	66
P. glacialis / norvegica	CI	0.02	0.00	3	93
	CII	0.06	0.02	10	510
	CIII	0.15	0.02	8	435
	CIV	0.45	0.05	6	191
	CV	1.61	0.46	34	424
	Male	1.48	0.34	5	33
P. glacialis	Egg sac	3.12	-	1	9
	Female	4.90	1.76	50	268
P. norvegica	Egg sac	1.36	0.04	2	28
	Female	3.99	0.94	51	312
P. polaris	Egg sac	0.67	-	1	3
	CII	0.14	-	1	6
	CIII	0.23	-	1	11
	CIV	0.63	-	1	23
	CV	1.83	0.39	2	47
	Female	3.47	0.15	2	11

Available results for *Pareuchaeta polaris* indicated that body mass did not substantially increase before the moult from CIII to CIV, although data on copepodite stage CI were lacking. The highest gain in dry mass occurred after the moult to stage CV (Table 3; Fig. 31). Compared to other congeners, growth from CV to adult females was relatively weak. In contrast to *P. glacialis* and *P. norvegica*, early stages (CII to CIV) of *P. polaris* were extremely large, whereas adults were considerably smaller. Thus, the total increase in individual biomass throughout the ontogenetic development was relatively poor.

The aetideid species *Aetideopsis minor*, *A. rostrata*, *Chiridius obtusifrons*, *Gaetanus brevispinus* and *G. tenuispinus* showed similar developments in body mass (Table 4, Fig. 32). In general, they doubled dry mass between successive copepodite stages. Compared to their respective mesopelagic congeners, however, the bathypelagic *A. rostrata* and *G. brevispinus* reached substantially larger sizes. Major differences also accompanied the last moult in males. *C. obtusifrons* and *G. tenuispinus* males remained at the mass of CV, whereas *G. brevispinus* and especially *A. rostrata* males considerably increased their body mass (Table 4; Fig. 32).

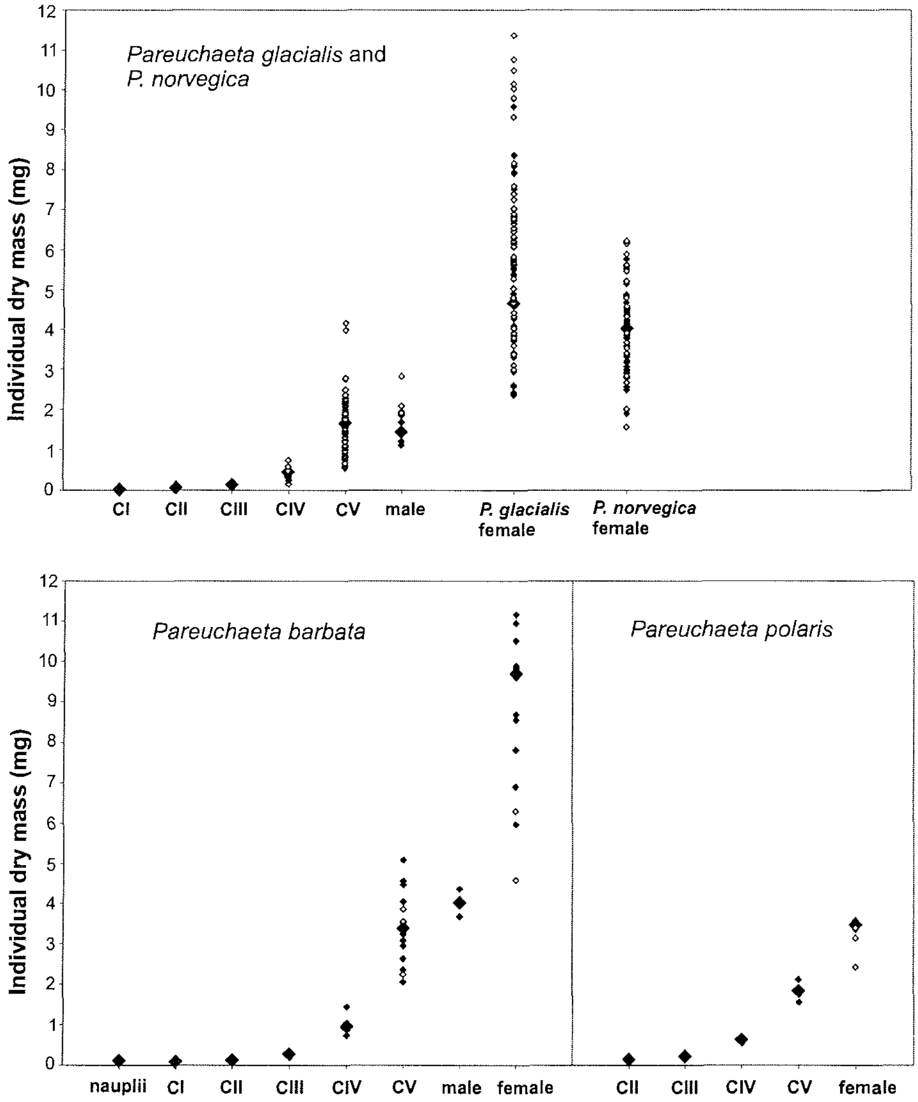

Fig. 31 Individual dry mass of *Pareuchaeta* species and stages. *black*: data from the Greenland Sea (ARK XIII/1+2), *white*: data from the central Arctic Ocean (ARK XII), *bold*: mean for Greenland Sea data

In comparison to other Aetideidae, *Chiridiella abyssalis* was characterised by very large CIII and CIV stages, but relatively light adult females (Fig. 32). This combination led to a relatively stable body mass throughout the ontogenetic development. Conversely, the moult from CIV to CV of *Pseudochirella spectabilis* was combined with an exceptional gain in mass. Copepodids CIV increased their mass of 0.52 mg DM nearly four times to 1.99 mg DM in the successive CV (Fig. 33). This strong growth made adult *P. spectabilis* females (3.88 mg DM) by far the largest Arctic Aetideidae.

Table 4 Individual dry mass data of aetideid species and stages in the Greenland Sea

Species	Stage	Individual dry mass (mg)		Number of samples	Total no. of individuals analysed
		Mean	SD		
Aetideopsis minor	CIII	0.05	-	1	10
	CIV	0.09	-	1	28
	CV	0.20	0.01	2	70
	Female	0.41	0.04	4	108
Aetideopsis rostrata	CII	0.06	-	1	6
	CIII	0.08	-	1	16
	CIV	0.16	-	1	30
	CV	0.41	0.02	2	54
	Male	0.62	-	1	24
	Female	0.60	0.02	3	72
Chiridius obtusifrons	Egg sac	0.17	-	1	14
	CIII	0.05	-	1	16
	CIV	0.11	-	1	32
	CV	0.27	0.02	3	109
	Male	0.26	-	1	3
	Female	0.64	0.08	8	226
Gaetanus brevispinus	CI	0.04	-	1	19
	CII	0.07	-	1	3
	CIII	0.08	0.01	3	79
	CIV	0.18	0.02	4	144
	CV	0.51	0.04	10	312
	Male	0.61	-	1	10
	Female	0.91	0.11	12	324
Gaetanus tenuispinus	CIII	0.05	-	1	13
	CIV	0.11	0.01	4	136
	CV	0.24	0.03	5	185
	Male	0.23	-	1	5
	Female	0.50	0.04	6	240
Chiridiella abyssalis	CIII	0.23	-	1	3
	CIV	0.24	-	1	2
	CV	0.30	-	1	6
	Female	0.31	-	1	11
Pseudochirella spectabilis	CII	0.11	-	1	2
	CIII	0.22	-	1	7
	CIV	0.52	-	1	8
	CV	1.99	-	1	5
	Female	3.88	-	1	7

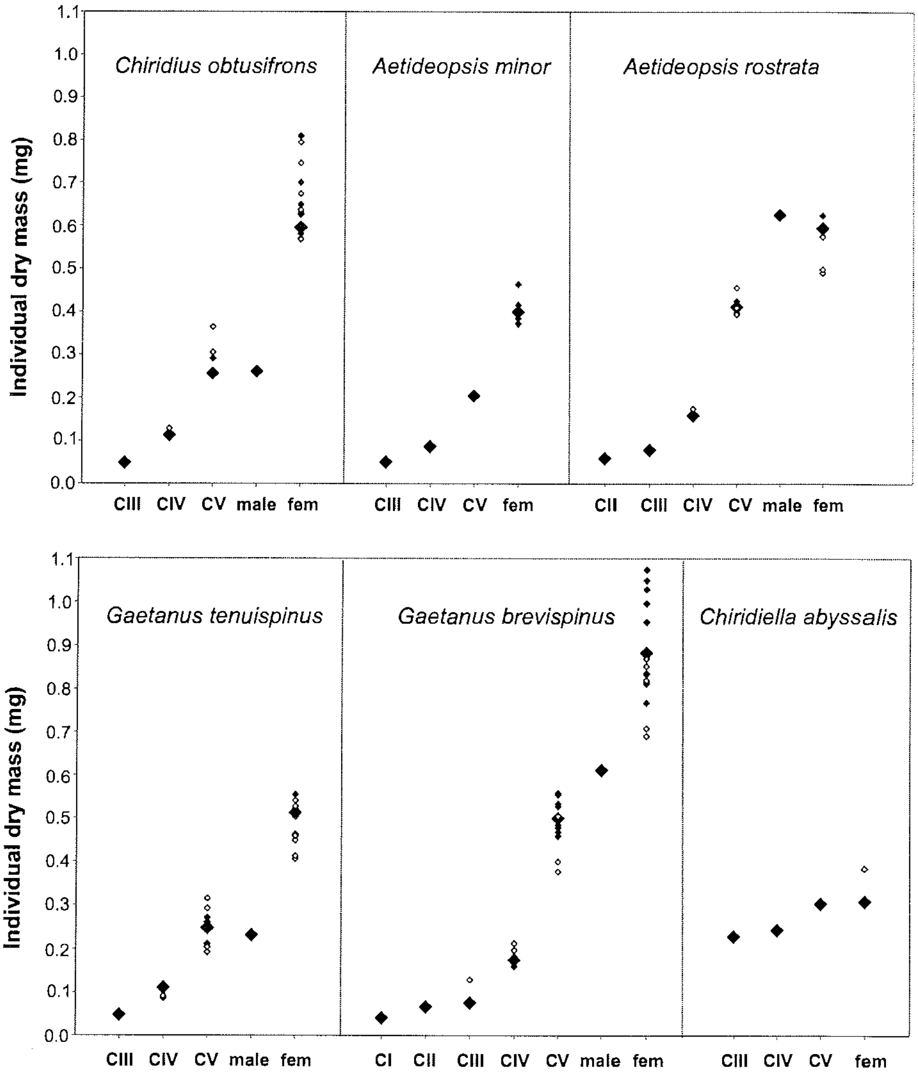

Fig. 32 Individual dry mass of aetideid species and stages. *black*: data from the Greenland Sea (ARK XIII/1+2), *white*: data from the central Arctic Ocean (ARK XII), *bold*: mean for Greenland Sea data

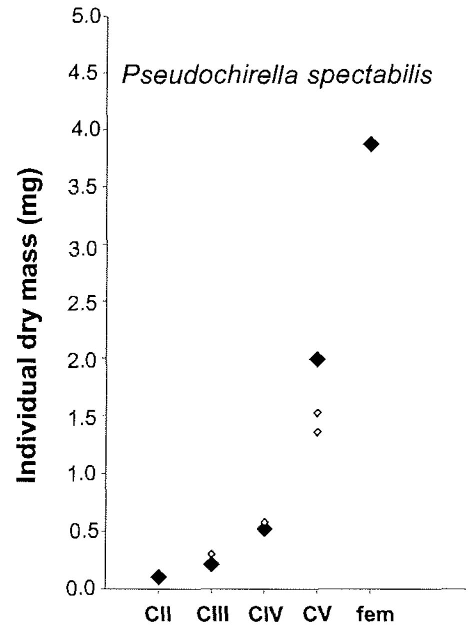

Fig. 33 Individual dry mass of *Pseudochirella spectabilis*. *black*: data from the Greenland Sea (ARK XIII/1+2), *white*: data from the central Arctic Ocean (ARK XII), *bold*: mean for Greenland Sea data

4.6 Total lipid content

In all *Pareuchaeta* species total lipid content displayed a characteristic trend during ontogenetic development. Eggs were very rich in lipid (59 to 93% of DM), resulting in high lipid contents (70%) of nauplii and copepodite stages CI (Table 5; Fig. 34). During subsequent development lipid reserves dramatically decreased to less than 20% in copepodite stage CIII of *Pareuchaeta glacialis* and *P. norvegica* or less than 30% in *P. barbata* CIV. Later stages again accumulated lipids, so that adult females contained high lipid amounts of more than 30% in *P. glacialis* and 40 to 50% in the other congeners.

The depletion in lipid content from the egg to copepodite stage CIII or CIV indicates that early development is largely fuelled by lipid reserves stored in the eggs. Especially bathypelagic *Pareuchaeta barbata* and *P. polaris* seem to depend strongly on stored energy reserves for development. Their delayed growth (see chapter 4.5) and prolonged lipid decomposition until CIV indicate that active feeding of young copepodids is only of limited importance for their energy budget. In contrast, *P. glacialis* and *P. norvegica* start continuous growth earlier and accumulate new lipid reserves already from CIII onwards. Thus, copepodids of these epi- to mesopelagic congeners probably start planktivorous feeding at a younger stage, and ingestion may account for a larger fraction of the developmental energy demands.

Aetideid copepods were generally characterised by low to moderate lipid amounts of 10 to 30% of DM (Table 5). They showed a different trend in lipid content during their ontogenetic development compared to the Euchaetidae (Fig. 35). In most species, e.g. *Chiridius obtusifrons*, *Aetideopsis rostrata*, *Gae-*

Table 5 Total lipid content of *Euchaetidae* and *Aetideidae* in the Greenland Sea

		Total lipid content (% of body DM)		Number of samples	Total no.of individuals analysed
		Mean	SD		
Pareuchaeta barbata	Egg sac	59.7	0.6	2	32
	Nauplius	81.9	-	1	32
	CI	67.3	-	1	28
	CII	37.1	-	1	48
	CIII	27.4	6.2	2	67
	CIV	26.4	5.6	5	88
	CV	35.4	4.9	7	66
	Male	40.8	2.1	2	15
	Female	43.8	3.6	11	62
P. glacialis / norvegica	CI	70.0	-	1	93
	CII	27.6	4.3	3	405
	CIII	15.3	3.7	4	435
	CIV	19.9	6.6	6	191
	CV	37.0	9.1	22	383
	Male	44.8	8.5	4	33
P. glacialis	Egg sac	63.8	-	1	9
	Female	33.9	8.4	28	255
P. norvegica	Egg sac	59.0	0.9	2	28
	Female	42.2	7.0	31	300
P. polaris	Egg sac	93.1	-	1	3
	CIV	42.4	-	1	23
	CV	43.0	5.2	2	47
	Female	50.5	4.5	2	11
Aetideopsis minor	CV	22.2	-	1	70
	Female	23.4	6.1	3	108
Aetideopsis rostrata	CIV	28.7	-	1	30
	CV	26.9	2.2	2	54
	Male	21.0	-	1	24
	Female	19.6	2.6	3	72
Chiridius obtusifrons	Egg sac	71.9	-	1	14
	CIV	34.7	-	1	32
	CV	26.1	2.7	3	109
	Female	18.7	7.7	8	226
Gaetanus brevispinus	CIII	26.4	-	1	79
	CIV	18.2	3.9	2	144
	CV	21.4	4.4	10	312
	Male	48.5	-	1	10
	Female	12.0	1.7	11	322
Gaetanus tenuispinus	CIV	17.0	3.9	2	136
	CV	18.8	5.0	5	185
	Female	11.6	2.2	6	240
Chiridiella abyssalis	Female	62.9	-	1	11
Pseudochirella spectabilis	CIV	20.8	-	1	8
	CV	48.7	-	1	5
	Female	30.3	-	1	7

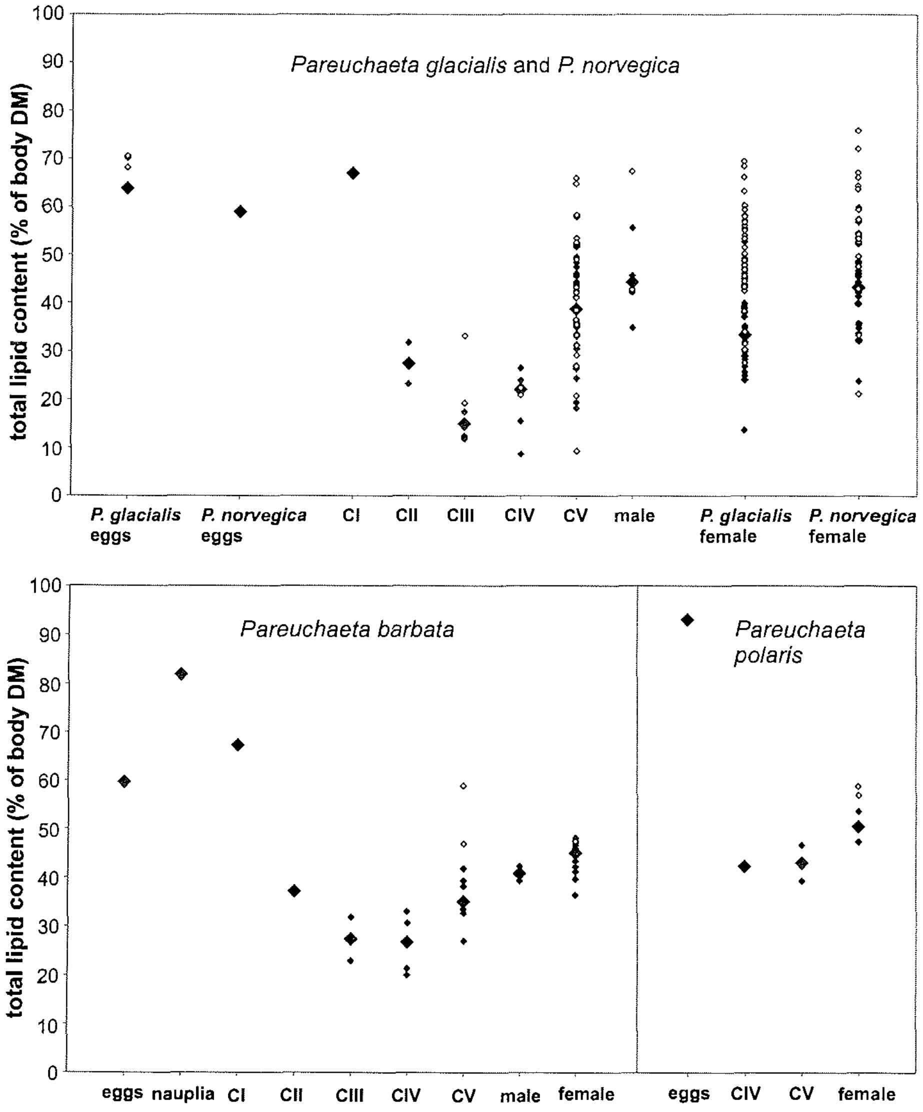

Fig. 34 Total lipid content of *Pareuchaeta* species and stages. *black*: data from the Greenland Sea (ARK XIII/1+2), *white*: data from the central Arctic Ocean (ARK XII), *bold*: mean for Greenland Sea data

tanus brevispinus and *G. tenuispinus*, total lipid content decreased from relatively high levels in eggs (*C. obtusifrons*) and young copepodite stages towards minimum amounts in adult females (Fig. 35). This ontogenetic decline was most pronounced in *C. obtusifrons*, where the lipid content of copepodids CIV was twice as high as that of females. Limited sample numbers of *A. minor*, *Chiridiella abyssalis* and *Pseudochirella spectabilis* prohibited detailed investigations of ontogenetic trends. However, exceptionally high lipid amounts of more than 48% and 62%, respectively, occurred in *G. brevispinus* males, *Pseudochirella spectabilis* CV and *Chiridiella abyssalis* females.

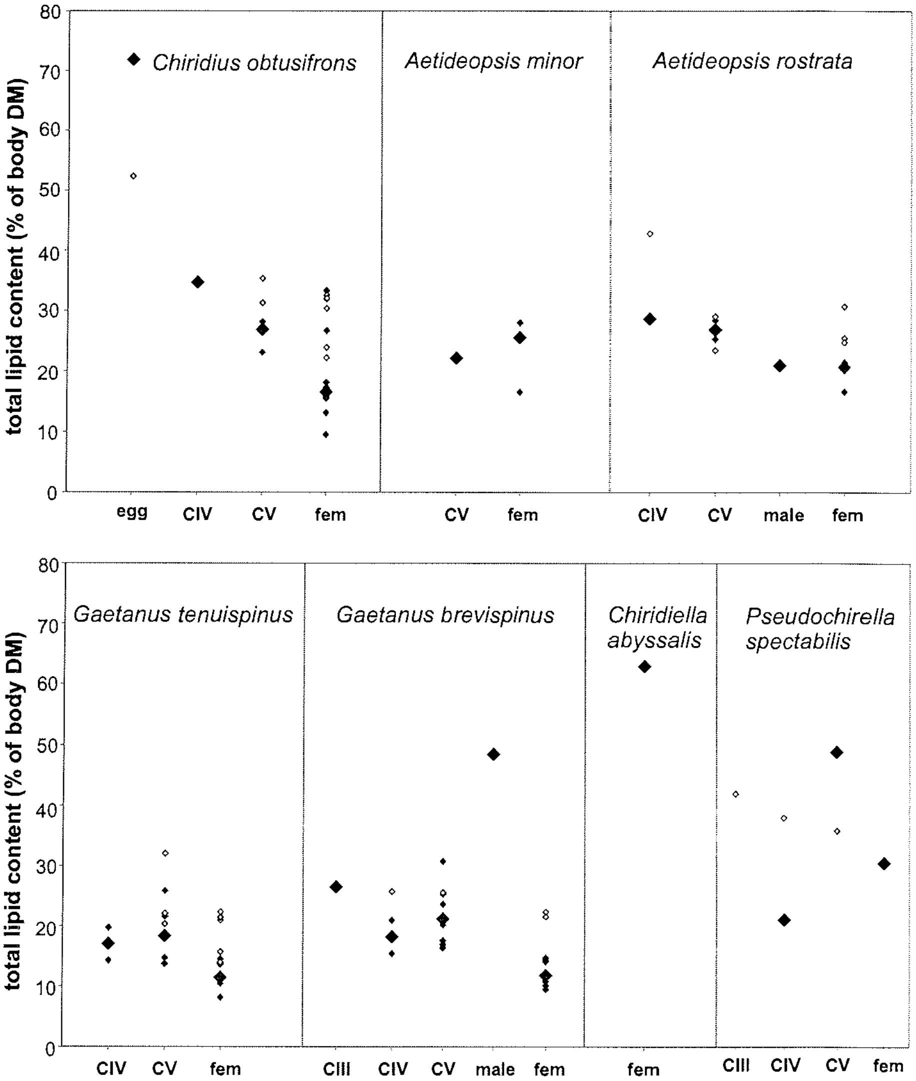

Fig. 35 Total lipid content of aetideid species and stages. *black*: data from the Greenland Sea (ARK XIII/1+2), *white*: data from the central Arctic Ocean (ARK XII), *bold*: mean for Greenland Sea data

4.7 Fatty acid and alcohol composition

The fatty acid and alcohol compositions of body lipids were analysed by gas-liquid-chromatography. A total of 16 samples was processed including females of three euchaetid and six aetideid species. In addition, the lipid compositions of male *Aetideopsis rostrata*, *Pareuchaeta barbata* and *P. glacialis/ norvegica*, as well as *P. glacialis /norvegica* CIII were analysed.

In comparison to standards of known composition, 30 fatty acids and five fatty alcohols were identified, accounting for more than 90% of the signal strength measured. 22 fatty acids only occurring in traces of less than 3% were omitted from the further analysis. The dominant fatty acids and fatty alcohols are listed in Table 6.

