

# Trophic structure of zooplankton in the Fram Strait in spring and autumn 2003

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Received in revised form 10 July 2007; accepted 19 August 2007

Available online 19 November 2007

## Abstract

The trophic structure of zooplankton was investigated in Fram Strait (north western Svalbard) in spring and autumn of 2003. Depth-stratified zooplankton samples were collected at 12 stations on the shelf (~200 m), across the shelf-slope (~500 m) and over deep water (> 750 m), using a Multiple Plankton Sampler equipped with 0.180-mm mesh size nets.

Higher zooplankton abundance and estimated biomass were found in the shelf area. Abundance and biomass were two times higher in August, when sea-surface temperature was higher than in May. Herbivores dominated numerically in May, and omnivores in August, suggesting a seasonal sequence of domination by different trophic groups. Cirripedia nauplii and *Fritillaria borealis* prevailed in spring, whereas copepod nauplii and *Calanus finmarchicus* were numerically the most important herbivores in autumn. Small copepods, *Oithona similis* and *Triconia borealis*, were the most numerous omnivorous species in both seasons, but their abundances increased in autumn. Chaetognatha (mainly *Eukrohnia hamata*) accounted for the highest abundance and biomass among predatory taxa at all deep-water stations and during both seasons. Regarding vertical distribution, herbivores dominated numerically in the surface layer (0–20 m), and omnivores were concentrated somewhat deeper (20–50 m) during both seasons. Maximum abundance of predators was found in the surface layer (0–20 m) in spring, and generally in the 20–50 m layer in autumn. This paper presents the first comprehensive summary of the zooplankton trophic structure in the Fram Strait area. Our goals are to improve understanding of energy transfer through this ecosystem, and of potential climate-induced changes in Arctic marine food webs.

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**Keywords:** Zooplankton; Trophic structure; Marine food web; Climate change; On Thin Ice

## 1. Introduction

For several reasons plankton are particularly good indicators of climate change in the marine

environment (Hays et al., 2005). First, unlike other marine species, such as fish and many intertidal invertebrates, only a few species of plankton are commercially exploited, and therefore any long-term changes can usually be attributed to environmental causes (e.g., climate change). Secondly, most species are short-lived and population size is for that reason less influenced by older generations, which leads to tight coupling between environmental

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change and plankton dynamics. Thirdly, plankton communities can exhibit dramatic changes in distribution because they are free floating or swimming and respond strongly to changes in the advective patterns of warm and cold oceanic current systems. Finally, recent evidence suggests that plankton organisms are more sensitive indicators of change than environmental variables because the nonlinear responses of biological communities can amplify subtle environmental perturbations (Hays et al., 2005).

It is widely believed that the effect of global climate change will be perceptible first in the polar regions. Studies of Arctic zooplankton started about a century ago during Nansen's 'Fram' expedition (Nansen, 1902). Sars (1900) first recognized similarities in the zooplankton species composition of the Arctic Ocean and the northern Atlantic. Long-term observations of mesozooplankton standing stocks and seasonal development have been conducted from drift ice stations since 1937 (Minoda, 1967; Hopkins, 1969a,b; Kosobokova, 1982). The next phase of investigations focused on the life cycles of epipelagic copepods in Fram Strait (Diel, 1991) and the Greenland Sea (Hirche, 1997). Smith (1988, 1990) and Hirche et al. (1991) examined metabolism, feeding, growth, and egg production of Fram Strait copepods. Some recent studies (Mumm, 1991; Mumm et al., 1998; Thibault et al., 1999) have revealed that zooplankton biomass in the upper 500 m of the central Arctic Ocean may be considerably higher than expected based on earlier records. Nevertheless, information on zooplankton from greater depths of the Arctic basins remains scarce (Kosobokova and Hirche, 2000; Auel and Hagen, 2002).

Fram Strait is the most important, and the only deep, passage between the Arctic Ocean and the Nordic Seas (Morison, 1991), yet information on the structure of pelagic biota in this region is still limited (e.g. Smith et al., 1985; Smith, 1988; Hirche et al., 1991). Thus, studying trophic relationships within Fram Strait plankton communities is of major importance. The present study was conducted within the On Thin Ice (OTI) project, which aimed to provide insight into the energy pathways and trophic structure of the Arctic marine ecosystem and its stability versus sensitivity to predicted future climate changes. Our objective is to give insight into the trophic structure of zooplankton in Fram Strait. The overview, one of the very first for this area, presents data on abundance as well as biomass, and from two different seasons (spring and autumn),

allowing an assessment of seasonal changes in the trophic structure of zooplankton. Because our sampling extended across the shelf-slope, we also were able to examine water-column depth as another factor affecting zooplankton community and trophic structure.