Table 6 Fatty acid and alcohol (A) composition of Aetideidae and Euchaetidae. Figures describe the fraction (%), which a certain fatty acid or alcohol contributes to the total fatty acid or alcohol content, respectively. The ratio given in the last row is a dimensionless coefficient. Fem.= female

	A. minor	*A. rostrata*		*C. obtusifrons*	*G. brevispinus*	*G. tenuispinus*	*P. spectabilis*
	Fem.	Fem.	Male	Fem.	Fem.	Fem.	Fem.
14:0	4.7	3.9	3.6	5.6	2.2	2.8	7.5
16:0	13.0	8.1	10.4	9.6	6.6	11.3	11.0
16:1(n-7)	6.9	8.2	6.4	7.5	6.6	5.8	8.2
18:1(n-7)	3.5	4.2	4.0	7.5	2.7	3.4	5.1
18:1(n-9)	11.4	11.2	11.6	9.4	17.6	16.7	17.9
20:1(n-9)	16.2	14.8	15.0	13.0	7.4	7.5	11.5
22:1(n-11)	14.6	12.5	11.3	11.7	7.0	4.9	9.9
20:5(n-3)	6.7	8.6	8.5	9.8	7.5	17.1	5.8
22:6(n-3)	7.0	10.6	11.6	8.0	14.1	14.1	7.2
14:0 A	14.8	7.8	22.9	15.3	19.4	9.7	9.8
16:0 A	12.2	7.1	31.2	11.3	21.2	41.0	17.0
16:1 A	1.3	1.1	0.0	10.7	1.1	1.8	1.0
20:1 A	38.2	35.1	12.6	33.4	21.4	19.3	27.0
22:1 A	33.6	49.0	33.3	29.3	28.2	18.4	38.5
Ratio 18:1(n-9) / 18:1(n-7)	3.3	2.7	2.9	1.3	6.5	4.9	3.5

	P. barbata			*P. glacialis*		*P. norvegica*		*P. glacialis/ norvegica*	
	Fem.	Fem.	Male	Fem.	Fem.	Fem.	Fem.	CIII	Male
14:0	1.6	2.7	1.0	3.7	4.3	3.4	2.5	1.6	2.7
16:0	3.1	3.9	1.7	2.0	2.5	2.5	2.0	6.1	1.8
16:1(n-7)	21.5	22.6	20.0	15.4	27.0	24.1	13.6	12.2	23.7
18:1(n-7)	1.2	1.6	0.5	0.8	1.0	1.0	0.9	1.5	0.8
18:1(n-9)	26.2	22.0	30.9	21.0	26.1	19.0	14.3	18.4	26.8
20:1(n-9)	8.5	9.3	6.5	19.8	7.7	9.1	15.4	10.1	6.4
22:1(n-11)	6.5	8.1	2.3	16.7	4.8	11.7	25.5	5.5	1.7
20:5(n-3)	4.1	4.8	4.7	3.2	4.9	5.7	4.3	8.3	4.6
22:6(n-3)	4.0	3.3	5.2	4.1	5.2	5.5	4.6	13.4	5.6
14:0 A	28.4	31.5	23.3	33.9	56.8	49.0	24.4	19.1	35.6
16:0 A	15.1	16.9	20.2	16.9	17.1	15.8	18.9	21.4	25.1
16:1 A	4.3	3.9	4.4	3.9	4.5	3.0	2.4	4.0	5.0
20:1 A	17.2	16.2	21.9	26.0	10.0	15.8	27.8	25.6	23.8
22:1 A	25.5	23.0	20.0	15.5	9.3	12.5	22.6	22.8	5.5
Ratio 18:1(n-9) / 18:1(n-7)	21.8	13.8	61.8	26.3	26.1	19.0	15.9	12.3	33.5

The lipid composition of *Pareuchaeta* adults was characterised by a strong dominance of only a few fatty acids. Usually, the fatty acids 16:1(n-7) and 18:1(n-9) each contributed more than 20% and together comprised about half of all fatty acids. Some variability occurred in *Pareuchaeta glacialis* and *P. norvegica* females, when the share of 16:1(n-7) and 18:1(n-9) was reduced and 20:1(n-9) and 22:1(n-11) became equally important. These long-chained monounsaturated fatty acids are typical components of herbivorous *Calanus* species. Therefore, high values occurring in carnivorous *P. glacialis* and *P. norvegica* probably reflect predator-prey relationships.

In contrast, aetideid body lipids were less dominated by certain fatty acids. They consisted mainly of a mixture of 16:0, 18:1(n-9), 20:1(n-9), 22:1(n-11) and 22:6(n-3). None of these species comprised more than 18% and other fatty acids, e.g. 18:1(n-7) and 20:5(n-3), were more important than in *Pareuchaeta*.

Considerable interspecific differences in the content of fatty acid biomarkers were detected between the genera. The lowest concentration of 18:1(n-9) generally considered as indicative for a carnivorous diet was measured in *Chiridius obtusifrons* females (9.4%). *Aetideopsis minor* and *A. rostrata* showed slightly higher values of more than 11%, whereas *Gaetanus brevispinus*, *G. tenuispinus* and *Pseudochirella spectabilis* accumulated amounts of 17%. Considerably higher values of 21 to 36% occurred in *Pareuchaeta glacialis* and *P. barbata* females. In *P. norvegica* females the value varied between 14% and 19%, whereas *Pareuchaeta* males showed the highest concentrations of 18:1(n-9) reaching 30%.

No clear trends emerged with regard to the concentration of 16:1(n-7) and 18:1(n-7) generally considered as typical biomarkers for diatoms. Small amounts (<1.6%) of 18:1(n-7) were detected in *Pareuchaeta* spp. Slightly higher levels of 6 to 8% occurred in aetideids. Conversely, 16:1(n-7) was less important in aetideids (3 to 8%) than in euchaetids (12 to 27%).

The concentrations of 20:1(n-9) and 22:1(n-11), which are typical components of body lipids from herbivorous *Calanus*, varied both between species and samples. *Pareuchaeta* males showed the lowest concentrations of these fatty acids. Low amounts were also detected in *P. barbata* and *Gaetanus* females, while moderate levels were measured in *Aetideopsis* spp. The highest concentrations and greatest variability occurred in *P. glacialis* and *P. norvegica* females and indicated predation on herbivorous Calanidae.

The ratio between the isomers 18:1(n-9) and 18:1(n-7) has been proposed as a relative measure for carnivory (Graeve et al. 1997). Low ratios indicate dietary compositions dominated by phytoplankton, whereas high values are indicative of a more carnivorous diet. *Chiridius obtusifrons* showed the lowest ratio of 1.3 in the present study. Higher values around 3 were determined in *Aetideopsis* spp. and *Pseudochirella spectabilis*. Among aetideid copepods *Gaetanus* spp. had the highest values of 5 to 6.5. In contrast, all Euchaetidae showed significantly higher values. Ratios increased from 12 in *Pareuchaeta glacialis/ norvegica* CIII, via *P. norvegica* females (12 to 16) and *P. barbata* females (14 to 22) to 26 in *P. glacialis* females. Extraordinarily high values were calculated for the non-feeding males of *P. glacialis/ norvegica* (33) and *P. barbata* (62). The relatively low ratio in *P. glacialis/norvegica* CIII might indicate that young stages of these epi- to mesopelagic species partly feed on phytoplankton.

Fatty alcohols are major components of wax esters. High amounts of the fatty alcohols 14:0, 16:0, 20:1 and 22:1 in all aetideid and euchaetid species analysed during the present study indicate that these species mainly synthesise wax esters as lipid reserves.

4.8 Reproductive strategies

Pareuchaeta species as well as some aetideid species, e.g. *Chiridius obtusifrons*, differ from the dominant herbivorous *Calanus* species in the way they care for their offspring. Females produce egg sacs and carry their clutches attached to the genital opening until the offspring hatches. Other Arctic aetideid species are known to release their eggs directly into the water.

Under laboratory conditions during the present study, however, it was observed that eggs of *Aetideopsis minor* also stuck to each other and stayed attached to their mother's genital somite, apparently similar to the egg sacs produced by *Chiridius obtusifrons*. Unlike *C. obtusifrons*, however, egg masses of *A. minor* were fragile and easily torn off. Therefore, it is uncertain whether *A. minor* produces attached egg masses only under sheltered laboratory conditions or also in the wild. Rough sampling procedures may destroy the fragile egg masses or detach them from the females, so that they are not usually found in mesozooplankton net samples.

In case of the more stable egg sacs of *Pareuchaeta* species and *Chiridius obtusifrons* various parameters were measured to evaluate the energetic investment of females in egg production and to elucidate different reproduction strategies (Table 7).

The fraction of females carrying egg sacs strongly differed between the four *Pareuchaeta* species. Among the bathypelagic *P. barbata* and *P. polaris* half to two thirds of all females had egg sacs attached to their genital somite. In contrast, only 11.5% of *P. glacialis* and 17.0% of *P. norvegica* females carried eggs. For *Chiridius obtusifrons* the fraction was even lower (8.4%). The extremely low value of 2.7% for *Aetideopsis minor* is probably the consequence of the highly fragile egg masses as explained above. Variations in the frequency of egg-carrying females may be explained by different breeding seasons or a reduced developmental speed in bathypelagic species, resulting in prolonged time periods until hatching.

Egg size, measured as diameter or dry mass, was not correlated with female size, since *Pareuchaeta polaris*, the smallest of the four congeners, produced larger eggs than *P. glacialis* or *P. norvegica*. Moreover, larger egg size in *P. polaris* was accompanied by extraordinarily high lipid contents of more than 90%, resulting in an elevated caloric content of 38.3 kJ g^{-1} (Table 7).

Table 7 Size and caloric content of eggs and clutches for copepod species with egg sacs

	Egg colour	Frequency of females carrying egg sacs (%)	Egg diameter (µm)	Egg number per clutch	Dry mass of clutch (mg)	Dry mass of egg (mg)	Lipid content of eggs (% DM)	Caloric content of eggs (kJ/g)	Energy ratio E_{egg}/E_{female} (%)	Energy ratio E_{clutch}/E_{female} (%)
Pareuchaeta polaris	violet	52.6	713 - 760	4 - 6 median 6	0.67	0.11	93.1	38.3	4.0	24.5
P. barbata	dark brown	66.7	665 - 831	10 - 19 median 15.5	2.00 - 2.07	0.13	59.7	31.9	1.5	23.1
P. glacialis	dark brown to black	11.5	428 - 523	46 - >50	3.12	0.06	63.8	32.7	1.6	81.5
P. norvegica	light blue	17.0	285 - 428	37 - >50	1.33 - 1.39	0.03	59.0	31.8	0.8	37.4
Chiridius obtusifrons	pink	8.4	238	22 - 34	0.17	<0.01	71.9	34.2	2.5	41.7
Aetideopsis minor	pink	(2.7)	-	see text	-	-	-	-	-	-

Apparently, the number of eggs per clutch was negatively correlated with depth of occurrence. Thus, egg numbers decreased from 40 to >50 per clutch in epipelagic *Pareuchaeta glacialis* and *P. norvegica* to less than 20 or 6, respectively, in the deep-sea congeners *P. barbata* and *P. polaris*. In relation to their body mass, *P. glacialis* females produced the largest clutches, exceeding 3 mg DM, which is equivalent to more than two thirds of the female's dry mass or 81.5% of the female's energy content.

Energetic investment per egg, however, was highest in *Pareuchaeta polaris*. Large size and high lipid content required 4% of the female's energy per egg. In contrast, other congeners invested only 0.8 to 1.6% of their energy into single eggs.

These results reveal pronounced differences in the reproductive strategies of epi- to mesopelagic and bathypelagic congeners. The deep-sea species *P. barbata* and, in particular, *P. polaris* produce low numbers of large eggs with relatively high energy content, whereas epi- to mesopelagic *P. glacialis* and *P. norvegica* produce high numbers of smaller eggs, resulting in a substantially higher energetic investment for the whole clutch.

Based on these data, it can be assumed that bathypelagic *P. polaris* and *P. barbata*, which invest less than a quarter of their body energy per clutch, can rely primarily on lipid reserves to fuel egg production. In contrast, high investments of 81.5% of body energy per clutch in *P. glacialis* are only possible if sufficient food is available.

4.9 Respiration rates

A total of 141 respiration measurements were conducted, including females of all *Pareuchaeta* species, *Pseudochirella spectabilis*, *Aetideopsis minor* and *A. rostrata*. Additionally, respiration rates of *Gaetanus brevispinus*, *P. spectabilis* and *P. barbata* CV and *P. barbata* CIV were measured (Table 8). As expected, absolute oxygen consumption increased with increasing body mass, whereas mass-specific respiration rates decreased with increasing body mass. Small aetideids, e.g. *Aetideopsis* and *Gaetanus*, and *P. barbata* CIV with body masses <0.51 mg C had high mass-specific respiration rates of more than 0.0065 d^{-1}, whereas larger *Pareuchaeta* and *Pseudochirella* (>1 mg C) showed lower rates of less than 0.0039 d^{-1}.

Ripe *Pareuchaeta glacialis* females had considerably higher oxygen demands than the average of all females, indicating that the production of eggs is a very energy-consuming process. However, this observation is based only on a limited number of measurements. The relatively high respiration rates of individuals carrying egg sacs may be explained by higher energetic costs for swimming against the increased drag created by the large egg sac.

Table 8 Respiration rates of Aetideidae and Euchaetidae. MSRR = mass-specific respiration rate

Species	Stage	n	Individual respiration rate				Dry mass	MSRR
			(µg O_2 h^{-1})		(µg C d^{-1})		(mg C)	(d^{-1})
			Mean ± SD	Max.	Mean	Max.		
Aetideopsis minor	female	4	0.37 ± 0.19	0.57	2.7	4.2	0.20	0.0133
Aetideopsis rostrata	female	3	0.28 ± 0.14	0.43	2.1	3.2	0.30	0.0069
Gaetanus brevispinus	CV	3	0.27 ± 0.11	0.38	2.0	2.8	0.25	0.0079
Pseudochirella spectabilis	CV	2	0.40 ± 0.02	0.42	3.0	3.1	1.00	0.0030
	female	5	0.47 ± 0.33	0.90	3.5	6.7	1.94	0.0018
Pareuchaeta barbata	CIV	3	0.44 ± 0.25	0.63	3.3	4.6	0.51	0.0065
	CV	5	0.91 ± 0.46	1.62	6.7	12.0	1.76	0.0038
	female	13	0.64 ± 0.43	1.49	4.7	11.0	4.61	0.0010
Pareuchaeta glacialis	female	82	0.58 ± 0.46	2.27	4.3	16.7	2.45	0.0018
	ripe female	2	1.29 ± 1.10	2.07	9.5	15.3	2.45	0.0039
	with egg sacs	12	0.87 ± 0.64	2.26	6.4	16.7	2.45	0.0026
Pareuchaeta norvegica	female	4	0.68 ± 0.78	1.83	5.0	13.5	2.00	0.0025
Pareuchaeta polaris	female	3	0.25 ± 0.13	0.39	1.8	2.9	1.74	0.0010

4.10 Ingestion rates of *Pareuchaeta glacialis* and *P. norvegica*

Ingestion rates of *Pareuchaeta norvegica* females as well as of *P. glacialis* females and CV were measured in feeding experiments with *Calanus* copepodids as prey. A total of 15 replicates were conducted with females of each species and two experiments with *P. glacialis* CV. However, only one third of the *P. glacialis* females actually fed, whereas all experiments with *P. norvegica* were successful. Replicates without feeding activity during the experimental period were excluded from the analysis.

Daily feeding rates of *Pareuchaeta norvegica* varied between 0.25 and 2.3 prey organisms per predator and day, equivalent to an average carbon ingestion of 0.15 ± 0.12 mg C d^{-1} or a mean turnover of 6.7% of body mass per day (Table 9). Predation rates of 0.5 to 1 ind. prey d^{-1} in *P. glacialis* females fell into the range determined for *P. norvegica* and resulted in an individual daily carbon ingestion of 0.12 ± 0.06 mg C d^{-1}, also similar to that of the congener.
However, mean turnover rates of less than 4% of body mass per day were considerably lower, since *P. glacialis* females were on average larger than individuals of *P. norvegica*. Moreover, the higher mean of 6.7% d^{-1} for *P. norvegica* was at least partly affected by the extraordinarily high maximum of 23.17% d^{-1}. The two replicates with *P. glacialis* CV showed very similar results. Predation rates of 0.25 and 0.29 ind. d^{-1}, equivalent to a carbon ingestion of 0.03 to 0.04 mg C d^{-1}, resulted in a turnover of approximately 4% d^{-1}, identical to the values for females.

Table 9 Daily ingestion rates of *Pareuchaeta norvegica* and *P. glacialis* derived from feeding experiments. Results are presented as predation rates (ind. d^{-1}), ingestion of dry mass (mg DM d^{-1}), carbon ingestion (mg C d^{-1}) and daily turnover of body mass (% d^{-1}).

	Minimum	Median	Maximum	Mean ± SD
***P. norvegica* females**				
ind. d^{-1}	0.25	0.67	2.33	0.76 ± 0.48
mg DM d^{-1}	0.08	0.22	1.06	0.29 ± 0.24
mg C d^{-1}	0.04	0.11	0.53	0.15 ± 0.12
% of body mass d^{-1}	1.89	4.92	23.17	6.70 ± 5.27
		Total number of experiments: 15		
		Fraction of individuals feeding: 100%		
***P. glacialis* female**				
ind. d^{-1}	0.50	1.00	1.00	0.80 ± 0.27
mg DM d^{-1}	0.11	0.22	0.36	0.23 ± 0.12
mg C d^{-1}	0.06	0.11	0.18	0.12 ± 0.06
% of body mass d^{-1}	2.31	2.94	7.18	3.98 ± 2.01
		Total number of experiments: 15		
		Fraction of individuals feeding: 33%		
***P. glacialis* CV**				
ind. d^{-1}	0.25	-	0.29	-
mg DM d^{-1}	0.06	-	0.07	-
mg C d^{-1}	0.03	-	0.04	-
% of body mass d^{-1}	3.92	-	4.57	-
		Total number of experiments: 2		
		Fraction of individuals feeding: 100%		

4.11 Dietary composition of Aetideidae

"Tastes differ.
Two men on board thought plankton were delicious,
two thought they were quite good,
and for two the sight of them was more than enough."

Thor Heyerdahl (1948) The Kon-Tiki expedition.

Qualitative feeding experiments were conducted with *Aetideopsis minor*, *A. rostrata*, *Chiridius obtusifrons*, *Gaetanus brevispinus*, *G. tenuispinus* and *Pseudochirella spectabilis*. Their reaction to different food items, e.g. phytoplankton, *Calanus* and *Pareuchaeta* nauplii, and copepodids of different sizes, was recorded. Results are shown in Table 10.

Most aetideid species fed opportunistically on all prey items offered. Some differences, however, were apparent between *Aetideopsis* species and *Chiridius obtusifrons* on the one hand and the *Gaetanus* species on the other. *Aetideopsis* spp. and *C. obtusifrons* took nauplii and small copepodids as well as phytoplankton. *Gaetanus brevispinus* and *G. tenuispinus* clearly preferred metazoan prey. They showed immediate and strong reactions to offered nauplii and copepodids, rapidly capturing prey with their maxillipeds. When drops of phytoplankton suspension were injected, *Gaetanus* spp. started filter-feeding, similar to *C. obtusifrons* and *Aetideopsis* spp. However, light and greenish faecal pellets produced by *Gaetanus* spp. fed with phytoplankton strikingly differed from the compact dark in-situ pellets produced shortly after capture. Thus, phytoplankton apparently was not an important component of their natural diet. In contrast to *C. obtusifrons* and *Aetideopsis* spp., both *Gaetanus* species also preyed on larger *Spinocalanus antarcticus* copepodids. These occurred abundantly in deeper waters of the Greenland Sea and Arctic Ocean and due to their rather sluggish behaviour probably made an easy prey for *Gaetanus* spp. and, especially, *Pseudochirella spectabilis*.

Table 10 Feeding behaviour of Aetideidae. **++** strong feeding activity, immediate reaction, faecal pellet production; **+** positive feeding reaction, faecal pellet production; **(+)** positive feeding reaction, but produced faecal pellets differed from "natural" in-situ pellets; **-** no feeding reaction

	Phytoplankton	Nauplii of *Calanus* and *Pareuchaeta*	*Microcalanus*, *Pseudocalanus* copepodids	*Spinocalanus antarcticus* copepodids
Aetideopsis minor females	++	+	+	-
A. rostrata females	+	+	+	-
Chiridius obtusifrons females	++	+	(+)	-
Gaetanus brevispinus females, CV	(+)	++	++	+
G. tenuispinus females	(+)	++	++	+
Pseudochirella spectabilis females	-	not tested	not tested	++

These results suggest that most aetideid species are principally able to utilise both phytoplankton and zooplankton. For *Gaetanus* spp., however, predatory feeding, especially on nauplii and small copepodids, seems to be more important, whereas *Aetideopsis* species and *Chiridius obtusifrons* take a higher portion of phytoplankton and/or phytodetritus.

Additional feeding experiments were conducted with *Pareuchaeta* species to elucidate their prey spectra. The high fraction of *Pareuchaeta glacialis* females, which did not feed on *Calanus* copepodids during the quantitative feeding experiments (see chapter 4.10), suggested that *Calanus* was not the adequate prey. Stimulated by data on the Antarctic relative *P. antarctica*, which primarily fed on *Metridia gerlachei* (Hopkins 1985a, b, 1987; Yen 1991), experiments were performed with *Metridia longa* CV and females as potential prey. However, *M. longa* was not eaten by *P. glacialis* either.

Females and CV of the deep-sea congeners *Pareuchaeta barbata* and *P. polaris* were tested with a variety of abundant calanoids. Potential prey organisms included CV and females of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Scaphocalanus magnus* and *Spinocalanus antarcticus*. Nevertheless, none of the offered prey items were taken. Thus, the prey spectra of both deep-sea euchaetids remain enigmatic.

4.12 Maximum ingestion of aetideid and euchaetid populations

Table 11 Individual maximum ingestion rates (I_{max}) of Aetideidae and Euchaetidae.
Am Aetideopsis minor, Ar A. rostrata, Co Chiridius obtusifrons, Gb Gaetanus brevispinus, Gt G. tenuispinus, Ps Pseudochirella spectabilis, Ca Chiridiella abyssalis, Pb Pareuchaeta barbata, Pg P. glacialis, Pn P. norvegica, Pp P. polaris, F female, M male

		I_{max} (μg C d^{-1})			I_{max} (μg C d^{-1})			I_{max} (μg C d^{-1})			I_{max} (μg C d^{-1})
Am	CIII	2.49	*Gb*	CI-II	2.15	*Ca*	CIII	7.73	*Pg/Pn*	CI-II	1.34
	CIV	3.73		CIII	3.43		CIV	8.09		CII	2.98
	CV	7.12		CIV	6.37		CV	9.57		CIII	5.55
	F	11.97		CV	14.04		F	9.68		CIV	12.86
Ar	CI-II	2.81		F	21.83					CV	33.44
	CIII	3.50	*Gt*	CIII	2.38	*Pb*	CI-II	4.57	*Pg*	F	77.13
	CIV	5.91		CIV	4.35		CI	3.96	*Pn*	F	66.02
	CV	12.03		CV	8.00		CII	5.19	*Pp*	CII	5.45
	F	16.01		F	14.00		CIII	8.92		CIII	7.66
	M	16.45	*Ps*	CII	4.37		CIV	23.56		CIV	16.47
Co	CIII	2.38		CIII	7.46		CV	60.08		CV	36.81
	CIV	4.56		CIV	14.42		F	123.86		F	59.45
	CV	8.66		CV	39.23						
	F	16.66		F	64.66						
	M	8.52									

Maximum ingestion rates I_{max} of aetideid and euchaetid stages were calculated according to an allometric relationship linking carbon demands with individual body mass (Table 11). Based on abundance data and stage compositions, the maximum ingestion of the total aetideid and euchaetid population was estimated (Fig. 36).

Highest I_{max} values of 12.5 to 15.8 mg C m^{-2} d^{-1} were determined for oceanic stations in the central Greenland Sea. In this region midwater populations between 500 and 1000 m depth accounted for the major fraction of I_{max}. In contrast, ingestion rates on the East Greenland shelf (transects B, C and western stations on transect A) and in the Nansen Basin (St. 79) were below 5 mg C m^{-2} d^{-1}. In the northwestern part of the investigation area I_{max} showed a bimodal distribution. A large fraction of the consumption occurred in the upper 50 m, where it coincided with high abundances of *Pareuchaeta glacialis*. Relatively high values were also determined in mesopelagic depths between 200 and 500 m.

The abundant aetideid and euchaetid communities over the Yermak Plateau consumed 5 to 10 mg C m^{-2} d^{-1}. Along transect D I_{max} values were distributed rather evenly throughout the water column with a slight increase towards the seafloor.

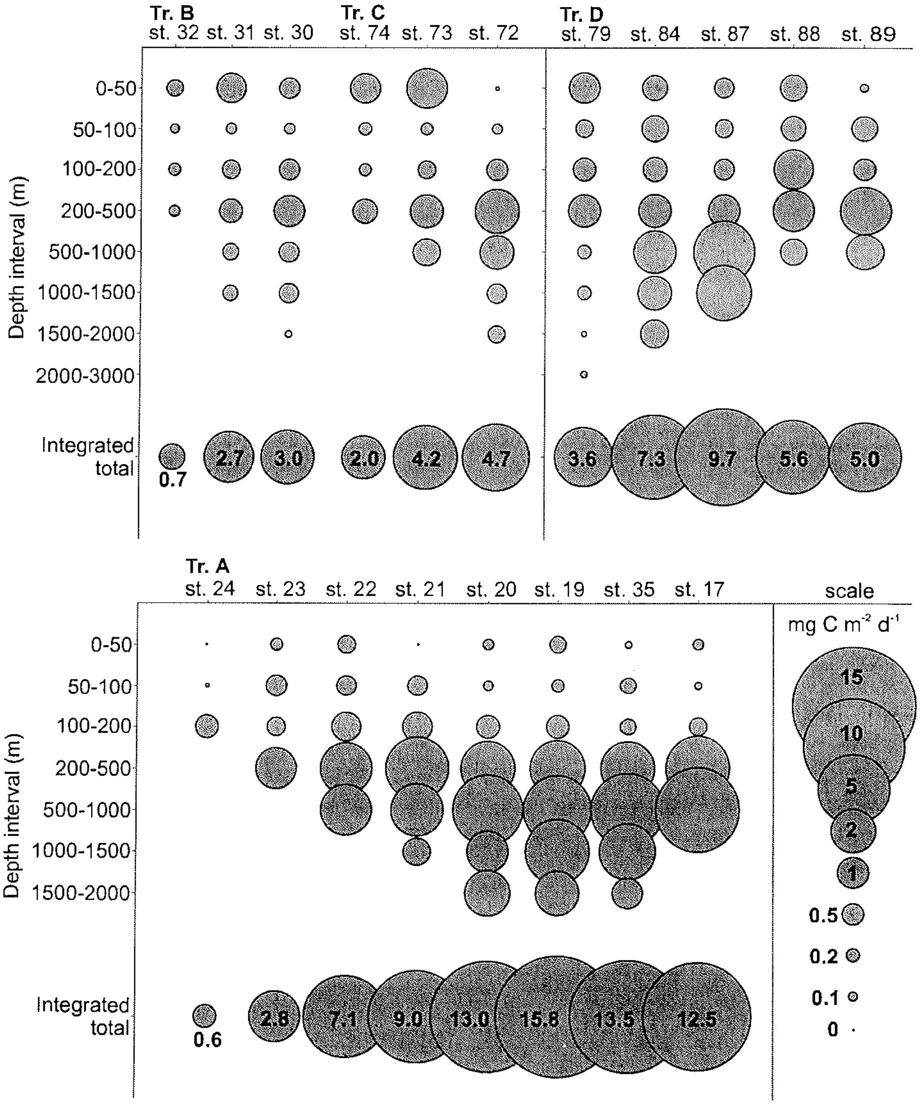

Fig. 36 Maximum ingestion rates of aetideid and euchaetid communities in the Greenland Sea. Circle areas are proportional to I_{max}. The scale exemplifies certain values for easier interpretation.