## 2. Materials and methods

### 2.1. The study area

Due to its width and deep sill, Fram Strait is the key area for the exchange of water masses and hence organic matter between the Arctic and North Atlantic Oceans (Quadfasel et al., 1987; Maslowski et al., 2004). In the east, Atlantic Water is carried north by the West Spitsbergen Current (WSC). In the west, the East Greenland Current exports Polar Water and ice from the Arctic Ocean. Branches of re-circulating Atlantic Water also cross Fram Strait and flow southward along East Greenland (Aagaard, 1982). These currents create three hydrographic domains (Hirche et al., 1991), aligned meridionally and separated by two frontal regions. The Arctic Front divides Atlantic and sub-Arctic Water from the Greenland Sea Gyres, and the East Greenland Polar Front separates sub-Arctic Water from Arctic Ocean Basin Water. The latter mostly coincides with the marginal ice zone (MIZ). The circulation pattern results in a spatially variable sea ice cover in Fram Strait, with permanent ice-covered areas in the west, permanent ice-free areas in the southeast and seasonally varying conditions in the central and eastern parts (Vinje, 1985).

### 2.2. Zooplankton sampling

Zooplankton were collected during two 2003 OTI cruises in the north-western Svalbard area of Fram Strait (Fig. 1). The spring cruise was carried out from the ice-strengthened R.V. *Jan Mayen* from 14 to 22 May, and the autumn cruise from R.V. *Lance* between 10 August and 6 September. For the present paper, a set of samples from six stations sampled in May and six stations sampled in August were selected (Table 1). In spring, sampling was carried out on the shelf (Ice Ia, Ice Ib, 405), on the continental slope (411 and 441) and over deep water in Sofiadypet (Ice II). In autumn, a transect from the shelf over Norskebanken to deep water was carried out (N1, N2, N3, Ice 3) together with two stations on the slope (Flaket 1, Flaket 2).

During sampling, the ships were drifting with the ice and the underlying near-surface water masses, while at the Ice stations the ships were anchored to the ice. Stratified vertical hauls were performed with a multiple plankton sampler (Hydro-Bios) consisting of five closing nets, each with 0.25 m<sup>2</sup> square opening and 0.180 mm mesh. At stations with depth <600 m, five depth-strata were sampled: 0–20 m (melt-water layer), 20–50 m (remaining euphotic zone), 50–100 m (upper 100 m zone), 100–200 m (mid-layer) and 200 m-bottom. At deep-water stations (depth >600 m), sampling strata included: 0–20 m (melt-water layer), 20–50 m (remaining euphotic zone), 50–200 m (mid-layer), 200–600 m (Atlantic layer) and 600 m-bottom. Net depths

down to 1400 m were determined using depth sensors (SIMRAD in May, Scanmar in August). For deeper sampling, the approximate sampler depth was estimated from the time taken to let out 100 m of wire.

Zooplankton samples were preserved in 4% borax-buffered formaldehyde immediately after collection. Organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer, following standard procedures (e.g., Harris et al., 2000).

Calculations of biomass of particular taxa were made using published mean individual dry weight data for copepods and small meroplanktonic organisms, and specific length/weight relationships for larger taxa (Uye, 1982; Berestovskij et al., 1989; Percy, 1989; Hirche, 1991; Mumm, 1991; Richter, 1994; Hanssen, 1997; Karnovsky et al., 2003). When neither individual DW factors nor length/weight regressions were available, relationships for species similar in shape were applied. Due to lack of appropriate conversion factors, *Oikopleura* spp. were excluded from biomass calculations.

Published descriptions of their diets and feeding behavior can be used to classify zooplankton taxa into broad trophic categories such as herbivores, omnivores and carnivores (Paffenhoefer, 1988). However, we generally agree with the opinion of Mauchline (1998) that exclusive or pure herbivory and carnivory are rare among zooplankters, and thus their dietary classification should be considered with caution. Being aware of the large flexibility in feeding patterns and preferences of zooplankters,

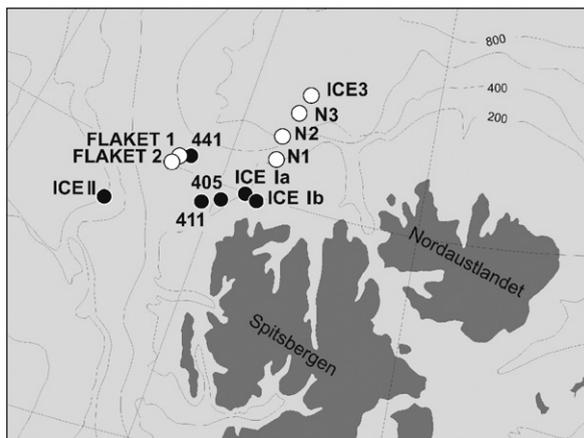


Fig. 1. Sampling area in Fram Strait (black circle—May 2003, white circle—August 2003 stations).

Table 1  
List of stations sampled in Fram Strait during spring and autumn 2003

On Thin Ice stations	Station ID	Date (2003)	Latitude (N)	Longitude (E)	Bottom depth (m)	Area	Sampled depths (m)
<i>May 2003</i>							
Ice Ia (day)	386	15 May	80° 03'	11° 05'	240	Shelf	219-200-100-50-20-0
Ice Ib (night)	398	16 May	79° 59.74'	11° 09.03'	205	Shelf	190-100-50-20-0
Norskebanken	405	16 May	79° 48.59'	10° 21.51'	258	Shelf	250-200-100-50-20-0
Slope of Norskebanken	411	17 May	79° 46.67'	09° 45.59'	406	Slope	400-200-100-50-20-0
Ice II	419	19 May	79° 32.64'	04° 53.71'	> 2700	Deep sea	1200-600-200-50-20-0
Ice III	441	21 May	80° 07.76'	08° 50.69'	508	Slope	483-200-100-50-20-0
<i>August/September 2003</i>							
Flaket	Flaket 1	13 Aug.	80° 07.3'	08° 47.2'	520	Slope	500-200-100-50-20-0
Flaket	Flaket 2	13 Aug.	80° 07.3'	08° 47.2'	516	Slope	500-200-100-50-20-0
Norskebanken (N1)	N1	13 Aug.	80° 18.1'	12° 00.5'	203	Shelf	190-100-50-20-0
Norskebanken (N2)	N2	14 Aug.	80° 30.7'	12° 00.2'	793	Deep sea	775-600-200-50-0
Norskebanken (N3)	N3	14 Aug.	80° 40.5'	12° 00.5'	1139	Deep sea	1120-600-200-50-20-0
Ice 3	ICE 3	1 Sept.	80° 50.9'	12° 48.9'	1683	Deep sea	~1600-600-200-50-20-0

which depend mainly on food availability or abundance, we divided mesozooplankton into the above mentioned groups based on different published sources (Alldredge and Madin, 1982; Paffenhoefer, 1993; Seiler and Brandt, 1997; Mauchline, 1998 and citations therein; Turner et al., 2001; Clark et al., 2003; Søreide et al., 2003) as well as on our own experience (Table 2).

### 3. Results

#### 3.1. Abundance

A total of 87 species/taxa were found in Fram Strait in spring and autumn 2003 (Table 2). Maximum abundances were at the shelf stations during both seasons (Table 3). Furthermore, two-times

Table 2

List of species or taxa from Fram Strait during spring and autumn 2003, with trophic levels indicated (h = herbivore, p = predator, o = omnivore)

Taxa/species	Trophic level	Taxa/species	Trophic level
<i>Calanus finmarchicus</i>	h	<i>Spinocalanus longicornis</i>	o
<i>Calanus glacialis</i>	h	<i>Spinocalanus polaris</i>	o
<i>Calanus hyperboreus</i>	h	<i>Spinocalanus</i> spp.	o
<i>Pseudocalanus</i> spp.	h	<i>Augaptilus glacialis</i>	o
<i>Scolecithricella minor</i>	h	<i>Acartia longiremis</i>	o
Copepoda nauplii	h	<i>Microsetella norvegica</i>	o
<i>Limacina helicina</i>	h	Harpacticoida indet.	o
<i>Limacina retroversa</i>	h	<i>Oithona similis</i>	o
<i>Paraeuchaeta</i> spp.	p	<i>Oithona atlantica</i>	o
<i>Heterorhabdus norvegicus</i>	p	<i>Triconia</i> (= <i>Oncaea</i> ) <i>borealis</i>	o
<i>Heterorhabdus compactus</i>	p	<i>Oncaea</i> spp. adults	o
<i>Aetideopsis minor</i>	p	Cyclopoida indet.	o
<i>Aetideopsis rostrata</i>	p	<i>Mormonilla minor</i>	o
<i>Gaetanus</i> ( <i>Gaidius</i> ) <i>brevispinus</i>	p	Ostracoda	o
<i>Gaetanus</i> ( <i>Gaidius</i> ) <i>tenuispinus</i>	p	Cirripedia nauplii	h
Aetideidae spp.	p	Cirripedia cypris	o
<i>Themisto libellula</i>	p	<i>Apherusa glacialis</i>	h
<i>Themisto abyssorum</i>	p	<i>Eusirus</i> sp.	o
<i>Aglantha digitale</i>	p	Gammaridea indet.	o
<i>Aglantha laurentii</i> larvae	p	Amphipoda indet.	o
<i>Bougainvilla</i> sp.	p	Isopoda Bopyridae	o
Hydromedusae indet.	p	Isopoda indet.	o
Hydromedusae larvae	p	Cumacea indet.	o
<i>Dimophyes arctica</i>	p	<i>Thysanoessa inermis</i>	o
Siphonophora indet.	p	<i>Thysanoessa longicaudata</i>	o
<i>Beroë cucumis</i>	p	<i>Thysanoessa raschii</i>	o
<i>Mertensia ovum</i>	p	Euphausiacea nauplii	o
Ctenophora larvae	p	Euphausiacea calyptopis	o
<i>Clione limacina</i>	p	Euphausiacea furcilia	o
<i>Eukrohnia hamata</i>	p	<i>Hymenodora glacialis</i>	o
<i>Sagitta elegans</i>	p	<i>Caridion</i> zoea	o
<i>Sagitta maxima</i>	p	<i>Eupagurus</i> zoea	o
Pisces larvae	p	<i>Hyas</i> megalopa	o
<i>Metridia longa</i>	o	Decapoda larvae	o
<i>Metridia lucens</i>	o	Gastropoda veliger	o
<i>Pleuromamma robusta</i>	o	Bivalvia veliger	o
<i>Microcalanus</i> spp.	o	<i>Tomopteris helgolandica</i>	o
<i>Temorites brevis</i>	o	Polychaeta indet.	o
<i>Chiridius obtusifrons</i>	o	Polychaeta larvae	o
<i>Scaphocalanus brevicornis</i>	o	Echinodermata larvae	o
<i>Scaphocalanus magnus</i>	o	<i>Fritillaria borealis</i>	h
<i>Spinocalanus antarcticus</i>	o	<i>Oikopleura</i> spp.	h
<i>Spinocalanus elongatus</i>	o	<i>Lucicutia</i> sp.	o
<i>Spinocalanus horridus</i>	o		