5 Discussion

5.1 Biodiversity and interspecific competition

Pelagic calanoid copepod communities of high latitudes are typically characterised by the sympatric occurrence of two or more closely-related or congeneric species. This feature is evident among the dominant herbivorous Calanidae (*Calanoides*, *Calanus* and *Neocalanus*) as well as among omnivorous Aetideidae (*Aetideopsis*, *Aetideus*, *Chiridiella*, *Chiridius*, *Gaetanus* and *Pseudochirella*) and, particularly, within the carnivorous genus *Pareuchaeta* in both hemispheres.

Sympatric distribution among Calanidae

The global distribution of dominant phytophagous copepods was summarised by Geynrikh (1986). At least nine species of Calanidae inhabited high latitudes of the northern hemisphere, four in the Atlantic and five in the Pacific. Latitudinally overlapping or onshore – offshore associations of two or more species occurred in both oceans (Conover 1988).
Epipelagic communities of the Arctic Ocean are dominated by the large herbivorous *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* (e.g. Kosobokova 1982; Hanssen 1993; Auel 1995; Mumm et al. 1998). In the Nansen Basin these three species comprised two thirds of the total mesozooplankton biomass (Mumm 1991). In the Atlantic domain of the Greenland Sea *C. finmarchicus* dominated in abundance (40%) and biomass (55%), whereas *C. hyperboreus* prevailed in terms of biomass (35%) in the Greenland Sea Gyre. However, the ranges of both species were widely overlapping, so that *C. finmarchicus* and *C. hyperboreus* co-occurred at most stations throughout the Greenland Sea (Richter 1994).

In the Northeast Water Polynya off Greenland *Calanus glacialis*, *C. hyperboreus* and *C. finmarchicus* dominated mesozooplankton samples both, numerically and by mass. On the East Greenland shelf the ranges of all three species overlapped considerably, resulting in a homogeneous species distribution (Hirche et al. 1994). At shelf stations in the Siberian Laptev Sea *Calanus glacialis* and *C. finmarchicus* contributed 60% and 7%, respectively, to total mesozooplankton biomass. Over the slope and in deeper offshore areas *C. glacialis* and *C. hyperboreus* together comprised 45 to 50% of biomass, while *C. finmarchicus* was also present in these waters (Kosobokova et al. 1998).

In the southern hemisphere a similar coexistence of Calanidae was reported from the Straits of Magellan, where *Calanoides patagoniensis*, *Calanus australis*, *C. simillimus* and *Neocalanus tonsus* occurred sympatrically (Guglielmo & Ianora 1995). In the ice-covered Weddell Sea *Calanoides acutus* and *Calanus propinquus* were very numerous (Boysen-Ennen & Piatkowski 1988) and dominated zooplankton biomass with more than 30% in oceanic regions and more than 47% on the northeastern shelf (Boysen-Ennen et al. 1991). Both species also co-occurred in samples collected through holes in the sea-ice of McMurdo Sound in the Ross Sea (Foster 1987).

Sympatric distribution of Aetideidae and Euchaetidae

Among omnivorous and carnivorous calanoids widely overlapping ranges and sympatric distribution patterns are also common. During the present study eight aetideid species were encountered in the Greenland Sea and Fram Strait. Among these, the genera *Aetideopsis*, *Gaetanus* and apparently *Chiridiella* were present with two species each. *Aetideopsis minor*, *A. rostrata*, *Gaetanus brevispinus* and *G. tenuispinus* together with *Chiridius obtusifrons* were also recorded in the Greenland Sea by Richter (1994, 1995) and occurred as dominant components in sediment trap samples from the same area (Seiler & Brandt 1997).

Corresponding results were obtained from the central Arctic Ocean. In samples from a drift-ice station (80° to 86° N) Markhaseva (1984) identified eight species of Aetideidae. Among those, the genera *Aetideopsis*, *Gaetanus* and *Pseudochirella* were represented by two species each. In addition, *Chiridius obtusifrons*, which strongly resembles *Aetideopsis*, and *Chiridiella abyssalis* were present. *Gaetanus brevispinus* and *G. tenuispinus* as well as *Pareuchaeta glacialis* and *P. norvegica* were collected in the upper 500 m of the Nansen Basin (Mumm 1991). *Aetideopsis armata*, *A. minor* and *A. rostrata* occurred together with *Chiridius obtusifrons* at slope and deep stations in the Laptev Sea. Similarly, *Gaetanus brevispinus* and *G. tenuispinus* sympatrically inhabited the same region (Kosobokova et al. 1998). For the north-eastern Atlantic two *Aetideopsis*, twelve *Gaetanus/Gaidius*, and three *Chiridius* species were listed by Vervoort (1952b, d, e, f).

In the Straits of Magellan species pairs of the aetideid genera *Aetideus* and *Chiridius* co-occurred with *Pareuchaeta antarctica* and *P. biloba* (Gugielmo & Ianora 1995). In the Antarctic *Aetideopsis rostrata* as well as *A. minor* were collected from layers below 400 m (Park 1978) and encountered as far south as the Filchner Depression in the Weddell Sea (Boysen-Ennen & Piatkowski 1988).

The most striking cases of sympatric coexistence have been documented within *Euchaeta/Pareuchaeta*, which is the largest calanoid group encompassing 102 species (Mauchline 1998). Four congeners, *Pareuchaeta barbata*, *P. glacialis*, *P. norvegica* and *P. polaris*, were identified in the Greenland Sea during the present study. The same species inhabited deeper parts of the Laptev Sea, whereas two species, *P. glacialis* and *P. norvegica*, were also found over the continental rise (Kosobokova et al. 1998).

Fourteen *Pareuchaeta* species, dominated by *P. norvegica*, co-occurred in the Rockall Trough, boreal NE Atlantic (Mauchline 1992, 1994a). The overwhelming dominance of *P. norvegica* in spite of the presence of many congeners apparently reflects a common feature of this genus (Mauchline 1995). Around South Georgia in the Southern Ocean, for instance, fourteen species of *Pareuchaeta* were also encountered, but only two of these, i.e. *P. antarctica* and, to a lesser extent, *P. biloba*, were dominant (Ward & Wood 1988).

The global distribution of the genus *Pareuchaeta* was reviewed by Park (1994b). Detailed descriptions focused on sympatric congeners and endemic species in different parts of the World Ocean. Besides co-occurring species, Park (1994b) also reported a number of allopatric pairs of closely related species with little or no overlap in distribution, differing only slightly from each other. Minor species-specific morphological variations were mainly restricted to certain secondary sex characteristics of the female genital segment and the male fifth pair of legs. The strict separation of distribution ranges suggested a cladogenesis, i.e. separation of species, through geographic speciation (Park 1994b).

Theory of competition

The widespread co-occurrence of closely-related species raises the question as to what mechanisms effectively minimise interspecific competition. Without such mechanisms competitive interactions between coexisting species occupying the same ecological niche would eliminate "less fit" competitors (Madin & Madin 1995). This aspect is particularly important in the vast and homogeneous environment of the pelagic deep-sea, where physical barriers are absent.

Competition is generally defined as "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability" (Keddy 1989). Competition may occur for various resources, including food, space, shelter or mates (Clapham & Brownell 1996). However, considerations on the competition among closely related calanoid copepods will be confined to food as a resource, since neither space nor shelter represent necessary commodities for pelagic organisms, and interspecific competition for mates can be ruled out.

Interspecific competition may occur between sympatric populations occupying similar ecological niches. The question of whether and how conspecifics or certain species outcompete others for available resources has long been debated in ecology. Connell (1983) reviewed experimental field studies on competition, both intra- and interspecific, and found that there was a greater incidence of competition among marine organisms than among terrestrial or freshwater species.

In order to demonstrate competition between species, several preconditions must be met. First, the species in question must be proven to be resource-limited (Milne 1961); that is, the availability of food cannot be effectively unbounded, either absolutely or in such areas as individuals are limited (by time, energetics, or other factors) to searching (Clapham & Brownell 1996). Second, there must be a substantial overlap in spatio-temporal distribution of the two species. Third, both species must occupy essentially similar ecological niches. Therefore, it is not necessarily sufficient to demonstrate that both feed on the same prey; they must also exploit similar types, e.g. size classes, of that prey, and forage at the same time and at similar depths (Clapham & Brownell 1996).

How do sympatric calanoid copepods avoid interspecific competition?

A substantial overlap in spatio-temporal distribution among dominant herbivorous as well as carnivorous calanoid copepods has already been demonstrated. With respect to resource limitation, which is the first prerequisite for competition, it is justified to assume that deep-sea ecosystems are generally food-limited. Since primary production is restricted to the euphotic zone, meso- and bathypelagic ecosystems depend on organic material, living or dead, sinking from the euphotic zone as an energy source. In polar oceans the ice-cover and strong seasonality of the light regime further limit primary production and food supplies for pelagic organisms. Due to their limited mobility in relation to the surrounding water body, planktonic organisms are especially dependent on a sufficient food supply within close range. Based on these considerations, one can expect that zooplankton is potentially vulnerable to food limitations and that competition for food sources may play an important role in deep-sea ecosystems.

In order to answer the question definitively as to how interspecific competition among Arctic deep-sea copepods is minimised, we have to focus on the third criterion, i.e. differences between the ecological niches of closely-related species. How have sympatric congeners found unique niches? In principal, there are three major ways of sharing a common deep-sea habitat without competition: vertical partitioning, vertical migration, or different life-cycle strategies.

Vertical partitioning of the water column

Sympatric species may find particular niches within the three-dimensional environment of the pelagic deep-sea by vertical partitioning of the water column. In this way, a spatial separation can be realised in spite of horizontally overlapping distribution ranges. In almost all parts of the ocean there are clear faunal differences between the meso- and bathypelagic depths, and the animals of those zones have very different life styles (Madin & Madin 1995).

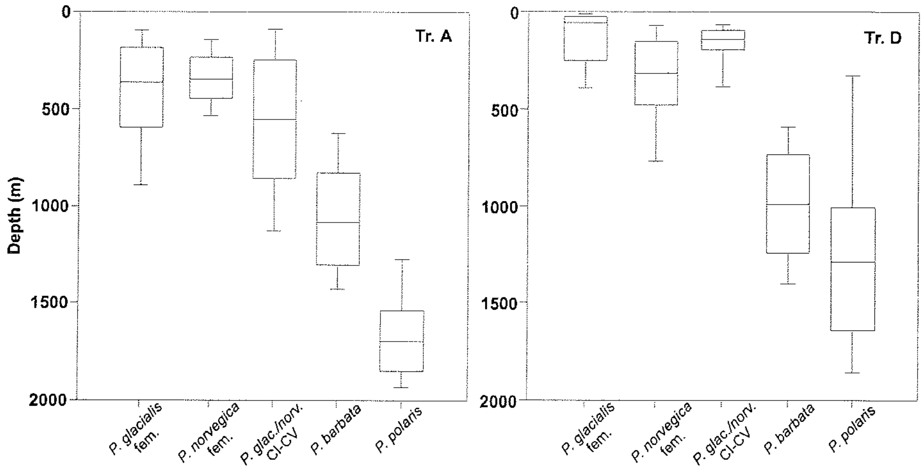

Fig. 37 Vertical distribution of Euchaetidae along the transects A and D. Boxes include 50% of the population, while whiskers encompass the 10th to the 90th percentile. The horizontal bar indicates the median depth.

The present study showed that in the central Greenland Sea congeneric copepod species were restricted to more or less discrete vertical ranges (Fig. 37, 38). *Aetideopsis rostrata* inhabited the deepest layers, whereas *A. minor* was distributed in the mesopelagic realm. The similar *Chiridius obtusifrons* was confined to the epi- and upper mesopelagial. Accordingly, *Gaetanus tenuispinus* prevailed between 200 and 500 m depth, while *G. brevispinus* dominated below

500 m. In the northern part of the investigation area vertical ranges of most species were shifted upwards (polar emergence), but the stratified distribution patterns persisted. Similar results were obtained for *Pareuchaeta* spp.: in the central Greenland Sea *P. glacialis* and *P. norvegica* inhabited the upper 500 m, whereas *P. barbata* dominated between 500 and 1500 m depth and *P. polaris* below 1000 m.

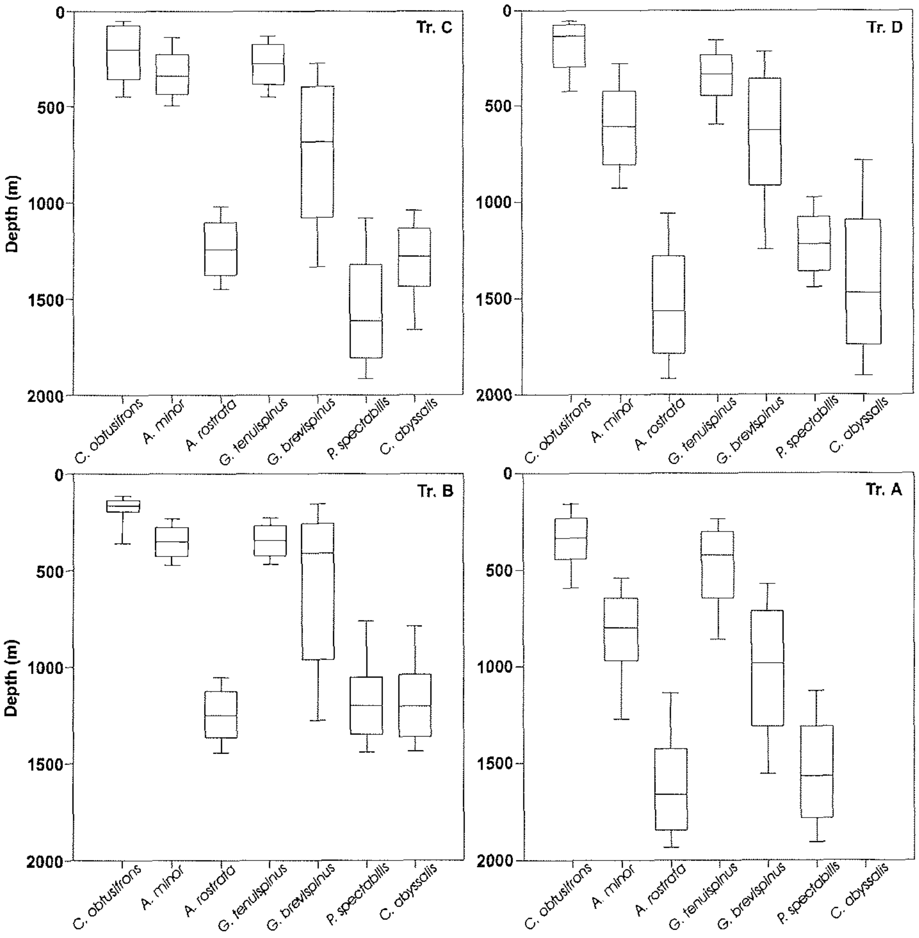

Fig. 38 Vertical distribution of Aetideidae along the four transects. Boxes include 50% of the population, while whiskers encompass the 10th to the 90th percentile. The horizontal bar depicts the median depth.

Supporting evidence for a vertical partitioning among Aetideidae in the Greenland Sea is provided by Richter (1995). In the Greenland Sea Gyre (75°N) the main fraction of the *Chiridius obtusifrons* population inhabited water depths from 300 m to 900 m, whereas *Aetideopsis minor* centred between 700 m and 1400 m and 75% of all *A. rostrata* occurred below 1500 m. Accordingly, 75% of the *Gaetanus tenuispinus* population were usually found above 900 m depth, while the same fraction of the *G. brevispinus* population occurred below 1000 m

(Richter 1995). In sediment trap samples retrieved from depths of 500 m, 1000 m and 2300 m in the Greenland Sea, high numbers of *Gaetanus tenuispinus* were confined to 500 m. At a depth of 1000 m *Aetideopsis minor* dominated abundance with 40% of all calanoid copepods in the sample. In contrast, *A. rostrata* comprised 80 to >90% of calanoid abundance in the deepest trap (Seiler & Brandt 1997).

A multi-layered vertical distribution of sympatric aetideids has also been reported from the Norwegian Sea (Østvedt 1955) and the North Atlantic (Grice & Hülsemann 1965). Raymont (1983) proposed that a lack of food specialisation among Aetideidae may have resulted in a vertical partitioning of the limited resources and in a stepwise arrangement of species with depth, allowing for a large generic radiation within the Aetideidae (Razouls 1993).

Several studies indicate that vertical partitioning among deep-sea copepods is also common in the Arctic Ocean (Markhaseva 1984; Grainger 1989). In contrast to *Pareuchaeta glacialis* and *P. norvegica*, the congeners *P. barbata* and *P. polaris* were absent from the continental slope of the Laptev Sea, but present in deeper parts of the adjacent Nansen Basin, indicating a preference for bathypelagic depths in the latter two species. In the central Arctic Ocean *Pareuchaeta glacialis*, *Chiridius obtusifrons* and *Gaetanus tenuispinus* were frequently encountered in the upper 50 m, whereas *Aetideopsis minor* and *G. brevispinus* usually inhabited deeper layers and only occasionally occurred at epipelagic depths. Between 50 and 1000 m many additional copepod species not reported from surface waters were identified, including *Aetideopsis rostrata*, *Chiridiella abyssalis*, *C. abyssalis*, *Pareuchaeta norvegica*, *P. polaris*, *P. barbata*, *Pseudaetideus armatus* and *Pseudochirella spectabilis* (Grainger 1989).

The most extraordinary example of vertical partitioning among congeneric copepods concerned the diverse *Pareuchaeta* community inhabiting the Rockall Trough. Fourteen species were partitioned vertically in the 2500 m water column (Mauchline 1992, 1994a, 1995). Thus, spatial separation by vertically partitioning the water column appears to be a widespread strategy to minimise competition among congeneric species with overlapping distribution ranges.

Vertical migration

A second potential mechanism to avoid competition and to utilise a homogeneous three-dimensional habitat is vertical migration, allowing a sort of time-sharing division of the water column. Species-specific migration cycles and patterns offer different species the opportunity to avoid each other and partitioning their environment on a time basis, thus realising a temporal separation within a common habitat (Madin & Madin 1995).

Diurnal and seasonal vertical migrations have been intensively studied mainly in dominant herbivorous Calanidae (Hirche 1996b). However, synchronising mechanisms and environmental triggers are poorly understood. Generally, it is believed that diurnal vertical migrations are restricted to epi- and mesopelagic organisms capable of detecting periodic changes in light intensity. Inhabitants of the aphotic bathypelagic realm do not perform vertical migrations.

Among the fourteen *Pareuchaeta* species occurring in the Rockall Trough, two mesopelagic species, *P. pseudotonsa* and *P. gracilis*, performed diel vertical migrations, and a third species, *P. hanseni*, appeared to migrate diurnally at times (Mauchline 1992). *P. norvegica* showed a eurybathic, but bimodal vertical distribution (300 to 1900 m). The upper part of the population centred at 500 to 600 m and performed regular diurnal migrations, but the behaviour of individuals in deeper layers was unknown (Mauchline 1995). In *Euchaeta marina*, an epipelagic relative from tropical latitudes, diel vertical migration was restricted to the upper 100 m with two migration cycles per day. At dusk adults and CV stages ascended from their daytime distribution at 50 m depth, reaching 20 to 30 m by nightfall. At midnight they returned to 40 to 60 m depth, before starting again a pre-dawn ascent to 10 to 15 m. Younger copepodids performed no midnight descent and remained at a depth of 30 m throughout the night (Morris & Hopkins 1983; Shuert & Hopkins 1987). In the Canadian Arctic *Pareuchaeta glacialis* performed seasonal vertical migrations (Hughes 1968).

Data on vertical migrations of Aetideidae are scarce and partly contradictory. Seiler & Brandt (1997) reported that in the Greenland Sea older copepodite stages and adults of *Aetideopsis rostrata* started seasonal vertical migrations in spring from 2300 m towards the 500 m depth level in summer, returning to greater depths in autumn. In contrast, Richter (1995) found that the same species, together with *A. minor*, *Chiridius obtusifrons*, *Gaetanus brevispinus* and *G. tenuispinus*, belonged to the meso- and bathypelagic "residents", characterised by a stationary depth distribution throughout the year. During the limited period of the present study (May to August) no indications were detected of diurnal vertical migrations or seasonal variations in the vertical distribution of aetideid or euchaetid species.

Life-cycle strategies

Different life-cycle strategies, including physiological adaptations, feeding and reproductive behaviour, are the third important possibility to separate ecological niches of sympatric species.

Intensive studies focused on the life-cycles of dominant herbivorous Calanidae in polar oceans, and detected significant differences in the reproductive biology of the sympatric Arctic *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. In *C. hyperboreus* egg production was independent of food availability, but fuelled by lipid reserves accumulated during the ontogenetic development. Spawning took place at great depth during winter, in advance of the phytoplankton bloom (Grainger 1963; Conover 1967). In contrast, reproduction of *C. finmarchicus* was closely coupled to food availability. During laboratory experiments fecundity responded directly to changes in phytoplankton concentration; egg production ceased under starvation, and resumed with feeding (Runge 1985; Hirche 1996a; Hirche et al. 1997). Females of *C. glacialis* were able to start egg production without food at the expense of lipid reserves. However, fecundity strongly increased under favourable feeding conditions (Hirche & Bohrer 1987; Hirche 1989). Thus, *C. glacialis* realised an opportunistic reproductive strategy, adapted to the highly seasonal and unpredictable food conditions in high-Arctic seas.

Different life-cycle strategies have also been reported for the co-occurring Antarctic species *Calanoides acutus* and *Calanus propinquus*. The life-cycle and overwintering strategies of *C. acutus* closely resembled those of its Arctic relatives. The species fed primarily on phytoplankton and survived food limitation during winter periods in a dormant state at great depth. In contrast, *Calanus propinquus* remained active in the upper 200 m for most of the year and changed to a more omnivorous diet, when phytoplankton was scarce (Schnack-Schiel & Hagen 1995). These differences in life-cycles were also reflected in the composition of body lipids. *C. acutus* accumulated long-chained wax esters typical of herbivorous Calanidae, whereas *C. propinquus* relied on triacylglycerols as energy reserves, more indicative of active overwintering (Hagen et al. 1993, Kattner et al. 1994, Kattner & Hagen 1995). These examples demonstrate how physiological adaptations and different life-cycle strategies enable sympatric species to find specific slots and thus minimise the risk of interspecific competition.

During the present study, feeding experiments and analyses of trophic biomarkers were conducted to elucidate the food preferences of sympatric deep-sea copepods. Further evidence for a differentiation of life-cycle strategies among co-occurring *Pareuchaeta* species was derived from observations of their reproductive behaviour.

Different food preferences were apparent between *Pareuchaeta glacialis* and *P. norvegica* on the one hand and the bathypelagic *P. barbata* and *P. polaris* on the other. Females of the first two species extensively preyed on *Calanus* copepodids during feeding experiments, whereas the bathypelagic congeners did not accept the offered prey at all. The analysis of biomarker fatty acids in body lipids supported this result. High and variable levels of the monounsaturated fatty acids 20:1(n-9) and 22:1(n-11), typical of herbivorous Calanidae, were detected in specimens of *P. glacialis* and *P. norvegica* from the field, indicating that *Calanus* specimens comprised a common food item for both species in the wild. In contrast, low amounts of these fatty acids in *P. barbata* suggested that *Calanus* was not an important component of its natural diet and thus explained the negative results of the feeding experiments.

The observations during qualitative feeding experiments with different Aetideidae and their generally diverse fatty acid compositions indicated a mainly omnivorous diet. However, the ratio between 18:1(n-9) and 18:1(n-7) fatty acid concentrations varied considerably between the different genera. The lowest value occurred in *Chiridius obtusifrons*, indicating that phytoplankton may be an important dietary component for this mainly epipelagic species. Occurring close to the surface, *C. obtusifrons* seems to benefit directly from primary production. Considerably higher ratios were measured in *Gaetanus* species, indicating a more carnivorous diet. Consistently, *G. brevispinus* and *G. tenuispinus* preyed heavily on nauplii, small copepodids and even large *Spinocalanus antarcticus* during the feeding experiments. When fed with phytoplankton, faecal pellets of *Gaetanus* spp. differed in form and colour from those produced under natural conditions. The genera *Aetideopsis* and *Pseudochirella* revealed intermediate ratios, indicative of an omnivorous diet consisting of small zooplankton and probably phytodetritus, since their deep range prohibited access to fresh phytoplankton.

Different reproductive strategies among Aetideidae were obvious, since *Chiridius obtusifrons* and possibly *Aetideopsis minor* carried their eggs attached to the genital opening, while the other species released their eggs directly into the water column. Even among congeneric *Pareuchaeta* species, which all produce egg sacs, different reproductive strategies could be identified. Compared to the epi- to mesopelagic congeners *P. glacialis* and *P. norvegica*, the bathypelagic forms *P. barbata* and *P. polaris* were characterised by larger egg size, combined with a reduction of egg numbers per sac. *P. polaris* females invested 4% of their body energy per egg, in comparison to only 0.8 to 1.6% in other congeners. Mauchline (1995, 1998) tried to explain the positive correlation between egg diameter and depth of occurrence as a consequence of a depth-dependent decrease in ambient temperature. However, the present study revealed that the same trend occurred under Arctic conditions in spite of stable temperature profiles throughout the water column.