Table 3  
Abundance and biomass of overall zooplankton at sampling stations in Fram Strait during spring and autumn 2003

Station ID	Abundance (ind. m <sup>-2</sup> )	Biomass (mg DW m <sup>-2</sup> )
<i>May 2003</i>		
Ice Ia	400 083	7042
Ice Ib	257 387	3797
405	272 633	7241
441	221 160	7003
411	276 401	18 000
Ice II	156 649	7296
<i>August 2003</i>		
N1	849 296	45 845
Flaket 2	335 188	8495
Flaket 1	582 018	5662
N2	540 104	24 408
N3	422 704	14 039
ICE 3	313 583	4309

higher overall zooplankton abundance (about  $850 \times 10^3$  ind. m<sup>-2</sup>) was found in autumn at the shallowest station N1 compared to the shelf station (Ice Ia) in spring (Table 3).

The zooplankton community was usually dominated numerically by herbivores in May, and by omnivores in August (Fig. 2). The two exceptions were that omnivores were the most abundant group at stations 441 and Ice II in spring, and herbivores at the shelf station (N1) in autumn. Seasonally ephemeral components of the zooplankton community prevailed during spring at the shelf stations: Cirripedia nauplii at stations Ice Ia and Ice Ib ( $172 \times 10^3$  and  $153 \times 10^3$  ind. m<sup>-2</sup>, respectively), and *Fritillaria borealis* at stations Ice Ia ( $103 \times 10^3$  ind. m<sup>-2</sup>) and 405 ( $58 \times 10^3$  ind. m<sup>-2</sup>). In autumn copepod nauplii (most of them *Calanus*) constituted the most important group within herbivores at all stations (maximum  $186 \times 10^3$  ind. m<sup>-2</sup> at Flaket 1) except shelf station N1, which was entirely dominated by older stages of *Calanus finmarchicus* ( $341 \times 10^3$  ind. m<sup>-2</sup>). *Oithona similis* and *Triconia borealis* were the most numerous omnivores in both seasons, although their abundances were higher in autumn (max.  $270 \times 10^3$  ind. m<sup>-2</sup> at Flaket 1 and  $69 \times 10^3$  ind. m<sup>-2</sup> at N2, respectively). Highest densities of predatory zooplankton were observed in both seasons at deep-water stations ( $6.7 \times 10^3$  ind. m<sup>-2</sup> at Ice II station in May, dominated by Chaetognatha, *Paraeuchaeta* spp. and *Clione limacina*; and  $10.5 \times 10^3$  ind. m<sup>-2</sup> at station N2 in August, dominated by Chaetognatha and *Aglantha digitale*).

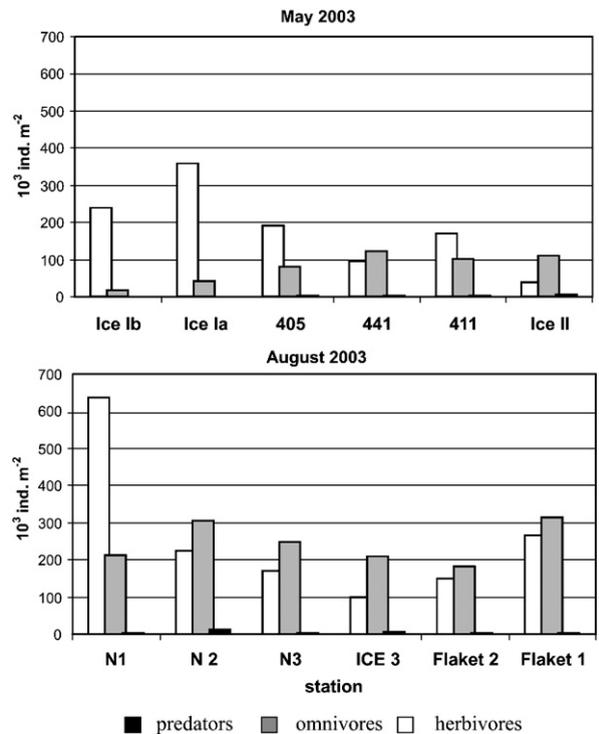


Fig. 2. Abundance (ind. m<sup>-2</sup>) of different trophic levels of Fram Strait zooplankton in spring and autumn 2003.

To assess the influence of bottom depth on the zooplankton trophic structure, we divided the six stations from each season into three bathymetric categories: shelf (~200 m), slope (~500 m), and deep water (>750 m), and calculated category mean abundance/biomass from three, two or single stations (two cases: deep-water station-Ice II in May and shelf station-N1 in August, see Table 1).

Vertical distribution of zooplankton, in terms of abundance, revealed a general dominance of herbivores in the surface-water layer (0–20 m) during both seasons except for the deep-water area in autumn. Omnivores were typically predominating in under-surface layers (20–50 m) except for the shelf and slope areas in May (Fig. 3). Maximum concentrations of predators were found near the surface (0–20 m) at all stations in spring, while in autumn the peak of their abundance was generally located somewhat deeper, in the 20–50 m depth interval.

### 3.2. Estimated biomass

Total zooplankton biomass reached its maximum in August at the shelf station (N1) and on the slope

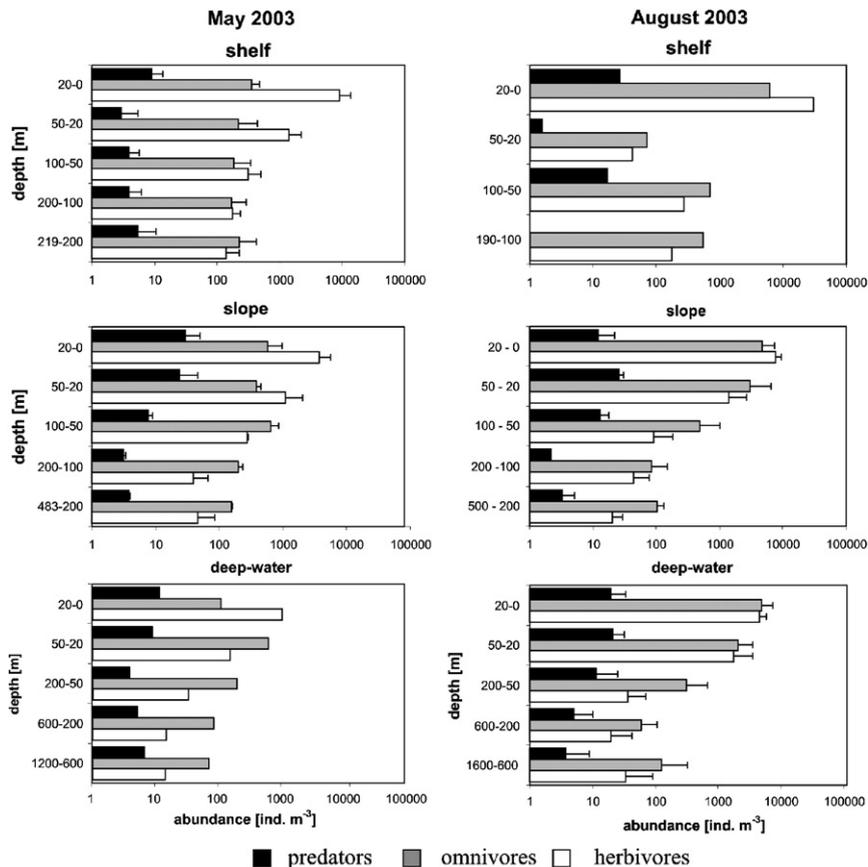


Fig. 3. Vertical distribution (ind. m<sup>-3</sup>) of different trophic levels of Fram Strait zooplankton in three depth categories of stations in spring and autumn 2003. Note the logarithmic scale.

(N2) (Table 3). Maximum total zooplankton biomass was 3 times higher in August (45.9 g DW m<sup>-2</sup> at station N1) than in May (18.0 g DW m<sup>-2</sup> at slope station 411).

The zooplankton trophic structure showed a different dominance pattern when described in terms of dry weights (Fig. 4). Herbivores dominated the biomass at all stations in both seasons, except at station Ice II in May (where predators dominated), and Ice 3 (where omnivores exceeded slightly the total dry weight of herbivores). The dominant herbivorous biomass component was usually *C. finmarchicus* in both seasons (maximum 25.5 g DW m<sup>-2</sup> at station N2 in August). However, Cirripedia nauplii (max. 2.1 g DW m<sup>-2</sup> at the shelf station Ice Ia), *F. borealis* (max. 1.9 g DW m<sup>-2</sup> at the shelf station Ice Ia) and *C. hyperboreus* (max. 1.6 g DW m<sup>-2</sup> at station 411) sometimes shared biomass dominance with *C. finmarchicus* during spring. In autumn, *Limacina helicina* reached dry weights comparable with *C. finmarchicus*, with a

peak at station N3, where the biomass of this pteropod (7.0 g DW m<sup>-2</sup>) was 4 times higher than for all *Calanus* species combined. During the same season, *C. hyperboreus* ranked third in biomass except at the shelf station (N1), where *C. glacialis* dry weights reached extremely high values (4.2 g DW m<sup>-2</sup>).

Omnivore biomass was dominated by *Metridia longa*. Its highest dry weights were at the deep stations 411 and 419 during May (1.3 and 1.2 g DW m<sup>-2</sup>, respectively), and at offshore station N3 in August (1.8 g DW m<sup>-2</sup>). The secondary dominant omnivore in terms of biomass was *O. similis* (max. 0.6 g DW m<sup>-2</sup> at August station N3).