Therefore, the following hypothesis is proposed to explain depth-dependent changes in egg size. Low numbers of large, energy-rich eggs in bathypelagic species can be interpreted as an adaptation to a food-limited environment. They enable early ontogenetic stages to rely on energy reserves within the yolk for development (lecithotrophic development), making them relatively independent of the adverse feeding conditions at bathypelagic depths. Thus, energy-rich eggs seem to be a successful reproductive strategy ensuring a higher survival rate of the new generation in the food-limited deep-sea. In contrast, epipelagic species produce a large number of relatively small eggs. The offspring probably does not depend on energy reserves, since it can benefit from the abundant food supply within the upper water layer (planktotrophic development). Moreover, the large number of eggs may be necessary to counter a higher predation risk in the epipelagic realm. Thus, bathypelagic species have realised a K-strategy to cope with adverse, but stable feeding conditions, while epipelagic species utilise their more variable environment by following a r-strategy. This hypothesis suggests that large eggs of bathypelagic species are more likely to be an adaptation to a depth-dependent decrease in food-availability than to depth-dependent temperature changes.

This interpretation is supported by several studies showing that in a number of copepod species egg size is negatively correlated with food availability, whereas egg number increases under favourable feeding conditions (Hutchinson 1967; Cooney & Gehrs 1980). Recent investigations on the marine copepod *Euterpina acutifrons* also revealed a trade-off between egg number and egg size (Guisande et al. 1996). At low food concentrations, both in the field and under experimental conditions, females produced fewer, but larger eggs, resulting in a faster development of nauplii and an increased reproductive success. Similarly, the mean volume of eggs produced by *Calanus helgolandicus* was inversely related to both food availability and fecundity (egg production per female and day), with increased numbers of smaller eggs produced during periods of high food availability (Pond et al. 1996). Moreover, it has been demonstrated that young copepodids are more vulnerable to starvation than older ones (Burns 1985; Borchers & Hutchings 1986; Tsuda 1994; Calbet & Alcaraz 1997). Thus an increase in egg-size at the expense of offspring number seems to be an advantageous strategy to maximise reproductive success under low food concentrations (Hutchinson 1967).

Indications that the ecological niches of sympatric *Pareuchaeta* species generally differ are also derived from morphological studies. Park (1994a, b) subdivided the genus into morphologically distinct species groups and noted that when two or more congeners dominated in a highly productive area, they were likely to belong to different species groups. This was evident for the dominant *P. norvegica*, *P. glacialis* and *P. barbata* in the northern Atlantic as well as for the sympatric *P. antarctica*, *P. biloba*, *P. rasa* and *P. barbata* in the Antarctic.

Avoidance of competition among deep-sea copepods in the Arctic

The present study reveals that sympatric deep-sea copepods have realised different strategies to minimise interspecific competition in the Greenland Sea.

Congeneric Aetideidae, e.g. *Aetideopsis* spp. and *Gaetanus* spp., respectively, occupied separate and distinct depth ranges, thus partitioning the water column vertically. A vertical separation of the bathypelagic realm was also apparent between *Pareuchaeta barbata* and *P. polaris*. By contrast, competition between different sympatric aetideid genera, e.g. *Aetideopsis* versus *Chiridius* or *Gaetanus*, appeared to be minimised by different dietary preferences or reproductive strategies. Distinct reproductive strategies were also detected for the epipelagic *Pareuchaeta glacialis* and *P. norvegica* on the one hand and bathypelagic congeners on the other.

Thus, species with similar diets lived at different depths and, vice versa, species encountered at the same depth substantially differed in dietary composition. Clearly separated niches and different life-cycle strategies generally ensured that sympatric species partition their uniform environment and avoid competition by not feeding on the same prey in the same place at the same time (Madin & Madin 1995).

However, this concept fails to explain the coexistence of *Pareuchaeta glacialis* and *P. norvegica* throughout the central Greenland Sea. Both species inhabit the same depth intervals, have similar diets and follow comparable reproductive strategies. How can such closely related species with seemingly similar demands coexist without competition that would eliminate the less fit competitor?

Small-scale heterogeneity in pelagic waters

Madin & Madin (1995) suggest that small to medium-scale hydrographic features at the surface and within the water column may form local and temporary patches differing in environmental properties and food abundance. This transient patchwork of varying environmental and feeding conditions could add heterogeneity to the environment and continually interrupt the interactions by which species compete with each other.

Rarity

Another key to understanding meso- and bathypelagic biodiversity may be the proportions of different species to total abundance. Usually a few species are very abundant in deep-sea samples, several are common and most are rare, with only a few individuals each. In fact, this has proven to be a characteristic feature of species-rich and highly diverse *Pareuchaeta* communities in different regions (Park 1994b, Ward & Wood 1988 for the Antarctic, Mauchline 1995 for the Rockall Trough). In general, it is estimated that over 80% of all oceanic species are rare (Madin & Madin 1995). Rarity may reduce competition simply because the individuals are too few and dispersed to interact very often.

Within the genus *Pareuchaeta* abundant species are usually endemic to highly productive regions, e.g. boreal seas and upwelling areas, whereas the majority of rare species are widely distributed in mainly oligotrophic seas. To explain these observations, Park (1994b) proposed the hypothesis that bathypelagic calanoids endemic to and abundant in productive areas are those adapted to eutrophic conditions of their habitats. Therefore, they cannot expand their ranges into the contiguous oligotrophic waters, even if the other environmental conditions are favourable and physical barriers absent. Usually rare species, on the other hand, are those not directly associated with local eutrophic conditions. They generally have extensive geographic ranges because of their survival ability in widely ranging oligotrophic conditions and the absence of physical barriers at bathypelagic depths of the World Ocean.

However, in the case of *Pareuchaeta glacialis* and *P. norvegica* rarity is not a suitable explanation for a coexistence without competition. Both forms belong to the "eutrophic" species (Park 1994b) and occur abundantly in the central Greenland Sea (present study). Thus, some other mechanism must be acting to minimise interspecific competition.

Continuous re-colonisation

The co-occurrence of *Pareuchaeta glacialis* and *P. norvegica* in the central Greenland Sea may be explained by advection processes. For both species the Greenland Sea does not represent the main distribution range. *P. norvegica* is primarily a boreal or sub-Arctic species, most abundant in the Faeroe Channel, Norwegian Sea and west of Iceland (With 1915, Park 1994b). It is transported northward together with Atlantic water masses by the West Spitsbergen Current. In contrast, *Pareuchaeta glacialis* is a typical polar species, mainly inhabiting the upper 300 m of the Arctic Ocean (Kosobokova 1982). During the present study highest abundances of *P. glacialis* were detected at the northernmost stations and in the Nansen Basin. The species is exported from the Arctic Ocean into the Greenland Sea by the East Greenland Current. Thus, the central Greenland Sea may be considered a "melting pot" for the boreal-Atlantic and polar congeners. Although both species are able to reproduce in the central Greenland Sea, a considerable portion of the population may consist of "expatriates", advected into the Greenland Sea by the opposing current regimes. Thus interspecific competition between *Pareuchaeta glacialis* and *P. norvegica* may occur in the central Greenland Sea, but may not result in the extinction of one competitor in the area, since new individuals of both species are permanently imported from their respective home ranges, replacing the populations within the Greenland Sea.

In conclusion, a combination of different mechanisms, including spatial separation by vertical partitioning (among congeners), different life-cycle strategies (between genera) and physical-biological interactions (in the case of *Pareuchaeta glacialis* and *P. norvegica*), ensure the maintenance of a high biodiversity in the homogeneous environment of the pelagic deep-sea.

5.2 Ecological role and effect on carbon flux

> *"Some day in the future, perhaps,*
> *men will think of harvesting plankton from the sea*
> *to the same extent as once, long ago,*
> *they had the idea of harvesting grain on land.*
> *A single grain is of no use either,*
> *but in large quantities it becomes food."*
>
> Thor Heyerdahl (1948) The Kon-Tiki expedition.

Comparison of carbon demands derived from different approaches

In order to assess the ecological role of Aetideidae and Euchaetidae and to evaluate their impact on the carbon and energy flux within Arctic marine ecosystems, the carbon demands of various species and stages were calculated applying an allometric relationship between body mass and maximum mass-specific ingestion rate proposed by Moloney & Field (1989). This mathematical approach was necessary, since experimental studies encompassed only a fraction of the species and size spectra recorded in the field.

In the following paragraph calculated maximum ingestion rates I_{max} will be compared to available results from respirometry and feeding experiments in order to confirm the validity of the allometric approach.

For most species calculated I_{max} values overestimated the respective data derived from respiration measurements by 30 to 40% (Table 12). This result was expected, since the allometric approach approximated the maximum potential ingestion rate under optimum conditions (Moloney & Field 1989; Gradinger et al. in press). Hence, in-situ measurements should generally reveal lower ingestion rates. For *Aetideopsis minor* measured values were slightly higher than I_{max}, but still in the same range.

However, strong deviations between calculated and measured ingestion rates occurred among bathypelagic *Pseudochirella spectabilis*, *Pareuchaeta polaris* and *P. barbata* females. For those species I_{max} values were about three to six times higher than the maximum consumption rates derived from respiration measurements. This overestimation suggests that bathypelagic carnivores may be able to severely reduce their metabolism as an adaptation to a food-limited environment. This hypothesis is also supported by personal observations that *Pareuchaeta barbata* females survived starvation for more than six months without apparent changes in activity or health status.

Table 12 Comparison of individual daily ingestion rates (µg C d^{-1}) derived from allometric equation (I_{max}), respiration measurements (I_{resp}) and feeding experiments (I_{feed}). R_b = measured basic metabolic needs

	I_{max}	I_{resp} ($I_{resp} = 3.58 \times R_b$)		$I_{max}/I_{resp\,max}$	I_{feed}	
		mean	max	(%)	mean	max
Aetideopsis minor female	12.0	9.7	15.0	80		
A. rostrata female	16.0	7.5	11.5	139		
Gaetanus brevispinus CV	14.0	7.2	10.0	140		
Pseudochirella spectabilis CV	39.2	10.7	11.1	**353**		
P. spectabilis female	64.7	12.5	24.0	**270**		
Pareuchaeta barbata CIV	23.6	11.8	16.5	143		
P. barbata CV	60.1	24.0	43.0	140		
P. barbata female	123.9	16.8	39.4	**314**		
P. glacialis CV	33.4				30 to 40	
P. glacialis female	77.1	15.4	59.8	129	120 ± 60	180
P. norvegica female	66.0	17.9	48.3	137	150 ± 120	530
P. polaris female	59.4	6.4	10.4	**571**		

Ingestion rates derived from feeding experiments with carnivorous *Pareuchaeta* were generally higher than I_{max} and respiration-based estimates. These differences can be explained by the design of the feeding experiments, where predation rates were calculated from the decrease in prey concentration during the experiments, regardless of whether killed prey was completely ingested or not. Thus, I_{feed} values overestimate actual ingestion. In addition, observations by Yen (1991) indicate that predatory behaviour of *Pareuchaeta* is probably a reflex, triggered by prey stimuli, but independent of the nutritional condition of the predator. Under these circumstances predation rates would mainly be a function of prey abundance determining the probability of predator-prey encounters. Relatively high predation rates during the feeding experiments might therefore be a consequence of higher prey concentrations than in the field. Accordingly, predation rates of the Antarctic carnivorous hyperiid amphipod *Themisto gaudichaudi* were considerably higher during feeding experiments than the respective estimates of daily ration derived from a respiration-based energy budget approach (Pakhomov & Perissinotto 1996).

In conclusion, the allometric approach generally provides fair approximations of the maximum potential ingestion of aetideid copepods. With respect to bathypelagic carnivores, however, I_{max} values considerably exceed actual carbon demands. In view of the total euchaetid and aetideid community, this overestimation is at least partly compensated by the fact that under favourable feeding conditions the predation impact of *Pareuchaeta glacialis* and *P. norvegica* might be even higher than estimated by I_{max}. Thus, the allometric approach may provide a valid estimate of the carbon demand of euchaetid and aetideid communities.

In general, daily rations of 2 to 23% of body carbon per day, measured in the present study, are in good accordance with published data for other calanoids or carnivorous zooplankton. Kleppel et al. (1996) reported mean daily rations of 11.2% of body C d^{-1} for a variety of actively feeding calanoid copepods on the West Florida continental shelf. In Antarctic waters, *Themisto gaudichaudi*, a carnivorous pelagic amphipod, consumed 8.5 to 21.8% of body mass d^{-1} (Pakhomov & Perissinotto 1996). The daily ingestion of *Pareuchaeta antarctica* accounted for 8.8% of its body mass d^{-1} (Yen 1991), whereas *P. norvegica* ingested 10.5% of body mass d^{-1} (Yen 1987).

Ecological role of Euchaetidae and Aetideidae

Members of the calanoid families Euchaetidae and Aetideidae are characteristic components of pelagic communities throughout the World Ocean. Since both families encompass primarily meso- to bathypelagic species, they are particularly important in oceanic midwater and deep-sea habitats.

Especially in boreal and polar regions, large Euchaetidae may contribute substantially to the mesozooplankton standing stock. In the central Arctic Ocean, for instance, *Pareuchaeta glacialis* belongs to the five dominant calanoid species and comprises 1 to 6% of the total biomass of all copepods (Kosobokova 1982; Grainger 1989). In deeper parts of the Siberian Laptev Sea *Pareuchaeta glacialis*, *P. norvegica*, *P. barbata* and *P. polaris* together accounted for 4.3 ± 1.9% (maximum 7.8%) of total mesozooplankton dry mass (Kosobokova et al. 1998). In the central Greenland Sea the same species represented on average 1.6% of mesozooplankton biomass and, thus, belonged to the ten most important taxa (Richter 1994). Similarly, the Antarctic congener *P. antarctica* comprised 2.0 to 3.1% of zooplankton biomass in the Weddell Sea (Boysen-Ennen et al. 1991) and more than 3.6% in McMurdo Sound, Ross Sea (Hopkins 1987).

Due to their smaller size Aetideidae are generally less important with respect to biomass. Their portion of the standing stock was 1.3 ± 0.6% in the Arctic Laptev Sea (Kosobokova et al. 1998) and 2% in oceanic regions of the Antarctic Weddell Sea (Boysen-Ennen et al. 1991). However, aetideids may significantly influence biodiversity of midwater habitats. In the Arctic Ocean, for instance, mesopelagic Aetideidae contributed to higher species numbers and biodiversity in midwater layers, compared to the Polar Surface Water (Grainger 1989; Auel 1995).

Euchaetidae are primarily carnivorous and actively prey on other zooplankton, while aetideid copepods are generally referred to as omnivorous (Hopkins 1985a; Richter 1995). The guts of seven Antarctic aetideid species contained phytoplankton with a high incidence of large frustules of Coscinodiscineae as well as *Euphausia superba* debris (in the form of bristles, fragments of appendages, pieces of the exoskeleton, eye pigment and ommatidia). The most common live prey of Antarctic aetideids were copepods, especially *Oncaea* spp., and the polychaete *Pelagobia longicirrata*. Among the dominant species, *Euchirella rostromagna* and *Gaetanus brevispinus* had the most diverse diets, whereas *Aetideopsis minor* fed mainly on phytoplankton and detritus (Hopkins 1985a). In other regions Aetideidae took phytoplankton debris, protozoans and small crustaceans (Esterly 1916; Geynrikh 1958; Chindonova 1959; Wickstead 1962; Mullin 1966; Arashkevich 1968; Harding 1974). The present study also underlines the generally opportunistic feeding behaviour of aetideids. However, Aetideidae comprise a very diverse group, so that significant variation in feeding behaviour and dietary composition is likely to occur, as has been demonstrated between *Gaetanus* and *Aetideopsis/Chiridius*.

Copepod feeding may have an important impact on the supply of carbon to deeper water layers and to the benthos (Ashjian et al. 1995). The repackaging of organic material via faecal pellet production can strongly affect sedimentation processes. Coprophagous and detritivorous feeding, in particular by aetideids, transforms sedimenting particles and therefore alters their sinking speed. Thus, meso- and bathypelagic copepods may control the vertical carbon flux.

Carnivorous *Pareuchaeta* are major predators on other mesozooplankton and fish larvae. They may even influence the recruitment of commercially important fish stocks, as has been demonstrated for Atlantic cod *Gadus morhua* and Pacific hake *Merluccius productus* (Bailey & Yen 1983; Yen 1987). A quantitative assessment of the daily predation impact of carnivorous *Pareuchaeta antarctica* on zooplankton communities in Gerlache Strait revealed that females and CV together could remove over 1% of both the small and the large copepod standing crop per day. Even higher impacts on small prey species occurred, when younger copepodids were included (Øresland 1995). In Kosterfjorden, Sweden, *Aetideopsis armata* and *Pareuchaeta norvegica* were responsible for 29 to 77% of the total energy flow through the carnivorous trophic level (Båmstedt 1981).

For the Greenland Sea Richter (1995) suggested that large bathypelagic aetideids may feed on *Calanus hyperboreus* CIII overwintering within their depth range. This was indicated by the co-occurrence of *Gaetanus brevispinus* with *C. hyperboreus* during the dark season, and by the apparent “inverse” seasonal vertical migration of *Aetideopsis rostrata* from the lower into the upper bathypelagial during the late winter period.

More recent investigations emphasise the important influence of predation on the structure of pelagic communities and generally question the longstanding paradigm of food availability as the governing factor determining plankton distribution (Verity & Smetacek 1996; Tiselius et al. 1997). It is now believed that the “top-down” control of zooplankton populations by predation may be equally important in determining zooplankton biomass and the ranges of certain species as the “bottom-up” mechanism. Thus, predation by Euchaetidae and Aetideidae may substantially affect the structure of pelagic communities.

Feeding ecology of *Pareuchaeta* spp.

The feeding ecology of carnivorous *Pareuchaeta* species has been studied intensively in boreal and Antarctic regions (Yen 1982, 1985, 1991). In contrast, data for Arctic populations are restricted to morphological investigations.

Electron-microscopic studies focusing on the distribution and structure of setae on the first antennae indicate that *Pareuchaeta norvegica* is a rheotactic predator (Kurbjeweit 1988). Setae on the first antennae function as mechanoreceptors and perceive vibrations and hydrodynamic stimuli emitted by prey organisms. Following a sit-and-wait strategy, *P. norvegica* stays motionless in the water column, until prey comes into reach. Then the predator rapidly spurts towards the prey by movements of the thoracopods and the first antennae and catches the victim with the enlarged maxillipeds.

In comparison to herbivorous or omnivorous species chemoreceptors are weakly developed, since the slow propagation by diffusion or turbulent mixing makes chemical signals useless for the detection of fast-moving prey (Kurbjeweit 1988).

The vibration sense of carnivorous chaetognaths, which also detect their prey by mechanoreception, even allows them to discriminate between different prey species (Horridge & Boulton 1967). Swimming or filter-feeding copepods create characteristic vibrations with their beating appendages. The frequency of the emitted vibrations is species-specific. Newbury (1972) demonstrated that attack responses of the chaetognath *Spadella cephaloptera* were triggered by vibration rates of 10 to 20 Hz, exactly corresponding with the bandwidth *Calanus finmarchicus* emitted during swimming or feeding activities. Similarly, *Pareuchaeta norvegica* was able to select between two species of *Acartia* (Tiselius et al. 1997). Thus, the vibration sense apparently enables rheotactic predators to actively select prey species.

Impact of Euchaetidae and Aetideidae on the carbon flux in the Arctic

In order to evaluate the impact of euchaetid and aetideid copepods on the carbon and energy flux within Arctic deep-sea environments, their carbon demands are discussed in relation to primary and secondary production, to mesozooplankton standing stock and vertical flux of particulate carbon.

For many decades primary production in ice-covered Arctic seas has been considered extremely low (Apollonio 1959; English 1961). However, during the last years we learned that ice algae greatly contribute to total primary production (Legendre et al. 1992) and may present up to two thirds of total primary production in ice-covered areas of the central Arctic Ocean (Wheeler et al. 1996). Haline stratification due to meltwater and river discharge stabilises the sunlit surface layer and triggers an early start of the pelagic production, especially in marginal ice zones and over the vast Siberian shelf regions. The production period in the Arctic Ocean may therefore extend to 120 days per year (Wheeler et al. 1996). Total annual primary production in oceanic areas of the central Arctic Ocean reaches 10 g C m^{-2} yr^{-1} (Subba Rao & Platt 1984; Wheeler et al. 1996). Higher values of 27 g C m^{-2} yr^{-1} were measured in Arctic shelf areas (<200 m water depth, Subba Rao & Platt 1984). In the southern Greenland Sea annual primary production reaches considerably higher rates of approximately 85 g C m^{-2} yr^{-1} (Bodungen et al. 1995).

A comparison between primary production and maximum ingestion rates of Aetideidae and Euchaetidae identified three regions with distinct regimes within the investigation area. High ingestion rates of 5.0 ± 0.5 g C m^{-2} yr^{-1} were calculated for aetideid and euchaetid populations in the central Greenland Sea. Due to the seasonal ice-cover and the more southerly position, however, primary production was also high. Consequently, the ratio of I_{max} and primary production was low with 5.9%.

Table 13 Estimates of annual primary production (g C m^{-2} yr^{-1}) and maximum ingestion (g C m^{-2} yr^{-1}) of Aetideidae and Euchaetidae from different regions of the Arctic Ocean. Data on primary production by Subba Rao & Platt (1984); Bodungen et al. (1995) and Wheeler et al. (1996).

Region	Primary production (P)	I_{max} of Aetideidae and Euchaetidae	Ratio I_{max}/P (%)
Nansen Basin	9	1.3	14.4
Yermak Plateau	9	2.5 ± 0.8	27.8
East Greenland Shelf & continental rise 81°N	27	1.1 ± 0.5	4.1
East Greenland Shelf & continental rise 75°N	27	1.8 ± 1.4	6.7
Central Greenland Sea	85	5.0 ± 0.5	5.9

In the permanently ice-covered areas of the East Greenland shelf primary production ranged around 27 g C m^{-2} yr^{-1} proposed by Subba Rao & Platt (1984) as a grand average for Arctic shelf areas. The lower primary production, however, coincided with a relatively low ingestion of 1 to 2 g C m^{-2} yr^{-1} for the aetideid and euchaetid community, so that their impact was comparable to the central Greenland Sea (4 to 7 %).

In contrast, the northern part of the investigation area was characterised by moderate I_{max} values of 1.3 g C m^{-2} yr^{-1} in the Nansen Basin and 2.5 g C m^{-2} yr^{-1} on the Yermak Plateau coinciding with an extremely low primary productivity of 9 g C m^{-2} yr^{-1}, which is typical of high-Arctic regions (Subbao Rao & Platt 1984; Wheeler et al. 1996). Due to this combination the ingestion of Aetideidae and Euchaetidae accounted for 14 to 28% of primary production (Table 13). Thus, aetideid and euchaetid copepods seem to have the strongest impact on the carbon flux in high-Arctic regions.

Comparisons between primary production and maximum ingestion of deep-sea copepods, however, underestimate their impact on the energy flux, since the prevailing euchaetid and some of the aetideid species are primarily carnivorous. Thus, they stand on a higher trophic level than the majority of epipelagic copepods and do not utilise primary production directly.

Compared to total mesozooplankton biomass, Aetideidae and Euchaetidae generally consumed less than 2% of the standing stock per day (Fig. 39). In the northwestern part of the investigation area (transects B and C) aetideid and euchaetid consumption was distributed evenly throughout the water column. A relatively stable vertical distribution of this consumption was also observed between 50 and 2000 m depth along transect D. In the central Greenland Sea, by contrast, the effect of daily consumption by Aetideidae and Euchaetidae on mesozooplankton standing stock increased with depth. Maximum daily consumption rates occurred in 1000 to 1500 m depth along the 75°N transect and accounted for 1.8% of total mesozooplankton biomass per day.

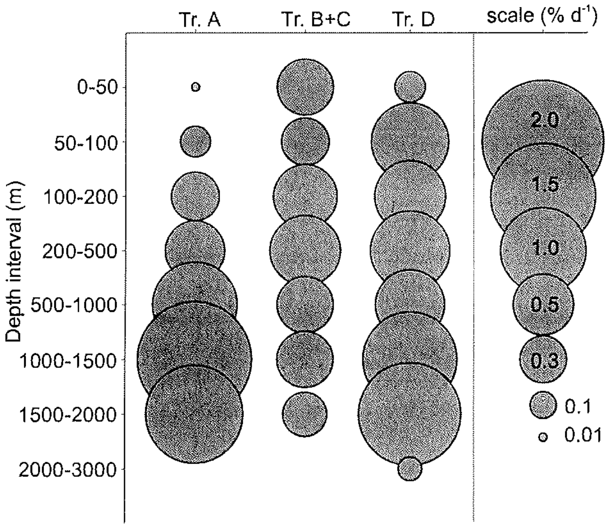

Fig. 39 Fraction of total mesozooplankton biomass consumed daily by Aetideidae and Euchaetidae in different areas of the Greenland Sea

Omnivorous Aetideidae rely to a large extent on detritus as a food resource (Hopkins 1985a and references therein). Thus, a comparison between the carbon demands of these detritivores and the annual vertical flux of organic carbon may provide an appropriate tool to evaluate their importance for pelagic remineralisation processes in the Greenland Sea. The annual vertical flux of particulate organic carbon in 500 m depth of the Greenland Sea ranged from 3.7 to 3.8 g C m^{-2} yr^{-1}, according to sediment trap data for 1988 to 1990 (Bodungen et al. 1995). Maximum ingestion rates of aetideid populations, integrated from 500 to 2000 m depth in the central Greenland Sea (Sts. 19, 20 and 35), measured 1.6 ± 0.1 g C m^{-2} yr^{-1}. Thus, Aetideidae possibly consume more than 40% of the available carbon supply.