Chaetognaths were the dominant predatory group during both seasons. They reached their highest biomass at two deep-water stations, Ice II and N2, where their maximum biomass in August (5.4 g DW m<sup>-2</sup> at station N2) was 2 times higher than in May at Ice II. Other important carnivorous species in terms of biomass were *Themisto libellula*

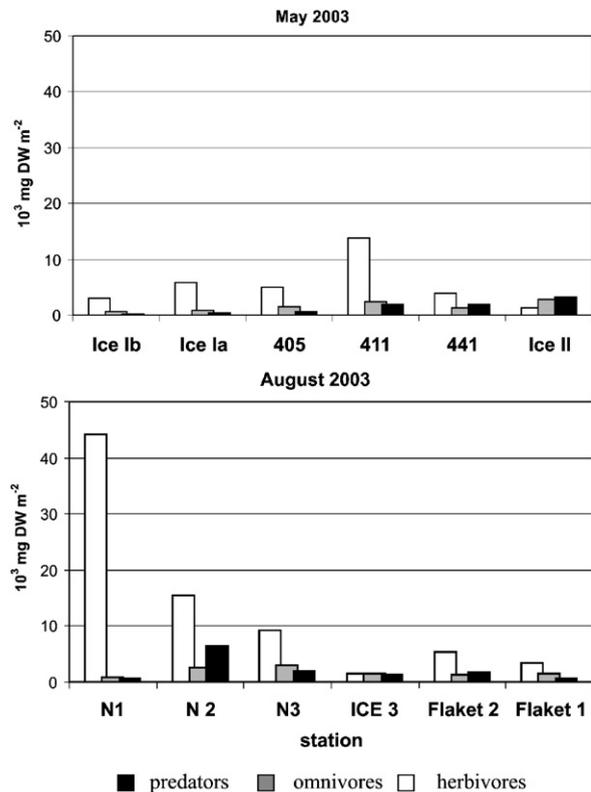


Fig. 4. Biomass ( $\text{mg DW m}^{-2}$ ) of different trophic levels of Fram Strait zooplankton in spring and autumn 2003.

(max.  $0.7 \text{ g DW m}^{-2}$  at Flaket 2), *Paraeuchaeta* spp. (max.  $0.6 \text{ g DW m}^{-2}$  at Ice II), *A. digitale* (max.  $0.5 \text{ g DW m}^{-2}$  at N2) and *C. limacina* (max.  $0.3 \text{ g DW m}^{-2}$  at N1).

Vertical distributions of biomass classified by trophic level (Fig. 5) show that the highest dry weights of herbivores were near the surface (0–20 m) except for the slope and deep-water area in August, where the maximum herbivore biomass was in the 20–50 m depth stratum. The maximum dry weight of predators also occurred in the uppermost water layers over the shelf and slope during spring, and over the shelf in autumn. At the deepest station (May) and in the slope area (August), peaks of carnivore biomass were concentrated deeper (in the 20–50 and 50–100 m layers, respectively). Autumn deep-water stations had relatively uniform profiles of predator biomass, but with a weak maximum in the deepest depth stratum.

#### 4. Discussion

The zooplankton community structure in our study area, with a pronounced dominance of

copepods, was similar to what has been reported previously (e.g., Mumm's, 1993). However, we found a higher diversity in zooplankton with 49 species and 38 higher taxa in our survey, in comparison with 45 species and 8 taxa reported by Mumm (1993) in the Nansen Basin during summer, and 45 species and 18 taxa noted by Auel and Hagen (2002) in the central Arctic Ocean in autumn. The increased diversity in our study area may be in part due to the general lower latitudinal position (closer to Svalbard) and the stronger influence of Atlantic water, our more detailed identification of the higher taxa, and our use of finer mesh nets. However, a climate component is also probable. According to Schauer et al. (2004), the influx of Atlantic water masses to the Arctic Ocean has increased considerably during the last decades. Direct measurements show that the Fram Strait branch of the WSC is strongly variable on a variety of time scales, including interannual. The Atlantic water transport in the WSC in the Fram Strait increased between 1997 and 2000 from 3 to 4 Sv (Schauer et al., 2004). According to Drinkwater (2006), climate warming also may change the migration patterns of "warmer water" species from the North Atlantic, causing their earlier arrivals and later departures. Ecosystem changes associated with climate warming may include a general northward movement of Atlantic/boreal species and in consequence, enhanced zooplankton diversity, as found in our study.

Another striking result from our study was that the mean total zooplankton abundance was 1 order of magnitude higher ( $385\,600 \text{ ind. m}^{-2}$ ) than average summer values of zooplankton in the Nansen Basin (Mumm, 1993). This might be partly explained by a larger mesh size ( $300 \mu\text{m}$ ) used in Mumm's (1993) study, in comparison with  $180 \mu\text{m}$  in our examination and, in consequence, an underestimation of small, and numerically important mesozooplankton species. Arashkevich et al. (2002) revealed a significant underestimation of small organisms sampled with the WP-2 net with the same mesh size ( $180 \mu\text{m}$ ) as in our investigation in comparison with samples collected with 10-l Niskin water bottles (with  $20\text{-}\mu\text{m}$  mesh size). In the upper 100-m layer, a difference between biomass of small zooplankton sampled with nets and that sampled with water bottles occasionally exceeded even 6 times (Arashkevich et al., 2002). On the other hand, small-mesh nets ( $64 \mu\text{m}$ ) will sample the small zooplankton fraction effectively but will lead to a

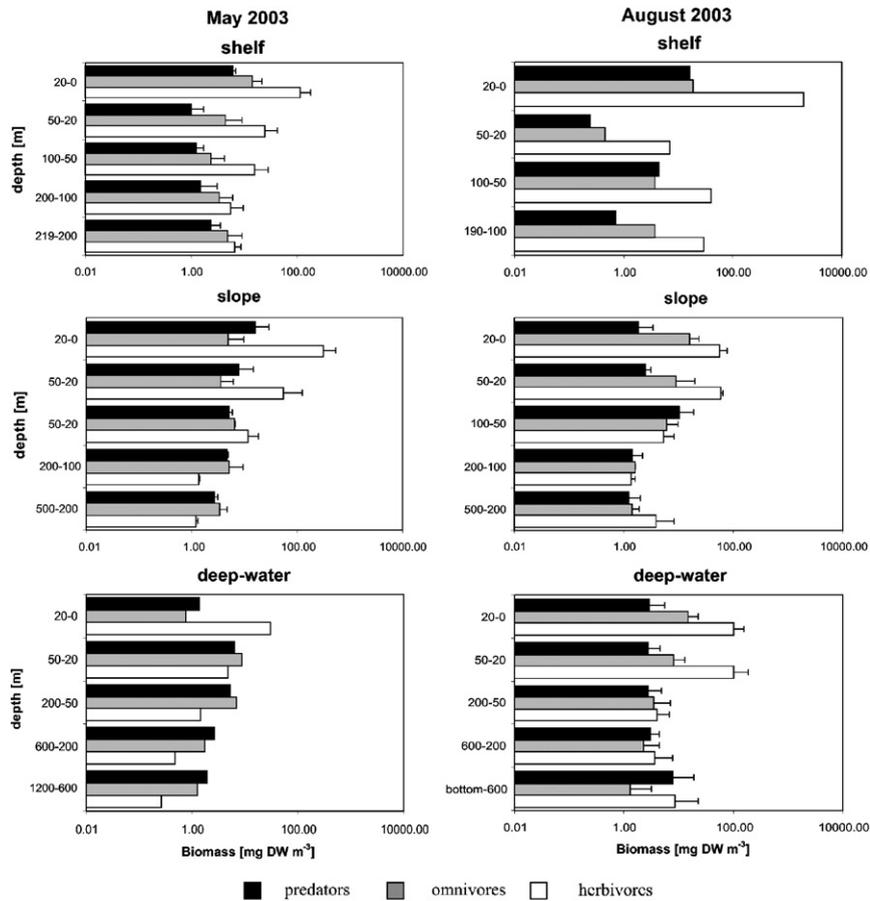


Fig. 5. Vertical fluctuations of biomass ( $\text{mg DW m}^{-3}$ ) of trophic levels of Fram Strait zooplankton in three depth categories of stations in spring and autumn 2003. Note the logarithmic scale.

higher avoidance rate by larger organisms, and thus may underestimate the mesozooplankton biomass (Hopkins, 1969a, b), which is in this area dominated by large copepods.

The Arctic Ocean was considered for a long-time to be a biological desert with very low mesozooplankton biomass. Exceptionally low values were obtained in the upper 500 m from drift-ice station during the “Arlis II” expedition in 1964/1965:  $0.29 \text{ g DW m}^{-2}$  in the Arctic Basin north of Greenland, increasing to  $4.5 \text{ g DW m}^{-2}$  in the East Greenland Current (Hopkins, 1969a). Winter biomass in the Arctic Basin was particularly low, only  $0.12 \text{ g DW m}^{-2}$  (Hopkins, 1969b). Higher biomass in the upper 100 m of the central Arctic basin ( $1.5\text{--}3 \text{ g DW m}^{-2}$ ) was reported by Kosobokova (1982) and Kosobokova et al. (1998). However, Thibault et al. (1999) measured  $7\text{--}13 \text{ g DW m}^{-2}$  in the upper 500 m of the Canadian Basin, similar to previous studies from the Eurasian Basin (Hirche

and Mumm, 1992; Mumm, 1993; Nielsen and Hansen, 1995). A recent investigation of mesozooplankton dry mass integrated over the upper 1500 m of the Arctic Ocean indicated low and surprisingly stable values of  $2.0 \text{ g DM m}^{-2}$  (Auel and Hagen, 2002), although the late sampling season (August–September 1991) might also have influenced the low result. A review of zooplankton dry weights from different Arctic regions shows that areas influenced by Atlantic Water masses (such as the WSC) and the Greenland Sea typically exhibit higher biomass values, suggesting higher productivity (Mumm et al., 1998). Therefore, the mean biomass of mesozooplankton ( $c. 13 \text{ g DW m}^{-2}$ ) found in our study from the Fram Strait supports a recently emerging paradigm (e.g., Ashjian et al., 2003) of a more productive Arctic Ocean than traditionally believed.