Accordingly, the potential ingestion of carnivorous *Pareuchaeta* populations can be evaluated in comparison to the secondary production of herbivorous Calanidae, which represent their principal prey. The maximum ingestion of *Pareuchaeta* populations ranged from 0.6 ± 0.3 g C m^{-2} yr^{-1} in polar areas of the East Greenland Shelf and Nansen Basin, via 1.7 ± 0.6 g C m^{-2} yr^{-1} on the Yermak Plateau to 3.2 ± 0.3 g C m^{-2} yr^{-1} in oceanic regions of the Greenland Sea. In contrast, annual production of *Calanus glacialis* and *C. hyperboreus* in the central Arctic Basin measured 1.7 to 5.6 g wet mass (WM) m^{-2} yr^{-1} (Kosobokova 1986). Considerably higher secondary production rates of 12 g WM m^{-2} yr^{-1} and 11.4 to 26.9 g WM m^{-2} yr^{-1}, respectively, were determined for *C. glacialis* in the White Sea (Kosobokova 1986) and populations of *C. finmarchicus* and *C. hyperboreus* in the Norwegian Sea (Timokhina 1968). According to Kosobokova (pers. communication) dry mass accounts for 16% of Arctic zooplankton wet mass. Based on a carbon content of 50% in dry mass (Richter 1994), secondary production rates of *Calanus* can be converted to 0.1 to 0.5 g C m^{-2} yr^{-1} in the central Arctic Ocean, 1.0 g C m^{-2} yr^{-1} in the White Sea and 0.9 to 2.2 g C m^{-2} yr^{-1} in the Norwegian Sea.

Assuming that the conditions in the northern part of the investigation area (e.g. Nansen Basin and NE Greenland shelf) are comparable to those in the central Arctic and that secondary production in the Norwegian Sea is representative also for the southern to central part of the Greenland Sea, the potential ingestion of *Pareuchaeta* populations is at least one third to one half higher than the annual secondary production by herbivorous *Calanus* species throughout the investigation area. These calculations demonstrate that predatory *Pareuchaeta* may be able to control the population growth of *Calanus* and the biomass concentrated in the herbivorous trophic level.

It can be argued that these calculations, based on abundance data from spring, may overestimate the annual mean, since abundance in winter could be lower. However, Aetideidae and Euchaetidae are known to stay active during winter and many species seem to reproduce throughout the year (e.g. Seiler & Brandt 1997 for *Aetideopsis minor*, *A. rostrata* and *Pareuchaeta* spp.). Moreover, Richter (1994) showed for the Greenland Sea that the abundance of Aetideidae did not vary seasonally.

The results of the present study therefore underline that deep-sea copepods of the families Euchaetidae and Aetideidae represent important components of Arctic zooplankton communities. Both families have a substantial influence on the carbon and energy flux in the ecosystem of the Greenland Sea. Meso- and bathypelagic copepods strongly contribute to the remineralisation of organic matter in the water column and affect sedimentation processes via production and transformation of sinking particles. Carnivorous copepods, particularly *Pareuchaeta* species, are able to control the population growth of dominant herbivorous zooplankton. Thus, the present study provides additional evidence that the "top-down" control of zooplankton biomass by predation may be as important as "bottom-up" mechanisms based on food availability.

Future investigations and models dealing with the energy flux in marine ecosystems should therefore include pelagic midwater and deep-sea communities. Moreover, the present study demonstrates that the species-rich and highly diverse families Euchaetidae and Aetideidae may provide particularly suitable study objects for the assessment of general questions regarding pelagic biodiversity and deep-sea ecology (c.f. Mauchline 1995). From this point of view, it would be an interesting topic to assess the phylogenetic development and evolution of both taxa, elucidating the reasons for their generic radiation.

After more than a century of large-scale oceanographic expeditions and at the end of the International Year of the Ocean 1998, scientific knowledge about meso- and bathypelagic organisms is still fragmentary. Now it is time for science to shed light on the life in the darkness of the deep-sea.

"However remote, unfamiliar, and uncomplicated the oceanic environment may seem compared to the land, we should not forget that it is the biggest biome on Earth, and its biota plays a significant role in global biological and chemical cycles. Our present, incomplete, knowledge of diversity and structure suggests that midwater communities are stable, but we have little basis for predicting what effect changes in global climate, carbon balance, or sea level might have on their structure and function. If these changes might be hastened by human activities, we would be wise to improve our understanding of oceanic biodiversity enough to be able to detect changes when they begin, and not after they are irreversible."

Laurence P. Madin & Katherine A. C. Madin (1995)

6 Acknowledgements

At first I would like to thank Prof. Michael Spindler for providing an excellent working place at the Institute for Polar Ecology. His constant interest in my work and his constructive comments on an earlier draft contributed significantly to this dissertation.

Many thanks go to Prof. Wilhelm Hagen for his encouragement, skilful supervision and for his fruitful contributions.

Special thanks to Prof. Lenz, whose lectures raised my interest in zooplankton ecology. He also acted as correferent for this dissertation.

I am very grateful to the whole staff of the Institute for Polar Ecology for their kindness, assistance and, especially, for the inspiring atmosphere making it a pleasure to work at the IPÖ. Special thanks go to Dr. Michael Schmid for the introduction to couloximetry, Dorothee Stübing for her assistance with the GC, Dr. Iris Werner for reviewing the manuscript and Werner Dzomla for the photographic work.

The fieldwork of the present study was carried out during three Arctic cruises of RV "Polarstern". I would like to thank the captains and crews of ARK XII, ARK XIII/1 and 2 for their skilful support. I am especially grateful to the chief scientist Prof. Spindler and all participants of ARK XIII/1, who contributed not only to the scientific success of the cruise, but made the journey a remarkable experience.

Special thanks go to my colleagues and members of the joint zooplankton task forces during the various cruises, e.g. Carola Albers, Birgit Strohscher, Silke Lischka, Birgit Obermüller, Dr. Ksenia Kosobokova, Till Scherzinger, Dr. Barbara Niehoff, Dr. Martin Graeve, Prof. Wilhelm Hagen and Dr. Hans-Jürgen Hirche. We were a great team!

I am very grateful to my friends and colleagues Dr. Dan Seiler, Christopher Krembs and Kirsten Tuschling, who shared their office with me for over two years. Fruitful discussions and many jokes contributed to the friendly and inspiring atmosphere.

This work was partly funded by the Federal Ministry for Education and Research (BMBF) in the framework of the AOSGE pilot project.

Last but not least I would like to thank my parents for their solicitude and cordially support. They always encouraged me and provided help in any way during my studies and this work.

7 References

Aagård K (1989) A synthesis of the Arctic Ocean circulation. Rapp PV Reun Cons Perm Int Explor Mer 188:11-22

Aagård K & Carmack EC (1989) The role of sea ice and other fresh water in the arctic circulation. J Geophys Res 94, C10:14485-14498

Anderson LG, Björk G, Holby O, Jones EP, Kattner G, Koltermann KP, Liljeblad B, Lindegren R, Rudels B & Swift J (1994) Water masses and circulation in the Eurasian Basin: Results from the Oden 91 expedition. J Geophys Res 99, C2:3273-3283

Anderson LG, Jones EP, Koltermann KP, Schlosser P, Swift JH & Wallace DWR (1989) The first oceanographic section across the Nansen Basin in the Arctic Ocean. Deep-Sea Res, Pt A 36:475-482

Apollonio S (1959) Hydrobiological measurements on IGY Drifting Station Bravo. Trans Am Geophys Union 40:316-319

Arashkevich Ye G (1968) The food and feeding of copepods in the northwestern Pacific. Oceanologia 9:695-709

Ashjian CJ, Smith SL & Lane PVZ (1995) The Northeast Water Polynya during summer 1992: distribution and aspects of secondary production of copepods. J Geophys Research 100(C3):4371-4388

Auel H (1995) Die horizontale und vertikale Verbreitung des Mesozooplanktons im europäischen Sektor des Nordpolarmeeres – Übersicht und neue Daten. Diploma thesis, University of Kiel. 97 pp.

Augstein E & cruise participants (1997) The expedition ARCTIC '96 of RV "Polarstern" (ARK XII) with the Arctic Climate System Study (ACSYS). Ber Polarforsch 234:1-54

Bailey KM & Yen J (1983) Predation by a carnivorous marine copepod, *Euchaeta elongata* (Esterly), on eggs and larvae of the Pacific hake, *Merluccius productus*. J Plankton Res 5:71-82

Bakke JLW (1977) Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Euchaeta norvegica* (Crustacea, Copepoda) from 1971 to 1974. Sarsia 63:49-55

Bakke JLW & Valderhaug VA (1978) Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population biology, biomass, and caloric content of *Chiridius armatus* (Crustacea, Copepoda). Sarsia 63:247-254

Båmsted U (1974) Biochemical studies on the deep-water pelagic community of Korsfjorden, western Norway. Methodology and sample design. Sarsia 56:71-86

Båmstedt U (1975) Studies on the deep-water pelagic community of Korsfjorden, western Norway. Ecological aspects of individual variations in weight and protein and lipid content of *Euchaeta norvegica* (Copepoda). Sarsia 59:31-46

Båmsted U (1978) Studies on the deep-water pelagic community of Korsfjorden, western Norway. Seasonal variation in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. Sarsia 63:145-154

Båmsted U (1981) Seasonal energy requirements of macrozooplankton from Kosterfjorden, western Sweden. Kieler Meeresforsch, Sonderh 5:140-152

Båmsted U & Holt MR (1978) Experimental studies on the deep-water pelagic community of Korsfjorden, western Norway. Prey-size preference and feeding of *Euchaeta norvegica* (Copepoda). Sarsia 63:225-236

Bjornberg TKS (1973) The planktonic copepods of the Marchile 1 expedition and of the "Eltanin" cruises 3-6 taken in the SE Pacific. Bolm Fac Filos Cienc Univ S Paulo, Zool Biol mar (n ser) 30:245-394

Blaume F (1992) Hochakkumulationsgebiete am norwegischen Kontinentalhang: Sedimentologische Abbilder Topographie-geführter Strömungsmuster. Ber Sonderforsch 313, University of Kiel 36:1-150

Bligh EG & Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911-917

Bodungen von B, Antia A, Bauerfeind E, Haupt O, Koeve W, Machado E, Peeken I, Peinert R, Reitmeier S, Thomsen C, Voss M, Wunsch M, Zeller U & Zeitschel B (1995) Pelagic processes and vertical flux of particles: an overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. Geol Rundsch 84:11-27

Borchers P & Hutchings L (1986) Starvation tolerance, development time and egg production of *Calanoides carinatus* in the Southern Benguela Current. J Plankton Res 8:917-925

Boysen-Ennen E, Hagen W, Hubold G & Piatkowski U (1991) Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. Marine Biology 111:227-235

Boysen-Ennen E & Piatkowski U (1988) Meso- and macrozooplankton communities in the Weddell Sea. Polar Biol 9:17-35

Bradford JM (1969) New species of *Aetideopsis* Sars and *Bradyidius* Giesbrecht (Copepoda: Calanoida) from the southern hemisphere. N Z J mar freshw Res 3:73-97

Bradford JM & Jillett JB (1980) The marine fauna of New Zealand: pelagic calanoid copepods: family Aetideidae. Memoirs of the New Zealand Oceanographic Institute 86:1-102

Brady GS (1918) Copepoda. Scient Rep Australas antarct Exped (C) 5(3):1-48

Brodskiy KA (1950) Calanoida of the far eastern seas and polar basin of the USSR. In: Pavlovskii EN (ed) Keys to the fauna of the USSR, No 35. Israel Progr Sci Transl, Jerusalem 1967, 440 pp.

Burns CW (1985) The effects of starvation on naupliar development and survivorship of three species of *Boeckella* (Copepoda: Calanoida). Arch Hydrobiol Beih 21:297-309

Calbet A & Alcaraz M (1997) Growth and survival rates of early developmental stages of *Acartia grani* (Copepoda: Calanoida) in relation to food concentration and fluctuations in food supply. Mar Ecol Prog Ser 147:181-186

Carmack E & Aagård K (1973) On the deep water of the Greenland Sea. Deep-Sea Res 20:687-715

Chindonova JG (1959) Feeding of some groups of macroplankton in the northwestern Pacific. Trudi Inst Okeanol 30:166-189

Christie WW (1982) Lipid analysis. Pergamon Press, Oxford. 207 pp.

Clapham PJ & Brownell Jr. RL (1996) The potential for interspecific competition in baleen whales. Rep Int Whal Commn 46:361-367

Clarke A (1983) Life in cold water: the physiological ecology of polar marine ectotherms. Oceanogr Mar Biol Ann Rev 21:341-453

Coachman LK & Aagård K (1974) Physical oceanography of Arctic and Subarctic seas. In: Herman Y (ed) Marine geology and oceanography of the Arctic seas. Springer Verlag, New York. pp. 1-72

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am Nat 122:661-696

Conover RJ (1967) Reproductive cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*. Crustaceana 13:61-72

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168:127-142

Conover RJ & Huntley M (1991) Copepods in ice-covered seas – Distribution, adaptations, growth patterns and life cycle strategies in polar seas. J Mar Systems 2:1-42

Cooney JD & Gehrs CW (1980) The relationship between egg size and naupliar size in the calanoid copepod *Diaptomus clavipes* Schacht. Limnol Oceanogr 25:549-552

Davis CC (1949) The pelagic Copepoda of the northeastern Pacific Ocean. University of Washington Publications in Biology 14:1-118

Diel S (1991) Zur Lebensgeschichte dominanter Copepodenarten (*Calanus finmarchicus, C. glacialis, C. hyperboreus, Metridia longa*) in der Framstraße. Ber Polarforsch 88:1-113

Diepenbroek M, Grobe H, Reinke M (1997) SEPAN – Sediment and paleoclimate data network. In: Lautenschlager M & Reinke M (eds) Climate and environmental data base systems. Kluwer, Boston, pp 147-161

Dorrien von CF (1993) Ökologie und Respiration ausgewählter arktischer Bodenfischarten. Ber Polarforsch 125:1-99

English TS (1961) Some biological oceanographic observations in the central North Polar Sea, Drift Station Alpha, 1957-1958. Arctic Inst No Am, Final Contract Rept AF 19 (604) 3073

Esterly CO (1911) Third report on the Copepoda of the San Diego region. Univ Calif Publ Zool 6:313-352

Esterly CI (1916) The feeding habits and food of pelagic copepods and the question of nutrition by organic substances in solution in the water. Univ California Pub Zool 16:171-184

Fahl K (1995) Biochemische Untersuchungen zum Lipidstoffwechsel antarktischer Copepoden. Ber Polarforsch 157:1-135

Farran GP (1929) Crustacea. Pt. 10. Copepoda. Brit. Antarctic (Terra Nova) Exped. Zool 1910. Nat Hist Rep Zool 8(3):203-306

Folch J, Lees M & Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. J biol Chem 226:497-509

Foster BA (1987) Composition and abundance of zooplankton under the spring sea-ice of McMurdo Sound, Antarctica. Polar Biol 8:41-48

Geynrikh AK (1958) On the nutrition of marine copepods in the tropical region. Dokl Akad Nauk SSSR 119:1028-1034

Geynrikh AK (1986) Mass species of oceanic phytophagous copepods and their ecology. Oceanology 26:213-217

Giguère LA, St-Pierre J-F, Bernier B, Vézina A, Rondeau J-G (1989) Can we estimate the true weight of zooplankton samples after chemical preservation? Can J Fish Aquat Sci 46:522-527

Gradinger R, Friedrich C & Spindler M (in press) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep-Sea Res

Graeve M, Kattner G & Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97-110

Graeve M, Kattner G & Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53-61

Grainger EH (1963) Copepods of the genus *Calanus* as indicators of eastern Canadian waters. In: Dunbar MJ (ed) Marine distributions. R Soc Can, Spec Publ 5, pp 68-94

Grainger EH (1989) Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey L, Alexander V (eds) Proc. 6th Conf. Comité Arctique Int. 1985, Brill, Leiden, pp. 48-60

Grice GD & Hülsemann K (1965) Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the northeast Atlantic. Journal of Zoology 146:213-262

Guglielmo L & Ianora A (eds 1995) Atlas of marine zooplankton. Straits of Magellan. Copepods. Springer, Berlin, 279 pp.

Guisande C, Sanchez J, Maneiro I & Miranda A (1996) Trade-off between offspring number and offspring size in the marine copepod *Euterpina acutifrons* at different food concentrations. Mar Ecol Prog Ser 143:37-44

Hagen W (1988) Zur Bedeutung der Lipide im antarktischen Zooplankton. Ber Polarforsch 49:1-129

Hagen W, Kattner G & Graeve M (1993) *Calanoides acutus* and *Calanus propinquus*, Antarctic copepods with different lipid storage modes via wax esters or triacylglycerols. Mar Ecol Prog Ser 97:135-142

Hagen W, Kattner G & Graeve M (1995) On the lipid biochemistry of polar copepods: compositional differences in the Antarctic calanoids *Euchaeta antarctica* and *Euchirella rostromagna*. Marine Biology 123:451-457

Hanssen H (1993) Zur Verteilung des oberflächennahen Zooplanktons im europäischen Nordpolarmeer. Diploma thesis, University of Kiel. 97 pp.

Harding GCH (1974) The food of deep-sea copepods. J mar biol Ass UK 54:141-155

Hardy AC & Gunther FR (1935) The plankton of the South Georgia Whaling grounds and adjacent waters, 1926-1927. Discovery Rep 11. 456 pp.

Hersch PA (1973) Couloximetry. Am Lab 5:29-36

Hirche H-J (1987) Temperature and plankton. II. Effect on respiration and swimming activity in copepods from the Greenland Sea. Marine Biology 94:347-356

Hirche H-J (1989) Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments. Marine Biology 103:311-318

Hirche H-J (1996a) The reproductive biology of the marine copepod, *Calanus finmarchicus* – a review. Ophelia 44:111-128

Hirche H-J (1996b) Diapause in the marine copepod, *Calanus finmarchicus* – a review. Ophelia 44:129-143

Hirche H-J (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128:607-618

Hirche H-J, Bohrer RN (1987) Reproduction of the Arctic copepod *Calanus glacialis* in Fram Strait. Marine Biology 94:11-17

Hirche H-J, Hagen W, Mumm N & Richter C (1994) The Northeast Water Polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. Polar Biol 14:491-503

Hirche H-J, Meyer U & Niehoff B (1997) Egg production of *Calanus finmarchicus*: effect of temperature, food and season. Marine Biology 127:609-620

Hopkins CCE (1978) The male genital system, and spermatophore production and function in *Euchaeta norvegica* Boeck (Copepoda: Calanoida). Journal of Experimental Marine Biology and Ecology 35:197-231

Hopkins CCE, Sargent JR & Nilssen EM (1993) Total lipid content, and lipid and fatty acid composition of the deep-water prawn *Pandalus borealis* from Balsfjord, northern Norway: growth and feeding relationships. Mar Ecol Prog Ser 96:217-228

Hopkins TL (1969a) Zooplankton standing crop in the Arctic Ocean. Limnol Oceanogr 14:80-85

Hopkins TL (1969b) Zooplankton biomass related to hydrography along the drift track of Arlis II in the Arctic Basin and East Greenland Current. J Fish Res Board Can 26:305-310

Hopkins TL (1985a) Food web of an Antarctic midwater ecosystem. Marine Biology 89:197-212

Hopkins TL (1985b) The zooplankton community of Croker Passage, Antarctic Peninsula. Polar Biol 4:161-170

Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Marine Biology 96:93-106

Horridge GA & Boulton PS (1967) Prey detection by Chaetognatha via a vibration sense. Proc Roy Soc B 168:413-419

Hughes KH (1968) Seasonal vertical distribution of copepods in the Arctic Water in the Canadian Basin of the North Polar Sea. Thesis. Univ. of Washington. 49 pp.

Hutchinson GE (1967) A treatise on limnology. II. Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York

Ikeda T & Hirakawa K (1996) Early development and estimated life cycle of the mesopelagic copepod *Pareuchaeta elongata* in the southern Japan Sea. Mar Biol 126:261-270

Kattner G & Fricke HSG (1986) Simple gas-liquid chromatographic method for simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. J Chromat 361:313-318

Kattner G, Graeve M & Hagen W (1994) Ontogenetic and seasonal changes in lipid and fatty acid/alcohol compositions of the dominant Antarctic copepods *Calanus propinquus*, *Calanoides acutus* and *Rhincalanus gigas*. Marine Biology 118:637-644

Kattner G & Hagen W (1995) Polar herbivorous copepods – different pathways in lipid biosynthesis. ICES J m Sci 52:329-335

Keddy PA (1989) Competition. Chapman and Hall, London. 202pp.

Kleppel GS, Burkart CA, Carter K & Tomas C (1996) Diets of calanoid copepods on the West Florida continental shelf: relationships between food concentration, food composition and feeding activity. Marine Biology 127:209-217

Kosobokova KN (1982) Composition and distribution of the biomass of zooplankton in the central Arctic Basin. Oceanology 22:744-750

Kosobokova (1986) Estimation of production of common herbivorous copepods of the central Arctic Basin. Oceanology 26:749-752

Kosobokova KN, Hanssen H, Hirche H-J & Knickmeier K (1998) Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. Polar Biol 19:63-76

Kurbjeweit F (1988) Untersuchungen zur Lage und Struktur von Sensillen bei calanoiden Copepoden (*Calanus glacialis*, *Pareuchaeta norvegica*, *Metridia longa*). Diploma thesis, University of Kiel.

Lee RF, Nevenzel JC & Paffenhöfer G-A (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Marine Biology 9:99-108

Legendre L, Ackley SF, Dieckmann GS, Gulliksen B, Horner R, Hoshiai T, Melnikov IA, Reeburgh WS, Spindler M & Sullivan CW (1992) Ecology of sea ice biota. 2. Global significance. Polar Biol 12:429-444

Madin LP & Madin KAC (1995) Diversity in a vast and stable habitat. Midwater is one of Earth's least explored environments. Oceanus 2 (fall/ winter):20-24

Mahaut M-L, Sibuet M & Shirayama Y (1995) Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Research 42:1575-1582

Markhaseva EL (1984) Aetideidae copepods (Copepoda, Calanoida) of the eastern sector of the central Arctic Basin. Oceanology 24:391-393

Markhaseva EL (1989) Review of the genus *Pseudochirella* (Copepoda, Calanoida). Issled Fauny Morei 41(49):33-60 (in Russian)

Markhaseva EL (1996) Calanoid copepods of the family Aetideidae of the world ocean, vol 268. Proc Zoology Institute, Russian Academy of Science, St. Petersburg

Mauchline J (1992) Restriction of body size spectra within species of deep-sea plankton. Mar Ecol Prog Ser 90:1-8

Mauchline J (1994a) Seasonal variation in some population parameters of *Euchaeta* species (Copepoda: Calanoida). Marine Biology 120:561-570

Mauchline J (1994b) Spermatophore transfer in *Euchaeta* species in a 2000 m water column. Hydrobiologia 293:309-316

Mauchline J (1995) Bathymetric adaptations of life history patterns of congeneric species (*Euchaeta*: Calanoida) in a 2000 m water column. ICES J mar Sci 52:511-516

Mauchline J (1998) The biology of calanoid copepods. In: Blaxter JHS, Southward AJ & Tyler PA (eds) Advances in marine biology. Academic Press, San Diego. 710 pp.

Milne A (1961) Definition of competition among animals. Symp Soc Exp Biol 15:40-61

Moloney CL & Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. Limnol Oceanogr 34:1290-1299

Morris RJ (1972) The occurrence of wax esters in crustaceans from the north-east Atlantic Ocean. Mar Biol 16:102-107

Morris MJ & Hopkins TL (1983) Biochemical composition of crustacean zooplankton from the eastern Gulf of Mexico. J Exp Mar Biol Ecol 69:1-19

Mullin MM (1966) Selective feeding by calanoid copepods from the Indian Ocean. In: Barnes H (ed) Some contemporary studies in marine science. George Allen and Unwin Ltd, London. pp. 313-334

Mumm N (1991) Zur sommerlichen Verteilung des Mesozooplanktons im Nansen-Becken, Nordpolarmeer. Ber Polarforsch 92:1-146

Mumm N, Auel H, Hanssen H, Hagen W, Richter C & Hirche H-J (1998) Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. Polar Biol 20:189-197

Nemoto T, Mauchline J & Kamada K (1976) Brood size and chemical composition of *Pareuchaeta norvegica* (Crustacea: Copepoda) in Loch Etive, Scotland. Mar Biol 36:151-157

Newbury TK (1972) Vibration perception by chaetognaths. Nature 236:459-460

Øresland V (1995) Winter population structure and feeding of the chaetognath *Eukrohnia hamata* and the copepod *Euchaeta antarctica* in Gerlache Strait, Antarctic Peninsula. Mar Ecol Prog Ser 115:77-86

Østvedt O-J (1955) Zooplankton investigations from weather ship "M" in the Norwegian Sea, 1948-49. Hvalradets Skrifter 40:1-93

Owre HB & Foyo M (1967) Copepods of the Florida Current. Fauna Caribaea 1, Crustacea, Part 1: Copepoda. pp. 1-137

Paffenhöfer GA (1971) Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar Biol 11:286-298

Pakhomov EA & Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91-100

Park T (1975a) Calanoid copepods of the genera *Aetideopsis*, *Pseudaetideus*, and *Chiridius* from the Gulf of Mexico. Bull mar Sci 25:272-290

Park T (1975b) Calanoid copepods of the genera *Gaetanus* and *Gaidius* from the Gulf of Mexico. Bull mar Sci 25:9-34

Park T (1978) Calanoid copepods from antarctic and subantarctic waters (Euchaetidae and Aetideidae). Antarct Res Ser 27:91-290

Park T (1994a) Taxonomy and distribution of the marine calanoid copepod family Euchaetidae. Bull Scripps Inst Oceanogr 29:1-203

Park T (1994b) Geographic distribution of the bathypelagic genus *Paraeuchaeta* (Copepoda, Calanoida). Hydrobiologia 292/293:317-332

Parkinson CL (1991) Interannual variability of the spatial distribution of sea ice in the North Polar region. J Geophys Res 96(C3):4791-4801

Parkinson CL & Cavalieri DJ (1989) Arctic sea ice 1973-1987: seasonal, regional, and interannual variability. J Geophys Res 94(C10):14499-14523

Peck LS & Uglow RF (1990) Two methods for the assessment of the oxygen content of small volumes of seawater. J Exp Mar Biol Ecol 141:53-62

Perkin RG & Lewis EL (1984) Mixing in the West Spitsbergen Current. J Phys Oceanogr 14:1315-1325

Piepenburg D & Schmid MK (1997) A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance, and estimates of biomass and organic carbon demand. Mar Ecol Prog Ser 147:63-75

Pond D, Harris R, Head R & Harbour D (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. Mar Ecol Prog Ser 143:45-63

Quadfasel D, Gascard J-C & Koltermann K-P (1987) Large-scale oceanography in Fram Strait during the 1984 Marginal Ice Zone Experiment. J Geophys Res 92(C7):6719-6728

Quadfasel D & Meincke J (1987) Note on the thermal structure of the Greenland Sea gyres. Deep-Sea Res 34:1883-1888

Raymont JEG (1983) Plankton and productivity in the oceans, 2. Zooplankton. Pergamon Press, Oxford. 824 pp.

Razouls C (1993) Bilan taxonomique actuel des copepodes planctoniques marins et des eaux saumatres. Proceedings of the first European Crustacean Conference 1992, 64:300-313

Rey L (1982) The Arctic Ocean. The hydrographic environment and the fate of pollutants. London. 433 pp.

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Ber Polarforsch 154:1-87

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

Ross RM (1982) Energetics of *Euphausia pacifica*. 1. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar Biol 68:1-13

Rudels B (1993) High latitude ocean convection. In: Stone DB & Runcorn SK (eds) Flow and creep in the solar system: Observations, modeling and theory. Kluwer Academic Publ. pp. 323-356

Rudels B (1995) The thermohaline circulation of the Arctic Ocean and the Greenland Sea. Phil Trans R Soc Lond A 352:287-299

Rudels B, Jones EP, Anderson LG & Kattner G (1994) On the Intermediate Depth Waters of the Arctic Ocean. In: Johannessen OM, Muench RD & Overland JE (eds) The polar oceans and their role in shaping the global environment. The Nansen Centennial Volume. Geophys Monogr Am Geophys Union 85:33-46

Runge JA (1985) Egg production rates of *Calanus finmarchicus* in the sea of Nova Scotia. Arch Hydrobiol (Beih Ergebn Limnol) 21:33-40

Sars GO (1900) Crustacea. In: Nansen F (ed) The Norwegian North Polar Expedition 1893-1896. Scient Res 1(5):1-137

Sars GO (1903) An account of the Crustacea of Norway, 4. Copepoda, Calanoida. – With short descriptions and figures of all the species. Bergen Museum, 171 pp.

Sars GO (1905) Liste preliminaire des Calanoides recueillis pendant les campagnes de S.A.S. le Prince Albert de Monaco, avec diagnoses des genres et des especes nouvelles (1-er partie). Bull Mus oceanogr. Monaco 26:1-22

Schmid MK (1996) Zur Verbreitung und Respiration ökologisch wichtiger Bodentiere in den Gewässern um Svalbard (Arktis). Ber Polarforsch 202:1-92

Schnack-Schiel SB & Hagen W (1995) Life-cycle strategies of *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. ICES J mar Sci 52:541-548

Scott A (1909) The Copepoda of the Siboga Expedition. Part I. Free-swimming, littoral and semi-parasitic Copepoda. Siboga Expeditie 29a:1-323

Seiler D & Brandt A (1997) Seasonal occurrence of planktic Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biol 17:337-349

Shih CT & Maclellan DC (1981) *Aetideopsis albatrossae*, new species (Crustacea: Copepoda) from east of Mindoro, the Philippines. J Crust Biol 1:567-572

Shuert PG & Hopkins TL (1987) The vertical distribution and feeding ecology of *Euchaeta marina* in the eastern Gulf of Mexico. Contributions in Marine Science 30:49-61

Skjoldal HR, Båmstedt U, Klinken J & Laing A (1984) Changes with time after capture in the metabolic activity of the carnivorous copepod *Euchaeta norvegica* Boeck. J Exp Mar Biol Ecol 83:195-210

Sommer U (1998) Biologische Meereskunde. Springer, Berlin. 475 pp.

Spindler M, Hagen W & Stübing D (eds, 1998) Scientific cruise report of the Arctic expedition ARK-XIII/1 of RV "Polarstern" in 1997. Ber Polarforsch 296:1-65

Steffensen JF (1989) Some errors in respirometry of aquatic breathers: how to avoid and correct for them. Fish Physiology and Biochemistry 6:49-59

Stein R & Fahl K (eds, 1997) Scientific cruise report of the Arctic expedition ARK-XIII/2 of RV "Polarstern" in 1997. Ber Polarforsch 255:1-235

St. John MA & Lund T (1996) Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar Ecol Prog Ser 131:75-85

Subba Rao DV & Platt T (1984) Primary production of Arctic waters. Polar Biol 3:191-201

Tanaka O (1957a) The pelagic copepods of the Izu Region, middle Japan. Systematic account. III. Family Aetideidae (Part 1). Publ Seto Mar Biol Lab 6:31-68

Tanaka O (1957b) The pelagic copepods of the Izu Region, middle Japan. Systematic account. IV. Family Aetideidae (Part 2). Publ Seto Mar Biol Lab 6:169-207

Tanaka O & Omori M (1968) Additional report on calanoid copepods from the Izu Region. Part 1. *Euchaeta* and *Pareuchaeta*. Publ Seto Mar Biol Lab 16:219-261

Tanaka O & Omori M (1970a) Additional report on calanoid copepods from the Izu Region. Part 3-A. *Euaetideus*, *Aetideopsis*, *Chiridius*, *Gaidius* and *Gaetanus*. Publ Seto Mar Biol Lab 18:109-141

Tanaka O & Omori M (1970b) Additional report on calanoid copepods from the Izu Region. Part 3-B. *Chirundina*, *Undeuchaeta*, *Pseudeuchaeta*, *Valdiviella* and *Chiridiella*. Publ Seto Mar Biol Lab 18:143-155

Timokhina AF (1968) Production by common species of zooplankton in the Norwegian Sea. Tr Polyarn n-issled in-ta morsk rybn kh-va I okeanogr 23:173

Tiselius P, Jonsson PR, Kaartvedt S, Olsen EM & Jørstad T (1997) Effects of copepod foraging behavior on predation risk: An experimental study of the predatory copepod *Pareuchaeta norvegica* feeding on *Acartia clausi* and *A. tonsa* (Copepoda). Limnol Oceanogr 42:164-170

Tsuda A (1994) Starvation tolerance of planktonic marine copepod *Pseudocalanus newmanni* Frost. J Exp Biol Ecol 181:81-89

Verity PG & Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130:277-293

Vervoort W (1949) Some new and rare Copepoda from East Indian Seas. Zool Verh Leiden 5:1-53

Vervoort W (1951) Plankton copepods from the Atlantic sector of the Antarctic. Verh ned Akad Wet, Afd Natuurk, Sect 2. 47(2):1-156

Vervoort W (1952a) Copepoda, suborder: Calanoida, family: Aetideidae. Key to the genera and references. Fich Ident Zoopl 41:1-4

Vervoort W (1952b) Copepoda, suborder: Calanoida, family: Aetideidae, genera: *Aetideus*, *Euaetideus*, *Aetideopsis*. Fich Ident Zoopl 42:1-4

Vervoort W (1952c) Copepoda, suborder: Calanoida, family: Aetideidae, genera: *Bradyidius*, *Bradyetes*, *Bryaxis*. Fich Ident Zoopl 43:1-4

Vervoort W (1952d) Copepoda, suborder: Calanoida, family: Aetideidae, genera: *Chiridius*, *Pseudaetideus*, *Chiridiella*. Fich Ident Zoopl 44:1-4

Vervoort W (1952e) Copepoda, suborder: Calanoida, family: Aetideidae, genus: *Gaidius*. Fich Ident Zoopl 45:1-4

Vervoort W (1952f) Copepoda, suborder: Calanoida, family: Aetideidae, genus: *Gaetanus*. Fich Ident Zoopl 46:1-5

Vervoort W (1952g) Copepoda, suborder: Calanoida, family: Aetideidae, genus: *Euchirella*. Fich Ident Zoopl 47:1-6

Vervoort W (1952h) Copepoda, suborder: Calanoida, family: Aetideidae, genus: *Pseudochirella*. Fich Ident Zoopl 48:1-4

Vervoort W (1952i) Copepoda, suborder: Calanoida, family: Aetideidae, genera: *Chirundina*, *Undeuchaeta*, *Pseudeuchaeta*. Fich Ident Zoopl 49:1-4

Vervoort W (1957) Copepods from Antarctic and sub-Antarctic plankton samples. Rep BANZ Antarctic Res Exped 1929-1931 (ser B) 3. 160 pp.

Vinberg GG (1956) Rate of metabolism and food requirements of fishes. Beloruss State University, Minsk (Fish Res Bd Can Transl Ser No 194, 1960), 253 pp.

Vinogradov ME & Shushkina EA (1987) Functioning of the planktonic communities in the epipelagic zone of the ocean. Nauka Press, Moscow (in Russian)

Ward P & Wood AG (1988) The distribution of the Euchaetidae (Copepoda: Calanoida) around South Georgia. Polar Biol 9:45-52

Weikert H & John H-C (1981) Experiences with a modified Be multiple opening-closing plankton net. J Plankton Res 3:167-176

Wheeler EH (1970) Atlantic deep-sea calanoid Copepoda. Smithsonian Contributions to Zoology 55:1-31

Wheeler PA, Gosselin M, Sherr E, Thibault D, Kirchman DL, Benner R & Whitledge TE (1996) Active cycling of organic carbon in the central Arctic Ocean. Nature 380:697-699

Wickstead JH (1962) Food and feeding in pelagic copepods. Proc Zool Soc Lond 139:545-555

Wieser W (1986) Bioenergetik. Thieme, Stuttgart

With C (1915) Copepoda 1. Calanoida. Amphascandria. Dan Ingolf Exped 3(4):1-260

Wolfenden RN (1904) Notes on the Copepoda of the North Atlantic Sea and the Faroe Channel. J mar biol Ass UK 7:110-146

Wolfenden RN (1911) Die marinen Copepoden: II. Die pelagischen Copepoden der Westwinddrift und des südlichen Eismeers. Deutsche Südpolar-Expedition 1901-1903, 12:181-380

Yen J (1982) Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. J Exp Mar Biol Ecol 63:105-117

Yen J (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. Marine Biology 75:69-77

Yen J (1985) Selective predation by the carnivorous marine copepod *Euchaeta elongata*: Laboratory measurements of predation rates verified by field observations of temporal and spatial feeding patterns. Limnol Oceanogr 30:577-597

Yen J (1987) Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua* L. J Exp Mar Biol Ecol 112:283-296

Yen J (1991) Predatory feeding behavior of an Antarctic marine copepod, *Euchaeta antarctica*. In: Sakshaug E, Hopkins CCE & Øritsland NA (eds) Proceedings of the Pro Mare Symposium on polar marine ecology, Trondheim, 12-16 May 1990. Polar Research 10:433-442

Zvereva JA (1976) About functional significance of morphological formations on genital segment of females *Pareuchaeta*. In: Explorations of the fauna of the seas, 18 (16). Functional morphology, growth and development of invertebrates of sea plankton. Academy of Sciences of the USSR, Zoological Inst, Leningrad. pp. 70-74

Folgende Hefte der Reihe „Berichte zur Polarforschung“ sind bisher erschienen:

* **Sonderheft Nr. 1/1981** – „Die Antarktis und ihr Lebensraum“
Eine Einführung für Besucher – Herausgegeben im Auftrag von SCAR

Heft Nr. 1/1982 – „Die Filchner-Schelfeis-Expedition 1980/81“
zusammengestellt von Heinz Kohnen

* **Heft-Nr. 2/1982** – „Deutsche Antarktis-Expedition 1980/81 mit FS ‚Meteor‘“
First International BIOMASS Experiment (FIBEX) – Liste der Zooplankton- und Mikronektonnetzfänge
zusammengestellt von Norbert Klages.

Heft Nr. 3/1982 – „Digitale und analoge Krill-Echolot-Rohdatenerfassung an Bord des Forschungsschiffes ‚Meteor‘“ (im Rahmen von FIBEX 1980/81, Fahrtabschnitt ANT III), von Bodo Morgenstern

Heft Nr. 4/1982 – „Filchner-Schelfeis-Expedition 1980/81“
Liste der Planktonfänge und Lichtstärkemessungen
zusammengestellt von Gerd Hubold und H. Eberhard Drescher

* **Heft Nr. 5/1982** – "Joint Biological Expedition on RRS 'John Biscoe', February 1982"
by G. Hempel and R. B. Heywood

* **Heft Nr. 6/1982** – „Antarktis-Expedition 1981/82 (Unternehmen ‚Eiswarte‘)“
zusammengestellt von Gode Gravenhorst

Heft Nr. 7/1982 – „Marin-Biologisches Begleitprogramm zur Standorterkundung 1979/80 mit MS ‚Polarsirkel‘ (Pre-Site Survey)“ – Stationslisten der Mikronekton- und Zooplanktonfänge sowie der Bodenfischerei
zusammengestellt von R. Schneppenheim

Heft Nr. 8/1983 – "The Post-Fibex Data Interpretation Workshop"
by D. L. Cram and J.-C. Freytag with the collaboration of J. W. Schmidt, M. Mall, R. Kresse, T. Schwinghammer

* **Heft Nr. 9/1983** – "Distribution of some groups of zooplankton in the inner Weddell Sea in summer 1979/80"
by I. Hempel, G. Hubold, B. Kaczmaruk, R. Keller, R. Weigmann-Haass

Heft Nr. 10/1983 – „Fluor im antarktischen Ökosystem“ – DFG-Symposium November 1982
zusammengestellt von Dieter Adelung

Heft Nr. 11/1983 – "Joint Biological Expedition on RRS 'John Biscoe', February 1982 (II)"
Data of micronecton and zooplankton hauls, by Uwe Piatkowski

Heft Nr. 12/1983 – „Das biologische Programm der ANTARKTIS-I-Expedition 1983 mit FS ‚Polarstern‘“
Stationslisten der Plankton-, Benthos- und Grundschleppnetzfänge und Liste der Probennahme an Robben und Vögeln, von H. E. Drescher, G. Hubold, U. Piatkowski, J. Plötz und J. Voß

* **Heft Nr. 13/1983** – „Die Antarktis-Expedition von MS ‚Polarbjörn‘ 1982/83“ (Sommerkampagne zur Atka-Bucht und zu den Kraul-Bergen), zusammengestellt von Heinz Kohnen

* **Sonderheft Nr. 2/1983** – „Die erste Antarktis-Expedition von FS ‚Polarstern‘ (Kapstadt, 20. Januar 1983 – Rio de Janeiro, 25. März 1983)“, Bericht des Fahrtleiters Prof. Dr. Gotthilf Hempel

Sonderheft Nr. 3/1983 – „Sicherheit und Überleben bei Polarexpeditionen“
zusammengestellt von Heinz Kohnen

* **Heft Nr. 14/1983** – „Die erste Antarktis-Expedition (ANTARKTIS I) von FS ‚Polarstern‘ 1982/83“
herausgegeben von Gotthilf Hempel

Sonderheft Nr. 4/1983 – "On the Biology of Krill *Euphausia superba*" – Proceedings of the Seminar and Report of the Krill Ecology Group, Bremerhaven 12.–16. May 1983, edited by S. B. Schnack

Heft Nr. 15/1983 – "German Antarctic Expedition 1980/81 with FRV 'Walther Herwig' and RV 'Meteor'" –
First International BIOMASS Experiment (FIBEX) – Data of micronekton and zooplankton hauls
by Uwe Piatkowski and Norbert Klages

Sonderheft Nr. 5/1984 – "The observatories of the Georg von Neumayer Station", by Ernst Augstein

Heft Nr. 16/1984 – "FIBEX cruise zooplankton data"
by U. Piatkowski, I. Hempel and S. Rakusa-Suszczewski

Heft Nr. 17/1984 – „Fahrtbericht (cruise report) der ‚Polarstern‘-Reise ARKTIS I, 1983“
von E. Augstein, G. Hempel und J. Thiede

Heft Nr. 18/1984 – „Die Expedition ANTARKTIS II mit FS ‚Polarstern‘ 1983/84“,
Bericht von den Fahrtabschnitten 1, 2 und 3, herausgegeben von D. Fütterer

Heft Nr. 19/1984 – „Die Expedition ANTARKTIS II mit FS ‚Polarstern‘ 1983/84“,
Bericht vom Fahrtabschnitt 4, Punta Arenas–Kapstadt (Ant-II/4), herausgegeben von H. Kohnen

Heft Nr. 20/1984 – „Die Expedition ARKTIS II des FS ‚Polarstern‘ 1984, mit Beiträgen des FS ‚Valdivia‘ und des Forschungsflugzeuges ‚Falcon 20‘ zum Marginal Ice Zone Experiment 1984 (MIZEX)“
von E. Augstein, G. Hempel, J. Schwarz, J. Thiede und W. Weigel

Heft Nr. 21/1985 – "Euphausiid larvae in plankton samples from the vicinity of the Antarctic Peninsula, February 1982" by Sigrid Marschall and Elke Mizdalski

Heft Nr. 22/1985 – "Maps of the geographical distribution of macrozooplankton in the Atlantic sector of the Southern Ocean" by Uwe Piatkowski

Heft Nr. 23/1985 – „Untersuchungen zur Funktionsmorphologie und Nahrungsaufnahme der Larven des Antarktischen Krills *Euphausia superba* Dana“ von Hans-Peter Marschall

Heft Nr: 24/1985 – „Untersuchungen zum Periglazial auf der König-Georg-Insel Südshetlandinseln/
Antarktika. Deutsche physiogeographische Forschungen in der Antarktis. – Bericht über die Kampagne
1983/84" von Dietrich Barsch, Wolf-Dieter Blümel, Wolfgang Flügel, Roland Mäusbacher, Gerhard
Stablein, Wolfgang Zick

* **Heft-Nr. 25/1985** – „Die Expedition ANTARKTIS III mit FS ‚Polarstern' 1984/1985"
herausgegeben von Gotthilf Hempel.

***Heft-Nr. 26/1985** – "The Southern Ocean"; A survey of oceanographic and marine meteorological
research work by Hellmer et al.

Heft Nr. 27/1986 – „Spatpleistozäne Sedimentationsprozesse am antarktischen Kontinentalhang
vor Kapp Norvegia, ostliche Weddell-See" von Hannes Grobe

Heft Nr. 28/1986 – „Die Expedition ARKTIS III mit ‚Polarstern' 1985"
mit Beiträgen der Fahrtteilnehmer, herausgegeben von Rainer Gersonde

* **Heft Nr. 29/1986** – „5 Jahre Schwerpunktprogramm ‚Antarktisforschung'
der Deutschen Forschungsgemeinschaft." Rückblick und Ausblick.
Zusammengestellt von Gotthilf Hempel, Sprecher des Schwerpunktprogramms

Heft Nr. 30/1986 – "The Meteorological Data of the Georg-von-Neumayer-Station for 1981 and 1982"
by Marianne Gube and Friedrich Obleitner

Heft Nr. 31/1986 – „Zur Biologie der Jugendstadien der Notothenioidei (Pisces) an der
Antarktischen Halbinsel" von A. Kellermann

Heft Nr. 32/1986 – „Die Expedition ANTARKTIS IV mit FS ‚Polarstern' 1985/86"
mit Beiträgen der Fahrtteilnehmer, herausgegeben von Dieter Fütterer

Heft Nr. 33/1987 – „Die Expedition ANTARKTIS-IV mit FS ‚Polarstern' 1985/86 –
Bericht zu den Fahrtabschnitten ANT-IV/3–4" von Dieter Karl Fütterer

Heft Nr. 34/1987 – „Zoogeographische Untersuchungen und Gemeinschaftsanalysen
an antarktischem Makroplankton" von U. Piatkowski

Heft Nr. 35/1987 – „Zur Verbreitung des Meso- und Makrozooplanktons in Oberflächenwasser
der Weddell See (Antarktis)" von E. Boysen-Ennen

Heft Nr. 36/1987 – „Zur Nahrungs- und Bewegungsphysiologie von *Salpa thompsoni* und *Salpa fusiformis*"
von M. Reinke

Heft Nr. 37/1987 – "The Eastern Weddell Sea Drifting Buoy Data Set of the Winter Weddell Sea Project
(WWSP)" 1986 by Heinrich Hoeber und Marianne Gube-Lehnhardt

Heft Nr. 38/1987 – "The Meteorological Data of the Georg von Neumayer Station for 1983 and 1984"
by M. Gube-Lenhardt

Heft Nr. 39/1987 – „Die Winter-Expedition mit FS ‚Polarstern' in die Antarktis (ANT V/1–3)"
herausgegeben von Sigrid Schnack-Schiel

Heft Nr. 40/1987 – "Weather and Synoptic Situation during Winter Weddell Sea Project 1986 (ANT V/2)
July 16–September 10, 1986" by Werner Rabe

Heft Nr. 41/1988 – „Zur Verbreitung und Ökologie der Seegurken im Weddellmeer (Antarktis)" von Julian Gutt

Heft Nr. 42/1988 – "The zooplankton community in the deep bathyal and abyssal zones
of the eastern North Atlantic" by Werner Beckmann

Heft Nr. 43/1988 – "Scientific cruise report of Arctic Expedition ARK IV/3"
Wissenschaftlicher Fahrtbericht der Arktis-Expedition ARK IV/3, compiled by Jörn Thiede

Heft Nr. 44/1988 – "Data Report for FV 'Polarstern' Cruise ARK IV/1, 1987 to the Arctic and Polar Fronts"
by Hans-Jürgen Hirche

Heft Nr. 45/1988 – „Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres
(Antarktis)" von Joachim Voß

Heft Nr. 46/1988 – "Meteorological and Oceanographic Data of the Winter-Weddell-Sea Project 1986
(ANT V/3)" by Eberhard Fahrbach

Heft Nr. 47/1988 – „Verteilung und Herkunft glazial-mariner Gerölle am Antarktischen Kontinentalrand
des östlichen Weddellmeeres" von Wolfgang Oskierski

Heft Nr. 48/1988 – „Variationen des Erdmagnetfeldes an der GvN-Station" von Arnold Brodscholl

* **Heft Nr. 49/1988** – „Zur Bedeutung der Lipide im antarktischen Zooplankton" von Wilhelm Hagen

Heft Nr. 50/1988 – „Die gezeitenbedingte Dynamik des Ekström-Schelfeises, Antarktis" von Wolfgang Kobarg

Heft Nr. 51/1988 – „Ökomorphologie nototheniider Fische aus dem Weddellmeer, Antarktis" von Werner Ekau

Heft Nr. 52/1988 – „Zusammensetzung der Bodenfauna in der westlichen Fram-Straße"
von Dieter Piepenburg

* **Heft Nr. 53/1988** – „Untersuchungen zur Ökologie des Phytoplanktons im südöstlichen Weddellmeer
(Antarktis) im Jan./Febr. 1985" von Eva-Maria Nöthig

Heft Nr. 54/1988 – „Die Fischfauna des östlichen und südlichen Weddellmeeres:
geographische Verbreitung, Nahrung und trophische Stellung der Fischarten" von Wiebke Schwarzbach

Heft Nr. 55/1988 – "Weight and length data of zooplankton in the Weddell Sea
in austral spring 1986 (Ant V/3)" by Elke Mizdalski

Heft Nr. 56/1989 – "Scientific cruise report of Arctic expeditions ARK IV/1, 2 & 3"
by G. Krause, J. Meincke und J. Thiede

Heft Nr. 57/1989 – „Die Expedition ANTARKTIS V mit FS ‚Polarstern' 1986/87"
Bericht von den Fahrtabschnitten ANT V/4–5 von H. Miller und H. Oerter

* **Heft Nr. 58/1989** – „Die Expedition ANTARKTIS VI mit FS ‚Polarstern' 1987/88"
von D. K. Fütterer

Heft Nr. 59/1989 – „Die Expedition ARKTIS V/1a, 1b und 2 mit FS ‚Polarstern' 1988"
von M. Spindler

Heft Nr. 60/1989 – „Ein zweidimensionales Modell zur thermohalinen Zirkulation unter dem Schelfeis"
von H. H. Hellmer

Heft Nr. 61/1989 – „Die Vulkanite im westlichen und mittleren Neuschwabenland,
Vestfjella und Ahlmannryggen, Antarktika" von M. Peters

* **Heft-Nr. 62/1989** – "The Expedition ANTARKTIS VII/1 and 2 (EPOS I) of RV 'Polarstern'
in 1988/89", by I. Hempel

Heft Nr. 63/1989 – „Die Eisalgenflora des Weddellmeeres (Antarktis): Artenzusammensetzung und Biomasse
sowie Ökophysiologie ausgewählter Arten" von Annette Bartsch

Heft Nr. 64/1989 – "Meteorological Data of the G.-v.-Neumayer-Station (Antarctica)" by L. Helmes

Heft Nr. 65/1989 – „Expedition Antarktis VII/3 in 1988/89" by I. Hempel, P. H. Schalk, V. Smetacek

Heft Nr. 66/1989 – „Geomorphologisch-glaziologische Detailkartierung
des arid-hochpolaren Borgmassivet, Neuschwabenland, Antarktika" von Karsten Brunk

Heft-Nr. 67/1990 – „Identification key and catalogue of larval Antarctic fishes",
edited by Adolf Kellermann

Heft-Nr. 68/1990 – „The Expediton Antarktis VII/4 (Epos leg 3) and VII/5 of RV 'Polarstern' in 1989",
edited by W. Arntz, W. Ernst, I. Hempel

Heft-Nr. 69/1990 – „Abhängigkeiten elastischer und rheologischer Eigenschaften des Meereises vom
Eisgefüge", von Harald Hellmann

Heft-Nr. 70/1990 – „Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des
Weddellmeeres, Antarktis", von Stefan Hain

Heft-Nr. 71/1990 – „Sedimentologie und Paläomagnetik an Sedimenten der Maudkuppe (Nordöstliches
Weddellmeer)", von Dieter Cordes.

Heft-Nr. 72/1990 – „Distribution and abundance of planktonic copepods (Crustacea) in the Weddell Sea
in summer 1980/81", by F. Kurbjeweit and S. Ali-Khan

Heft-Nr. 73/1990 – „Zur Frühdiagenese von organischem Kohlenstoff und Opal in Sedimenten des südlichen
und östlichen Weddellmeeres", von M. Schlüter

Heft-Nr. 74/1990 – „Expeditionen ANTARKTIS-VIII/3 und VIII/4 mit FS ‚Polarstern' 1989"
von Rainer Gersonde und Gotthilf Hempel

Heft-Nr. 75/1991 – „Quartäre Sedimentationsprozesse am Kontinentalhang des Süd-Orkey-Plateaus im
nordwestlichen Weddellmeer (Antarktis)", von Sigrun Grünig

Heft-Nr. 76/1990 – „Ergebnisse der faunistischen Arbeiten im Benthal von King George Island
(Südshetlandinseln, Antarktis)", von Martin Rauschert

Heft-Nr. 77/1990 – „Verteilung von Mikroplankton-Organismen nordwestlich der Antarktischen Halbinsel
unter dem Einfluß sich ändernder Umweltbedingungen im Herbst", von Heinz Klöser

Heft-Nr. 78/1991 – „Hochauflösende Magnetostratigraphie spätquartärer Sedimente arktischer
Meeresgebiete", von Norbert R. Nowaczyk

Heft-Nr. 79/1991 – „Ökophysiologische Untersuchungen zur Salinitäts- und Temperaturtoleranz
antarktischer Grünalgen unter besonderer Berücksichtigung des ß-Dimethylsulfoniumpropionat
(DMSP) - Stoffwechsels", von Ulf Karsten

Heft-Nr. 80/1991 – „Die Expedition ARKTIS VII/1 mit FS ‚Polarstern' 1990",
herausgegeben von Jörn Thiede und Gotthilf Hempel

Heft-Nr. 81/1991 – „Paläoglaziologie und Paläozeanographie im Spätquartär am Kontinentalrand des
südlichen Weddellmeeres, Antarktis", von Martin Melles

Heft-Nr. 82/1991 – „Quantifizierung von Meereseigenschaften: Automatische Bildanalyse von
Dünnschnitten und Parametrisierung von Chlorophyll- und Salzgehaltsverteilungen", von Hajo Eicken

Heft-Nr. 83/1991 – „Das Fließen von Schelfeisen - numerische Simulationen
mit der Methode der finiten Differenzen", von Jürgen Determann

Heft-Nr. 84/1991 – „Die Expedition ANTARKTIS-VIII/1-2, 1989 mit der Winter Weddell Gyre Study
der Forschungsschiffe „Polarstern" und „Akademik Fedorov", von Ernst Augstein,
Nikolai Bagriantsev und Hans Werner Schenke

Heft-Nr. 85/1991 – „Zur Entstehung von Unterwassereis und das Wachstum und die Energiebilanz
des Meereises in der Atka Bucht, Antarktis", von Josef Kipfstuhl

Heft-Nr. 86/1991 – „Die Expedition ANTARKTIS-VIII mit „FS Polarstern" 1989/90. Bericht vom
Fahrtabschnitt ANT-VIII / 5", von Heinz Miller und Hans Oerter

Heft-Nr. 87/1991 –"Scientific cruise reports of Arctic expeditions ARK VI / 1-4 of RV "Polarstern"
in 1989", edited by G. Krause, J. Meincke & H. J. Schwarz

Heft-Nr. 88/1991 – „Zur Lebensgeschichte dominanter Copepodenarten (*Calanus finmarchicus,*
C. glacialis, C. hyperboreus, Metridia longa) in der Framstraße", von Sabine Diel

Heft-Nr. 89/1991 – „Detaillierte seismische Untersuchungen am östlichen Kontinentalrand des Weddell-Meeres vor Kapp Norvegia, Antarktis", von Norbert E. Kaul

Heft-Nr. 90/1991 – „Die Expedition ANTARKTIS-VIII mit FS „Polarstern" 1989/90. Bericht von den Fahrtabschnitten ANT-VIII/6-7", herausgegeben von Dieter Karl Fütterer und Otto Schrems

Heft-Nr. 91/1991 – "Blood physiology and ecological consequences in Weddell Sea fishes (Antarctica)", by Andreas Kunzmann

Heft-Nr. 92/1991 – „Zur sommerlichen Verteilung des Mesozooplanktons im Nansen-Becken, Nordpolarmeer", von Nicolai Mumm

Heft-Nr. 93/1991 – „Die Expedition ARKTIS VII mit FS „Polarstern", 1990. Bericht vom Fahrtabschnitt ARK VII/2", herausgegeben von Gunther Krause

Heft-Nr. 94/1991 – „Die Entwicklung des Phytoplanktons im östlichen Weddellmeer (Antarktis) beim Übergang vom Spätwinter zum Frühjahr", von Renate Scharek

Heft-Nr. 95/1991 – „Radioisotopenstratigraphie, Sedimentologie und Geochemie jungquartärer Sedimente des östlichen Arktischen Ozeans", von Horst Bohrmann

Heft-Nr. 96/1991 – „Holozäne Sedimentationsentwicklung im Scoresby Sund, Ost-Grönland", von Peter Marienfeld

Heft-Nr. 97/1991 – „Strukturelle Entwicklung und Abkühlungsgeschichte der Heimefrontfjella (Westliches Dronning Maud Land/Antarktika)", von Joachim Jacobs

Heft-Nr. 98/1991 – „Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca)", von Angelika Brandt

Heft-Nr. 99/1992 – "The Antarctic ice sheet and environmental change: a three-dimensional modelling study", by Philippe Huybrechts

* **Heft-Nr. 100/1992** – „Die Expeditionen ANTARKTIS IX/1-4 des Forschungsschiffes „Polarstern" 1990/91", herausgegeben von Ulrich Bathmann, Meinhard Schulz-Baldes, Eberhard Fahrbach, Victor Smetacek und Hans-Wolfgang Hubberten

Heft-Nr. 101/1992 – „Wechselbeziehungen zwischen Schwermetallkonzentrationen (Cd, Cu, Pb, Zn) im Meewasser und in Zooplanktonorganismen (Copepoda) der Arktis und des Atlantiks", von Christa Pohl

Heft-Nr. 102/1992 – „Physiologie und Ultrastruktur der antarktischen Grünalge *Prasiola crispa* ssp. *antarctica* unter osmotischem Streß und Austrocknung", von Andreas Jacob

Heft-Nr. 103/1992 – „Zur Ökologie der Fische im Weddelmeer", von Gerd Hubold

Heft-Nr. 104/1992 – „Mehrkanalige adaptive Filter für die Unterdrückung von multiplen Reflexionen in Verbindung mit der freien Oberfläche in marinen Seismogrammen", von Andreas Rosenberger

Heft-Nr. 105/1992 – „Radiation and Eddy Flux Experiment 1991 *(REFLEX I)*", von Jörg Hartmann, Christoph Kottmeier und Christian Wamser

Heft-Nr. 106/1992 – „Ostracoden im Epipelagial vor der Antarktischen Halbinsel - ein Beitrag zur Systematik sowie zur Verbreitung und Populationsstruktur unter Berücksichtigung der Saisonalität", von Rüdiger Kock

Heft-Nr. 107/1992 – „ARCTIC '91: Die Expedition ARK-VIII/3 mit FS „Polarstern" 1991", von Dieter K. Fütterer

Heft-Nr. 108/1992 – „Dehnungsbeben an einer Störungszone im Ekström-Schelfeis nördlich der Georg-von-Neumayer Station, Antarktis. – Eine Untersuchung mit seismologischen und geodätischen Methoden", von Uwe Nixdorf.

Heft-Nr. 109/1992 – „Spätquartäre Sedimentation am Kontinentalrand des südöstlichen Weddellmeeres, Antarktis", von Michael Weber.

Heft-Nr. 110/1992 – „Sedimentfazies und Bodenwasserstrom am Kontinentalhang des nordwestlichen Weddellmeeres", von Isa Brehme.

Heft-Nr. 111/1992 – „Die Lebensbedingungen in den Solekanälchen des antarktischen Meereises", von Jürgen Weissenberger.

Heft-Nr. 112/1992 – „Zur Taxonomie von rezenten benthischen Foraminiferen aus dem Nansen Becken, Arktischer Ozean", von Jutta Wollenburg.

Heft-Nr. 113/1992 – „Die Expedition ARKTIS VIII/1 mit FS "Polarstern" 1991", herausgegeben von Gerhard Kattner.

* **Heft-Nr. 114/1992** – „Die Gründungsphase deutscher Polarforschung, 1865-1875", von Reinhard A. Krause.

Heft-Nr. 115/1992 – „Scientific Cruise Report of the 1991 Arctic Expedition ARK VIII/2 of RV "Polarstern" (EPOS II)", by Eike Rachor.

Heft-Nr. 116/1992 – „The Meteorological Data of the Georg-von-Neumayer-Station (Antarctica) for 1988, 1989, 1990 and 1991", by Gert König-Langlo.

Heft-Nr. 117/1992 – „Petrogenese des metamorphen Grundgebirges der zentralen Heimefrontfjella (westliches Dronning Maud Land / Antarktis)", von Peter Schulze.

Heft-Nr. 118/1993 – „Die mafischen Gänge der Shackleton Range / Antarktika: Petrographie, Geochemie, Isotopengeochemie und Paläomagnetik", von Rüdiger Hotten.

* **Heft-Nr. 119/1993** – „Gefrierschutz bei Fischen der Polarmeere", von Andreas P.A. Wöhrmann.

* **Heft-Nr. 120/1993** – „East Siberian Arctic Region Expedition '92: The Laptev Sea - its Significance for Arctic Sea-Ice Formation and Transpolar Sediment Flux", by D. Dethleff, D. Nürnberg, E. Reimnitz, M. Saarso and Y. P. Sacchenko. – „Expedition to Novaja Zemlja and Franz Josef Land with RV.'Dalnie Zelentsy'", by D. Nürnberg and E. Groth.

* **Heft-Nr. 121/1993** – „Die Expedition ANTARKTIS X/3 mit FS 'Polarstern' 1992", herausgegeben von Michael Spindler, Gerhard Dieckmann und David Thomas.

Heft-Nr. 122/1993 – „Die Beschreibung der Korngestalt mit Hilfe der Fourier-Analyse: Parametrisierung der morphologischen Eigenschaften von Sedimentpartikeln", von Michael Diepenbroek.

* **Heft-Nr. 123/1993** – „Zerstörungsfreie hochauflösende Dichteuntersuchungen mariner Sedimente", von Sebastian Gerland.

Heft-Nr. 124/1993 – „Umsatz und Verteilung von Lipiden in arktischen marinen Organismen unter besonderer Berücksichtigung unterer trophischer Stufen", von Martin Graeve.

Heft-Nr. 125/1993 – „Ökologie und Respiration ausgewählter arktischer Bodenfischarten", von Christian F. von Dorrien.

Heft-Nr. 126/1993 – „Quantitative Bestimmung von Paläoumweltparametern des Antarktischen Oberflächenwassers im Spätquartär anhand von Transferfunktionen mit Diatomeen", von Ulrich Zielinski

Heft-Nr. 127/1993 – „Sedimenttransport durch das arktische Meereis: Die rezente lithogene und biogene Materialfracht", von Ingo Wollenburg.

Heft-Nr. 128/1993 – „Cruise ANTARKTIS X/3 of RV 'Polarstern': CTD-Report", von Marek Zwierz.

Heft-Nr. 129/1993 – „Reproduktion und Lebenszyklen dominanter Copepodenarten aus dem Weddellmeer, Antarktis", von Frank Kurbjeweit

Heft-Nr. 130/1993 – „Untersuchungen zu Temperaturregime und Massenhaushalt des Filchner-Ronne-Schelfeises, Antarktis, unter besonderer Berücksichtigung von Anfrier- und Abschmelzprozessen", von Klaus Grosfeld

Heft-Nr. 131/1993 – „Die Expedition ANTARKTIS X/5 mit FS 'Polarstern' 1992", herausgegeben von Rainer Gersonde

Heft-Nr. 132/1993 – „Bildung und Abgabe kurzkettiger halogenierter Kohlenwasserstoffe durch Makroalgen der Polarregionen", von Frank Laturnus

Heft-Nr. 133/1994 – "Radiation and Eddy Flux Experiment 1993 *(REFLEX II)*", by Christoph Kottmeier, Jörg Hartmann, Christian Wamser, Axel Bochert, Christof Lüpkes, Dietmar Freese and Wolfgang Cohrs

* **Heft-Nr. 134/1994** – "The Expedition ARKTIS-IX/1", edited by Hajo Eicken and Jens Meincke

Heft-Nr. 135/1994 – „Die Expeditionen ANTARKTIS X/6-8", herausgegeben von Ulrich Bathmann, Victor Smetacek, Hein de Baar, Eberhard Fahrbach und Gunter Krause

Heft-Nr. 136/1994 – „Untersuchungen zur Ernährungsökologie von Kaiserpinguinen *(Aptenodytes forsteri)* und Königspinguinen *(Aptenodytes patagonicus)*", von Klemens Pütz

* **Heft-Nr. 137/1994** – „Die känozoische Vereisungsgeschichte der Antarktis", von Werner U. Ehrmann

Heft-Nr. 138/1994 – „Untersuchungen stratosphärischer Aerosole vulkanischen Ursprungs und polarer stratosphärischer Wolken mit einem Mehrwellenlängen-Lidar auf Spitzbergen *(79° N, 12° E)*", von Georg Beyerle

Heft-Nr. 139/1994 – „Charakterisierung der Isopodenfauna (Crustacea, Malacostraca) des Scotia-Bogens aus biogeographischer Sicht: Ein multivariater Ansatz", von Holger Winkler.

Heft-Nr. 140/1994 – „Die Expedition ANTARKTIS X/4 mit FS 'Polarstern' 1992", herausgegeben von Peter Lemke

Heft-Nr. 141/1994 – „Satellitenaltimetrie über Eis – Anwendung des GEOSAT-Altimeters über dem Ekströmisen, Antarktis", von Clemens Heidland

Heft-Nr. 142/1994 – "The 1993 Northeast Water Expedition. Scientific cruise report of RV'Polarstern' Arctic cruises ARK IX/2 and 3, USCG 'Polar Bear' cruise NEWP and the NEWLand expedition", edited by Hans-Jürgen Hirche and Gerhard Kattner

Heft-Nr. 143/1994 – „Detaillierte refraktionsseismische Untersuchungen im inneren Scoresby Sund Ost-Grönland", von Notker Fechner

Heft-Nr. 144/1994 – „Russian-German Cooperation in the Siberian Shelf Seas: Geo-System Laptev Sea", edited by Heidemarie Kassens, Hans-Wolfgang Hubberten, Sergey M. Pryamikov und Rüdiger Stein

* **Heft-Nr. 145/1994** – „The 1993 Northeast Water Expedition. Data Report of RV 'Polarstern' Arctic Cruises IX/2 and 3", edited by Gerhard Kattner and Hans-Jürgen Hirche.

Heft-Nr. 146/1994 – "Radiation Measurements at the German Antarctic Station Neumayer 1982-1992", by Torsten Schmidt and Gert König-Langlo.

Heft-Nr. 147/1994 – „Krustenstrukturen und Verlauf des Kontinentalrandes im Weddell Meer / Antarktis", von Christian Hübscher.

Heft-Nr. 148/1994 – "The expeditions NORILSK/TAYMYR 1993 and BUNGER OASIS 1993/94 of the AWI Research Unit Potsdam", edited by Martin Melles.

** **Heft-Nr. 149/1994** – "Die Expedition ARCTIC' 93. Der Fahrtabschnitt ARK-IX/4 mit FS 'Polarstern' 1993", herausgegeben von Dieter K. Fütterer.

Heft-Nr. 150/1994 – "Der Energiebedarf der Pygoscelis-Pinguine: eine Synopse", von Boris M. Culik.

Heft-Nr. 151/1994 – „Russian-German Cooperation: The Transdrift I Expedition to the Laptev Sea", edited by Heidemarie Kassens and Valeriy Y. Karpiy.

Heft-Nr. 152/1994 – „Die Expedition ANTARKTIS-X mit FS 'Polarstern' 1992. Bericht von den Fahrtabschnitten / ANT-X / 1a und 2", herausgegeben von Heinz Miller.

Heft-Nr. 153/1994 – "Aminosäuren und Huminstoffe im Stickstoffkreislauf polarer Meere", von Ulrike Hubberten.

Heft-Nr. 154/1994 – "Regional und seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea", by Claudio Richter.

Heft-Nr. 155/1995 – "Benthos in polaren Gewässern", herausgegeben von Christian Wiencke und Wolf Arntz.

Heft-Nr. 156/1995 – "An adjoint model for the determination of the mean oceanic circulation, air-sea fluxes und mixing coefficients", by Reiner Schlitzer.

Heft-Nr. 157/1995 – "Biochemische Untersuchungen zum Lipidstoffwechsel antarktischer Copepoden", von Kirsten Fahl.

** **Heft-Nr. 158/1995** – "Die Deutsche Polarforschung seit der Jahrhundertwende und der Einfluß Erich von Drygalskis", von Cornelia Lüdecke.

Heft-Nr. 159/1995 – The distribution of ∂^{18}O in the Arctic Ocean: Implications for the freshwater balance of the haloclin and the sources of deep and bottom waters", by Dorothea Bauch.

* **Heft-Nr. 160/1995** – "Rekonstruktion der spätquartären Tiefenwasserzirkulation und Produktivität im östlichen Südatlantik anhand von benthischen Foraminiferenvergesellschaftungen", von Gerhard Schmiedl.

Heft-Nr. 161/1995 – "Der Einfluß von Salinität und Lichtintensität auf die Osmolytkonzentrationen, die Zellvolumina und die Wachstumsraten der antarktischen Eisdiatomeen *Chaetoceros* sp. und *Navicula* sp. unter besonderer Berücksichtigung der Aminosäure Prolin", von Jürgen Nothnagel.

Heft-Nr. 162/1995 – "Meereistransportiertes lithogenes Feinmaterial in spätquartären Tiefseesedimenten des zentralen östlichen Arktischen Ozeans und der Framstraße", von Thomas Letzig.

Heft-Nr. 163/1995 – "Die Expedition ANTARKTIS-XI/2 mit FS "Polarstern" 1993/94", herausgegeben von Rainer Gersonde.

Heft-Nr. 164/1995 – "Regionale und altersabhängige Variation gesteinsmagnetischer Parameter in marinen Sedimenten der Arktis", von Thomas Frederichs.

Heft-Nr. 165/1995 – "Vorkommen, Verteilung und Umsatz biogener organischer Spurenstoffe: Sterole in antarktischen Gewässern", von Georg Hanke.

Heft-Nr. 166/1995 – "Vergleichende Untersuchungen eines optimierten dynamisch-thermodynamischen Meereismodell mit Beobachtungen im Weddellmeer", von Holger Fischer.

Heft-Nr. 167/1995 – "Rekonstruktionen von Paläo-Umweltparametern anhand von stabilen Isotopen und Faunen-Vergesellschaftungen planktischer Foraminiferen im Südatlantik", von Hans-Stefan Niebler

Heft-Nr. 168/1995 – "Die Expedition ANTARKTIS XII mit FS 'Polarstern' 1993/94. Bericht von den Fahrtabschnitten ANT XII/1 und 2", herausgegeben von Gerhard Kattner und Dieter Karl Fütterer.

Heft-Nr. 169/1995 – "Medizinische Untersuchung zur Circadianrhythmik und zum Verhalten bei Überwinterern auf einer antarktischen Forschungsstation", von Hans Wortmann.

Heft-Nr. 170/1995 – DFG-Kolloquium: Terrestrische Geowissenschaften - Geologie und Geophysik der Antarktis.

Heft-Nr. 171/1995 – "Strukturentwicklung und Petrogenese des metamorphen Grundgebirges der nördlichen Heimefrontfjella (westliches Dronning Maud Land/Antarktika)", von Wilfried Bauer.

Heft-Nr. 172/1995 – "Die Struktur der Erdkruste im Bereich des Scoresby Sund, Ostgrönland: Ergebnisse refraktionsseismischer und gravimetrischer Untersuchungen", von Holger Mandler.

Heft-Nr. 173/1995 – "Paläozoische Akkretion am paläopazifischen Kontinentalrand der Antarktis in Nordvictorialand – P-T-D-Geschichte und Deformationsmechanismen im Bowers Terrane", von Stefan Matzer.

Heft-Nr. 174/1995 – "The Expedition ARKTIS-X/2 of RV 'Polarstern' in 1994", edited by Hans-W. Hubberten.

Heft-Nr. 175/1995 – "Russian-German Cooperation: The Expedition TAYMYR 1994", edited by Christine Siegert and Dmitry Bolshiyanov.

Heft-Nr. 176/1995 – "Russian-German Cooperation: Laptev Sea System", edited by Heidemarie Kassens, Dieter Piepenburg, Jörn Thiede, Leonid Timokhov, Hans-Wolfgang Hubberten and Sergey M. Priamikov.

Heft-Nr. 177/1995 – "Organischer Kohlenstoff in spätquartären Sedimenten des Arktischen Ozeans: Terrigener Eintrag und marine Produktivität", von Carsten J. Schubert.

Heft-Nr. 178/1995 – "Cruise ANTARKTIS XII/4 of RV 'Polarstern' in 1995: CTD-Report", by Jüri Sildam.

Heft-Nr. 179/1995 – "Benthische Foraminiferenfaunen als Wassermassen-, Produktions- und Eisdriftanzeiger im Arktischen Ozean", von Jutta Wollenburg.

Heft-Nr. 180/1995 – "Biogenopal und biogenes Barium als Indikatoren für spätquartäre Produktivitätsänderungen am antarktischen Kontinentalhang, atlantischer Sektor", von Wolfgang J. Bonn.

Heft-Nr. 181/1995 – "Die Expedition ARKTIS X/1 des Forschungsschiffes ‚Polarstern' 1994", herausgegeben von Eberhard Fahrbach.

Heft-Nr. 182/1995 – "Laptev Sea System: Expeditions in 1994", edited by Heidemarie Kassens.

Heft-Nr. 183/1996 – "Interpretation digitaler Parasound Echolotaufzeichnungen im östlichen Arktischen Ozean auf der Grundlage physikalischer Sedimenteigenschaften", von Uwe Bergmann.

Heft-Nr. 184/1996 – "Distribution and dynamics of inorganic nitrogen compounds in the troposphere of continental, coastal, marine and Arctic areas", by María Dolores Andrés Hernández.

Heft-Nr. 185/1996 – "Verbreitung und Lebensweise der Aphroditiden und Polynoiden (Polychaeta) im östlichen Weddell meer und im Lazarevmeer (Antarktis)", von Michael Stiller.

Heft-Nr. 186/1996 – "Reconstruction of Late Quaternary environmental conditions applying the natural radionuclides ^{230}Th, ^{10}Be, ^{231}Pa and ^{238}U: A study of deep-sea sediments from the eastern sector of the Antrctic Circumpolar Current System", by Martin Frank.

Heft-Nr. 187/1996 – "The Meteorological Data of the Neumayer Station (Antarctica) for 1992, 1993 and 1994", by Gert König-Langlo and Andreas Herber.

Heft-Nr. 188/1996 – "Die Expedition ANTARKTIS-XI/3 mit FS 'Polarstern' 1994", herausgegeben von Heinz Miller und Hannes Grobe.

Heft-Nr. 189/1996 – "Die Expedition ARKTIS-VII/3 mit FS 'Polarstern' 1990", herausgegeben von Heinz Miller und Hannes Grobe.

Heft-Nr. 190/1996 – “Cruise report of the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign in 1994”, edited by Wolf Arntz and Matthias Gorny.

Heft-Nr. 191/1996 – “Leitfähigkeits- und Dichtemessung an Eisbohrkernen”, von Frank Wilhelms.

Heft-Nr. 192/1996 – “Photosynthese-Charakteristika und Lebensstrategie antarktischer Makroalgen”, von Gabriele Weykam.

Heft-Nr. 193/1996 – “Heterogene Raktionen von N_2O_5 und HBr und ihr Einfluß auf den Ozonabbau in der polaren Stratosphäre”, von Sabine Seisel.

Heft-Nr. 194/1996 – “Ökologie und Populationsdynamik antarktischer Ophiuroiden (Echinodermata)”, von Corinna Dahm.

Heft-Nr. 195/1996 – “Die planktische Foraminifere *Neogloboquadrina pachyderma* (Ehrenberg) im Weddellmeer, Antarktis”, von Doris Berberich.

Heft-Nr. 196/1996 – “Untersuchungen zum Beitrag chemischer und dynamischer Prozesse zur Variabilität des stratosphärischen Ozons über der Arktis”, von Birgit Heese.

Heft-Nr. 197/1996 – “The Expedition ARKTIS-XI/2 of 'Polarstern' in 1995”, edited by Gunther Krause.

Heft-Nr. 198/1996 – “Geodynamik des Westantarktischen Riftsystems basierend auf Apatit-Spaltspuranalysen“, von Frank Lisker.

Heft-Nr. 199/1996 – “The 1993 Northeast Water Expedition. Data Report on CTD Measurements of RV 'Polarstern' Cruises ARKTIS IX/2 and 3“, by Gereon Budéus and Wolfgang Schneider.

Heft-Nr. 200/1996 – “Stability of the Thermohaline Circulation in analytical and numerical models“, by Gerrit Lohman

Heft-Nr. 201/1996 – “Trophische Beziehungen zwischen Makroalgen und Herbivoren in der Potter Cove (King George-Insel, Antarktis)“, von Katrin Iken.

Heft-Nr. 202/1996 – “Zur Verbreitung und Respiration ökologisch wichtiger Bodentiere in den Gewässern um Svalbard (Arktis)“, von Michael K. Schmid.

Heft-Nr. 203/1996 – “Dynamik, Rauhigkeit und Alter des Meereises in der Arktis - Numerische Untersuchungen mit einem großskaligen Modell“, von Markus Harder.

Heft-Nr. 204/1996 – “Zur Parametrisierung der stabilen atmosphärischen Grenzschicht über einem antarktischen Schelfeis“, von Dörthe Handorf.

Heft-Nr. 205/1996 – “Textures and fabrics in the GRIP ice core, in relation to climate history and ice deformation“, by Thorsteinn Thorsteinsson.

Heft-Nr. 206/1996 – “Der Ozean als Teil des gekoppelten Klimasystems: Versuch der Rekonstruktion der glazialen Zirkulation mit verschieden komplexen Atmosphärenkomponenten“, von Kerstin Fieg.

Heft-Nr. 207/1996 – “Lebensstrategien dominanter antarktischer Oithonidae (Cyclopoida, Copepoda) und Oncaeidae (Poecilostomatoida, Copepoda) im Bellingshausenmeer“, von Cornelia Metz.

Heft-Nr. 208/1996 – “Atmosphäreneinfluß bei der Fernerkundung von Meereis mit passiven Mikrowellenradiometern“ von Christoph Oelke.

Heft-Nr. 209/1996 – “Klassifikation von Radarsatellitendaten zur Meereiserkennung mit Hilfe von Line-Scanner-Mess gen“, von Axel Bochert.

Heft-Nr. 210/1996 – “Die mit ausgewählten Schwämmen (Hexactinellida und Demospongiae) aus dem Weddellmeer, Antarktis, vergesellschaftete Fauna“, von Kathrin Kunzmann.

Heft-Nr. 211/1996 – “Russian-German Cooperation: The Expediton TAYMYR 1995 and the Expedition KOLYMA 199 by Dima Yu. Bolshiyanov and Hans-W. Hubberten.

Heft-Nr. 212/1996 – “Surface-sediment composition and sedimentary processes in the central Arctic Ocean and alor the Eurasian Continental Margin“, by Ruediger Stein, Gennadij I. Ivanov, Michael A. Levitan, and Kirsten Fahl.

Heft-Nr. 213/1996 – “Gonadenentwicklung und Eiproduktion dreier *Calanus*-Arten (Copepoda): Freilandbeobachtung Histologie und Experimente“, von Barbara Niehoff.

Heft-Nr. 214/1996 – “Numerische Modellierung der Übergangszone zwischen Eisschild und Eisschelf“, von Christopl Mayer.

Heft-Nr. 215/1996 – “Arbeiten der AWI-Forschungsstelle Potsdam in Antarktika, 1994/95“, herausgegeben von Ulricl Wand.

Heft-Nr. 216/1996 – “Rekonstruktion quartärer Klimaänderungen im atlantischen Sektor des Südpolarmeeres anhanc von Radiolarien“, von Uta Brathauer.

Heft-Nr. 217/1996 – “Adaptive Semi-Lagrange-Finite-Elemente-Methode zur Lösung der Flachwassergleichungen: Implementierung und Parallelisierung“, von Jörn Behrens.

Heft-Nr. 218/1997 – “Radiation and Eddy Flux Experiment 1995 (REFLEX III)“, by Jörg Hartmann, Axel Bochert, Dietmar Freese, Christoph Kottmeier, Dagmar Nagel and Andreas Reuter.

Heft-Nr. 219/1997 – “Die Expedition ANTARKTIS-XII mit FS 'Polarstern' 1995. Bericht vom Fahrtabschnitt ANT-XII/3“ herausgegeben von Wilfried Jokat und Hans Oerter.

Heft-Nr. 220/1997 – “Ein Beitrag zum Schwerefeld im Bereich des Weddellmeeres, Antarktis. Nutzung von Altimetermessungen des GEOSAT und ERS-1”, von Tilo Schöne.

Heft-Nr. 221/1997 – “Die Expeditionen ANTARKTIS-XIII/1-2 des Forschungsschiffes 'Polarstern' 1995/96”, herausgegeben von Ulrich Bathmann, Mike Lucas und Victor Smetacek.

Heft-Nr. 222/1997 – “Tectonic Structures and Glaciomarine Sedimentation in the South-Eastern Weddell Sea from Seismic Reflection Data”, by László Oszkó.

Heft-Nr. 223/1997 – “Bestimmung der Meereisdicke mit seismischen und elektromagnetisch-induktiven Verfahren”, von Christian Haas.

Heft-Nr. 224/1997 – “Troposphärische Ozonvariationen in Polarregionen”, von Silke Wessel.

Heft-Nr. 225/1997 – “Biologische und ökologische Untersuchungen zur kryopelagischen Amphipodenfauna des arktischen Meereises”, von Michael Poltermann.

Heft-Nr. 226/1997 – “Scientific Cruise Report of the Arctic Expedition ARK-XI/1 of RV 'Polarstern' in 1995”, edited by Eike Rachor.

Heft-Nr. 227/1997 – “Der Einfluß kompatibler Substanzen und Kyroprotektoren auf die Enzyme Malatdehydrogenase (MDH) und Glucose-6-phosphat-Dehydrogenase (G6P-DH) aus Acrosiphonia arcta (Chlorophyta) der Arktis“, von Katharina Kück.

Heft-Nr. 228/1997 – “Die Verbreitung epibenthischer Mollusken im chilenischen Beagle-Kanal”, von Katrin Linse.

Heft-Nr. 229/1997 – “Das Mesozooplankton im Laptevmeer und östlichen Nansen-Becken - Verteilung und Gemeinschaftsstrukturen im Spätsommer”, von Hinrich Hanssen.

Heft-Nr. 230/1997 – “Modell eines adaptierbaren, rechnergestützten, wissenschaftlichen Arbeitsplatzes am Alfred-Wegener-Institut für Polar- und Meeresforschung”, von Lutz-Peter Kurdelski.

Heft-Nr. 231/1997 – “Zur Ökologie arktischer und antarktischer Fische: Aktivität, Sinnesleistungen und Verhalten”, von Christopher Zimmermann.

Heft-Nr. 232/1997 – “Persistente clororganische Verbindungen in hochantarktischen Fischen”, von Stephan Zimmermann.

Heft-Nr. 233/1997 – “Zur Ökologie des Dimethylsulfoniumpropionat (DMSP)-Gehaltes temperierter und polarer Phytoplanktongemeinschaften im Vergleich mit Laborkulturen der Coccolithophoride *Emiliania huxleyi* und der antarktischen Diatomee *Nitzschia lecointei“,* von Doris Meyerdierks.

Heft-Nr. 234/1997 – “Die Expedition ARCTIC '96 des FS 'Polarstern' (ARK XII) mit der Arctic Climate System Study (ACSYS)”, von Ernst Augstein und den Fahrtteilnehmern.

Heft-Nr. 235/1997 – “Polonium-210 und Blei-219 im Südpolarmeer: Natürliche Tracer für biologische und hydrographische Prozesse im Oberflächenwasser des Antarktischen Zirkumpolarstroms und des Weddellmeeres“, von Jana Friedrich.

Heft-Nr. 236/1997 – “Determination of atmospheric trace gas amounts and corresponding natural isotopic rations by means of ground-based FTIR spectroscopy in the high Arctic“, by Arndt Meier.

Heft-Nr. 237/1997 – “Russian-German Cooperation: The Expedition TAYMYR / SEVERNAYA ZEMLYA 1996“, edited by Martin Melles, Birgit Hagedorn and Dmitri Yu. Bolshiyanow.

Heft-Nr. 238/1997 – “Life strategy and ecophysiology of Antarctic macroalgae“, by Iván M. Gómez.

Heft-Nr. 239/1997 – “Die Expedition ANTARKTIS XIII/4-5 des Forschungsschiffes 'Polarstern' 1996“, herausgegeben von Eberhard Fahrbach und Dieter Gerdes.

Heft-Nr. 240/1997 – “Untersuchungen zur Chrom-Speziation im Meerwasser, Meereis und Schnee aus ausgewählten Gebieten der Arktis“, von Heide Giese.

Heft-Nr. 241/1997 – “Late Quaternary glacial history and paleoceanographic reconstructions along the East Greenland continental margin: Evidence from high-resolution records of stable isotopes and ice-rafted debris“, by Seung-Il Nam.

Heft-Nr. 242/1997 – “Thermal, hydrological and geochemical dynamics of the active layer at a continuouse permafrost site, Taymyr Peninsula, Siberia”, by Julia Boike.

Heft-Nr. 243/1997 – “Zur Paläoozeanographie hoher Breiten: Stellvertreterdaten aus Foraminiferen“, von Andreas Mackensen.

Heft-Nr. 244/1997 – “The Geophysical Observatory at Neumayer Station, Antarctica. Geomagnetic and seismological observations in 1995 and 1996“, by Alfons Eckstaller, Thomas Schmidt, Viola Gaw, Christian Müller and Johannes Rogenhagen.

Heft-Nr. 245/1997 – “Temperaturbedarf und Biogeographie mariner Makroalgen - Anpassung mariner Makroalgen an tiefe Temperaturen“, von Bettina Bischoff-Bäsmann.

Heft-Nr. 246/1997 – “Ökologische Untersuchungen zur Fauna des arktischen Meereises“, von Christine Friedrich.

Heft-Nr. 247/1997 – “Entstehung und Modifizierung von marinen gelösten organischen Substanzen“, von Berit Kirchhof

Heft-Nr. 248/1997 – “Laptev Sea System: Expeditions in 1995“, edited by Heidemarie Kassens.

Heft-Nr. 249/1997 – “The Expedition ANTARKTIS XIII/3 (EASIZ I) of RV 'Polarstern' to the eastern Weddell Sea in 1996“ edited by Wolf Arntz and Julian Gutt.

Heft-Nr. 250/1997 – “Vergleichende Untersuchungen zur Ökologie und Biodiversität des Mega-Epibenthos der Arktis und Antarktis“, von Andreas Starmans.

Heft-Nr. 251/1997 – “Zeitliche und räumliche Verteilung von Mineralvergesellschaftungen in spätquartären Sedimenten des Arktischen Ozeans und ihre Nützlichkeit als Klimaindikatoren während der Glazial/Interglazial-Wechsel“, von Christoph Vogt.

Heft-Nr. 252/1997 – “Solitäre Ascidien in der Potter Cove (King George Island, Antarktis). Ihre ökologische Bedeutung und Populationsdynamik“, von Stephan Kühne.

Heft-Nr. 253/1997 – “Distribution and role of microprotozoa in the Southern Ocean“, by Christine Klaas.

Heft-Nr. 254/1997 – “Die spätquartäre Klima- und Umweltgeschichte der Bunger-Oase, Ostantarktis“, von Thomas Kulbe.

Heft-Nr. 255/1997 – “Scientific Cruise Report of the Arctic Expedition ARK-XIII/2 of RV ’Polarstern’ in 1997”, edited by Ruediger Stein and Kirsten Fahl.

Heft-Nr. 256/1998 – “Das Radionuklid Tritium im Ozean: Meßverfahren und Verteilung von Tritium im Südatlantik und im Weddellmeer”, von Jürgen Sültenfuß.

Heft-Nr. 257/1998 – “Untersuchungen der Saisonalität von atmosphärischem Dimethylsulfid in der Arktis und Antarkt von Christoph Kleefeld.

Heft-Nr. 258/1998 – “Bellinghausen- und Amundsenmeer: Entwicklung eines Sedimentationsmodells”, von Frank-Oliver Nitsche.

Heft-Nr. 259/1998 – “The Expedition ANTARKTIS-XIV/4 of RV ’Polarstern’ in 1997”, by Dieter K. Fütterer.

Heft-Nr. 260/1998 – “Die Diatomeen der Laptevsee (Arktischer Ozean): Taxonomie und biogeographische Verbreitun von Holger Cremer.

Heft-Nr. 261/1998 – “Die Krustenstruktur und Sedimentdecke des Eurasischen Beckens, Arktischer Ozean: Resultate aus seismischen und gravimetrischen Untersuchungen”, von Estella Weigelt.

Heft-Nr. 262/1998 – “The Expedition ARKTIS-XIII/3 of RV ’Polarstern’ in 1997”, by Gunther Krause.

Heft-Nr. 263/1998 – “Thermo-tektonische Entwicklung von Oates Land und der Shackleton Range (Antarktis) basiere auf Spaltspuranalysen”, von Thorsten Schäfer.

Heft-Nr. 264/1998 – “Messungen der stratosphärischen Spurengase ClO, HCl, O_3, N_2O, H_2O und OH mittels flugzeug tragener Submillimeterwellen-Radiometrie”, von Joachim Urban.

Heft-Nr. 265/1998 – “Untersuchungen zu Massenhaushalt und Dynamik des Ronne Ice Shelfs, Antarktis“, von Astrid Lambrecht.

Heft-Nr. 266/1998 – “Scientific Cruise Report of the Kara Sea Expedition of RV ’Akademik Boris Petrov’ in 1997“, edited by Jens Matthiessen and Oleg Stepanets.

Heft-Nr. 267/1998 – “Die Expedition ANTARKTIS-XIV mit FS ’Polarstern’ 1997. Bericht vom Fahrtabschnitt ANT-XIV/ herausgegeben von Wilfried Jokat und Hans Oerter.

Heft-Nr. 268/1998 – “Numerische Modellierung der Wechselwirkung zwischen Atmosphäre und Meereis in der arktischen Eisrandzone“, von Gerit Birnbaum.

Heft-Nr. 269/1998 – “Katabatic wind and Boundary Layer Front Experiment around Greenland (KABEG ’97)“, by Günther Heinemann.

Heft-Nr. 270/1998 – “Architecture and evolution of the continental crust of East Greenland from integrated geophysical studies“, by Vera Schlindwein.

Heft-Nr. 271/1998 – “Winter Expedition to the Southwestern Kara Sea - Investigations on Formation and Transport o Turbid Sea-Ice“, by Dirk Dethleff, Peter Loewe, Dominik Weiel, Hartmut Nies, Gesa Kuhlmann, Christian Bahe and Gennady Tarasov.

Heft-Nr. 272/1998 – “FTIR-Emissionsspektroskopische Untersuchungen der arktischen Atmosphäre”, von Edo Becke

Heft-Nr. 273/1998 – “Sedimentation und Tektonik im Gebiet des Agulhas Rückens und des Agulhas Plateaus (’SETA-RAP’)”, von Gabriele Uenzelmann-Neben.

Heft-Nr. 274/1998 – “The Expedition ANTARKTIS XIV/2”, by Gerhard Kattner.

Heft-Nr. 275/1998 – “Die Auswirkung der ‘NorthEastWater’ Polynya auf die Sedimentation vor NO-Grönland und Unt suchungen zur Paläo-Ozeanographie seit dem Mittelweichsel”, von Hanne Notholt.

Heft-Nr. 276/1998 – “Interpretation und Analyse von Potentialfelddaten im Weddellmeer, Antarktis: der Zerfall des Superkontinents Gondwana”. von Michael Studinger.

Heft-Nr. 277/1998 – “Koordiniertes Programm Antarktisforschung“. Berichtskolloquium im Rahmen des Koordinierte Programms “Antarktisforschung mit vergleichenden Untersuchungen in arktischen Eisgebieten“, herausgegeben von Hubert Miller.

Heft-Nr. 278/1998 – “Messung stratosphärischer Spurengase über Ny-Ålesund, Spitzbergen, mit Hilfe eines bodengebundenen Mikrowellen-Radiometers“, von Uwe Raffalski.

Heft-Nr. 279/1998 – “Arctic Paleo-River Discharge (APARD). A New Research Programme of the Arctic Ocean Scienc Board (AOSB)“, edited by Ruediger Stein.

Heft-Nr. 280/1998 – “Fernerkundungs- und GIS-Studien in Nordostgrönland“, von Friedrich Jung-Rothenhäusler.

Heft-Nr. 281/1998 – “Rekonstruktion der Oberflächenwassermassen der östlichen Laptevsee im Holozän anhand aquatischen Palynomorphen“, von Martina Kunz-Pirrung.

Heft-Nr. 282/1998 – “Scavenging of ^{231}Pa and ^{230}Th in the South Atlantic: Implications for the use of the ^{231}Pa/^{230}Th rati as a paleoproductivity proxy“, by Hans-Jürgen Walter.

Heft-Nr. 283/1998 – “Sedimente im arktischen Meereis - Eintrag, Charakterisierung und Quantifizierung“, von Frank Lindemann.

Heft-Nr. 284/1998 – “Langzeitanalyse der antarktischen Meereisbedeckung aus passiven Mikrowellendaten“, von Christian H. Thomas.

Heft-Nr. 285/1998 – “Mechanismen und Grenzen der Temperaturanpassung beim Pierwurm *Arenicola marina* (L.)“, von Angela Sommer.

Heft-Nr. 286/1998 – “Energieumsätze benthischer Filtrierer der Potter Cove (King George Island, Antarktis)“, von Jens Kowalke.

Heft-Nr. 287/1998 – “Scientific Cooperation in the Russian Arctic: Research from the Barents Sea up to the Laptev Sea“, edited by Eike Rachor.

Heft-Nr. 288/1998 – “Alfred Wegener. Kommentiertes Verzeichnis der schriftlichen Dokumente seines Lebens und Wirkens“, von Ulrich Wutzke.

Heft-Nr. 289/1998 – “Retrieval of Atmospheric Water Vapor Content in Polar Regions Using Spaceborne Microwave Radiometry“, by Jungang Miao.

Heft-Nr. 290/1998 – “Strukturelle Entwicklung und Petrogenese des nördlichen Kristallingürtels der Shackleton Range Antarktis: Proterozoische und Ross-orogene Krustendynamik am Rand des Ostantarktischen Kratons“, von Axel Brommer.

Heft-Nr. 291/1998 – “Dynamik des arktischen Meereises - Validierung verschiedener Rheologieansätze für die Anwendung in Klimamodellen“, von Martin Kreyscher.

Heft-Nr. 292/1998 – “Anthropogene organische Spurenstoffe im Arktischen Ozean. Untersuchungen chlorierter Biphenyle und Pestizide in der Laptevsee, technische und methodische Entwicklungen zur Probenahme in der Arktis und zur Spurenstoffanalyse“, von Sven Utschakowski.

Heft-Nr. 293/1998 – “Rekonstruktion der spätquartären Klima- und Umweltgeschichte der Schirmacher Oase und des Wohlthat Massivs (Ostantarktika)“, von Markus Julius Schwab.

Heft-Nr. 294/1998 – “Besiedlungsmuster der benthischen Makrofauna auf dem ostgrönländischen Kontinentalhang“, von Klaus Schnack.

Heft-Nr. 295/1998 – “Gehäuseuntersuchungen an planktischen Foraminiferen hoher Breiten: Hinweise auf Umweltveränderungen während der letzten 140.000 Jahre“, von Harald Hommers.

Heft-Nr. 296/1998 – “Scientific Cruise Report of the Arctic Expedition ARK-XIII/1 of RV ’Polarstern’ in 1997“, edited by Michael Spindler, Wilhelm Hagen and Dorothea Stübing.

Heft-Nr. 297/1998 – “Radiometrische Messungen im arktischen Ozean - Vergleich von Theorie und Experiment“, von Klaus-Peter Johnsen.

Heft-Nr. 298/1998 – “Patterns and Controls of CO_2 Fluxes in Wet Tundra Types of the Taimyr Peninsula, Siberia - the Contribution of Soils and Mosses“, by Martin Sommerkorn.

Heft-Nr. 299/1998 – “The Potter Cove coastal ecosystem, Antarctica. Synopsis of research performed within the frame of the Argentinean-German Cooperation at the Dallmann Laboratory and Jubany Station (King George Island, Antarctic 1991-1997)“, by Christian Wiencke, Gustavo Ferreyra, Wolf Arntz & Carlos Rinaldi.

Heft-Nr. 300/1999 – “The Kara Sea Expedition of RV ‘Akademik Boris Petrov’ 1997: First results of a Joint Russian-German Pilot Study“, edited by Jens Matthiessen, Oleg V. Stepanets, Ruediger Stein, Dieter K. Fütterer, and Eric M. Galimov.

Heft-Nr. 301/1999 – “The Expedition ANTARKTIS XV/3 (EASIZ II)“, edited by Wolf E. Arntz and Julian Gutt.

Heft-Nr. 302/1999 – “Sterole im herbstlichen Weddellmeer (Antarktis): Großräumige Verteilung, Vorkommen und Umsatz“, von Anneke Mühlebach.

Heft-Nr. 303/1999 – “Polare stratosphärische Wolken: Lidar-Beobachtungen, Charakterisierung von Entstehung und Entwicklung“, von Jens Biele.

Heft-Nr. 304/1999 – “Spätquartäre Paläoumweltbedingungen am nördlichen Kontinentalrand der Barents- und Kara-See. Eine Multi-Parameter-Analyse“, von Jochen Knies.

Heft-Nr. 305/1999 – “Arctic Radiation and Turbulence Interaction Study (ARTIST)“, by Jörg Hartmann, Frank Albers, Stefania Argentini, Axel Bochert, Ubaldo Bonafé, Wolfgang Cohrs, Alessandro Conidi, Dietmar Freese, Teodoro Georgiadis, Alessandro Ippoliti, Lars Kaleschke, Christof Lüpkes, Uwe Maixner, Giangiuseppe Mastrantonio, Fabrizio Ravegnan Andreas Reuter, Giuliano Trivellone and Abgelo Viola.

Heft-Nr. 306/1999 – “German-Russian Cooperation: Biogeographic and biostratigraphic investigations on selected sediment cores from the Eurasian continental margin and marginal seas to analyze the Late Quaternary climatic variability”, edited by Robert F. Spielhagen, Max S. Barash, Gennady I. Ivanov, and Jörn Thiede.

Heft-Nr. 307/1999 – “Struktur und Kohlenstoffbedarf des Makrobenthos am Kontinentalhang Ostgrönlands“, von Dan Seiler.

Heft-Nr. 308/1999 – “ARCTIC ’98: The Expedition ARK-XIV/1a of RV ’Polarstern’ in 1998”, edited by Wilfried Jokat.

Heft-Nr. 309/1999 – “Variabilität der arktischen Ozonschicht: Analyse und Interpretation bodengebundener Millimeterwellenmessungen”, von Björn-Martin Sinnhuber.

Heft-Nr. 310/1999 – “Rekonstruktion von Meereisdrift und terrigenem Sedimenteintrag im Spätquartär: Schwermineralassoziationen in Sedimenten des Laptev-See-Kontinentalrandes und des zentralen Arktischen Ozeans”, von Marion Behrends.

Heft-Nr. 311/1999 – “Parameterisierung atmosphärischer Grenzschichtprozesse in einem regionalen Klimamodell der Arktis”, von Christoph Abegg.

Heft-Nr. 312/1999 – “Solare und terrestrische Strahlungswechselwirkung zwischen arktischen Eisflächen und Wolken”, von Dietmar Freese.

Heft-Nr. 313/1999 – “Snow accumulation on Ekströmisen, Antarctica”, by Elisabeth Schlosser, Hans Oerter and Wolfgang Graf.

Heft-Nr. 314/1999 – “Die Expedition ANTARKTIS XV/4 des Forschungsschiffes ’Polarstern’ 1998”, herausgegeben von Eberhard Fahrbach.

Heft-Nr. 315/1999 – “Expeditions in Siberia in 1998”, edited by Volker Rachold.

Heft-Nr. 316/1999 – “Die postglaziale Sedimentationsgeschichte der Laptewsee: schwermineralogische und sedimentpetrographische Untersuchungen”, von Bernhard Peregovich.

Heft-Nr. 317/1999 – “Adaptation an niedrige Temperaturen: Lipide in Eisdiatomeen”, von Heidi Lehmal.

Heft-Nr. 318/1999 – “Effiziente parallele Lösungsverfahren für elliptische partielle Differentialgleichungen in der numerischen Ozeanmodellierung”, von Natalja Rakowsky.

Heft-Nr. 319/1999 – “The Ecology of Arctic Deep-Sea Copepods (Euchaetidae and Aetideidae). Aspects of their Distribution, Trophodynamics and Effect on the Carbon Flux”, by Holger Auel.

* vergriffen / out of print.

** nur noch beim Autor / only from the author.