The Arctic Ocean and its marginal seas have the most extreme seasonal regime of all marine ecosystems (e.g., Falk-Petersen et al., 2000). The importance

of seasonality was highlighted by Kosobokova (1982), who observed a 6–8 fold increase of zooplankton biomass between June and August in the central Arctic Basin. In Fram Strait, we found 2-times higher mean biomass in August ( $17 \text{ g DW m}^{-2}$ ) than in May ( $8 \text{ g DW m}^{-2}$ ). Our data fit the general pattern of a seasonal plankton cycle in the Arctic described by Cushing (1975): a single summer peak of phytoplankton abundance (in May/June) followed by a later zooplankton maximum (in August). During our surveys, mean chlorophyll-*a* values for the integrated 0–75 m water layer ranged from  $1.7$  to  $3.3 \mu\text{g l}^{-1}$  in May and from  $0.5$  to  $1.1 \mu\text{g l}^{-1}$  in August (E.N. Hegseth, unpubl. data), suggesting spring-bloom and autumn post-bloom situations in our survey.

Our study confirmed a sharp decrease of mean biomass from the Spitsbergen shelf towards the high-Arctic deep-sea basins (Table 3; stations N1, N2, N3 and ICE 3). A similar seaward decline was reported by Mumm et al. (1998):  $4.6 \text{ g DW m}^{-2}$  over the continental slope of Nansen Basin versus  $1\text{--}2 \text{ g DW m}^{-2}$  over the northern basin. The decrease of mesozooplankton biomass towards the central Arctic deep-sea basins can be accompanied by shifts in their vertical distribution. According to Mumm et al. (1998), 57–75% of the total zooplankton biomass was concentrated in the upper 100 m over the deep-sea basins in July–August 1987, whereas only 25% of the biomass from the upper 500 m was located in the top 100 m of the area influenced by the WSC. On the contrary, Kosobokova et al. (1998) found a pronounced maximum of zooplankton biomass in the surface layer of the slope and in deep areas, with a rapid decrease below 50 m and described it as a typical vertical distribution of zooplankton for the Arctic summer season. Our study seems to confirm this latter pattern. We found 71–90% of the total zooplankton biomass in spring and 82–96% in autumn 2003 in the upper water layer (0–50 m) of Fram Strait. Even a more pronounced vertical gradient was observed in abundance, with 80–88% of zooplankton concentrated at the surface in May and 95–98% in August. Smidt (1979) also indicated that the bulk of zooplankton was in the upper water layers of the Southwest Greenland in April–September, and Ashjian et al. (2003) observed that most zooplankton biomass (> 50%) was concentrated between 200 and 1500 m depth in the western Arctic Ocean except in summer when most of the total was in the upper 100 m.

With regard to trophic levels, the mesozooplankton community of Fram Strait was numerically dominated by herbivores in spring and by omnivores in autumn, although predators also played an essential role, especially at depth. Longhurst (1985) estimated that predatory mesozooplankton represent only 23% of the zooplankton community in the Arctic, compared to 38% in temperate waters and 47% in tropical oceans. The proportion of predators in total zooplankton biomass fluctuated from a few percent in the shelf area up to 30–40% in the deepest waters in the present study.

In spring, Cirripedia nauplii were the most abundant herbivorous zooplankton in the shelf area of Fram Strait. Similar findings were reported from the coastal area of southwest Greenland in April–May (Smidt, 1979), from the southernmost part of Nansen Basin in summer (Mumm, 1993), and in the shallow waters of the Laptiev Sea (Kosobokova et al., 1998). The appendicularian *F. borealis* was also abundant in our spring samples, which is in agreement with previous results from the Nansen Basin (Mumm, 1993) and from Atlantic waters of the Barents Sea (Arashkevich et al., 2002).

In autumn, copepod nauplii and *C. finmarchicus* were the most abundant herbivores in our study area. Total zooplankton biomass in Fram Strait was strongly dominated by the large *Calanus* species in both seasons, as in the central Arctic Ocean (Auel and Hagen, 2002). The smallest of *Calanus* species and the most important component of biomass in our study, *C. finmarchicus*, is considered to be limited to Atlantic waters in Fram Strait and parts of Nansen Basin (Grainger, 1961; Hirche, 1991; Daase and Eiane, 2007). An alteration in the inflow of Atlantic water could modify the dispersion of this species and ultimately change the energy flow to higher trophic levels (Weslawski and Kwasniewski, 1990; Karnovsky et al., 2003; Falk-Petersen et al., 2006). The relatively low abundances of *C. glacialis* found in our study are in accord with the statement by Ashjian et al. (2003) that this species may not be self-sustaining in the Arctic Ocean. Association of *C. glacialis* with shelf/shallow regions (Conover, 1988) was confirmed by our observation of maximum numbers and biomass at the shelf station (N1) in autumn. *Calanus hyperboreus* ranked third in total mesozooplankton biomass especially in deeper water (this study), which agrees with findings of Hassel (1986) that this species, in addition to being an Arctic species, also is a deep-water resident in the Greenland Sea and in the Arctic Ocean.

Small copepods, *O. similis* and *T. borealis*, were the most numerous omnivorous species in both seasons of our study, but their abundances increased in autumn. According to Hansen et al. (1999), large copepods (*Calanus* spp.) migrate to the deeper water and start hibernation around midsummer, leaving the near-surface productive layers free for occupation by protozooplankton, smaller copepod species and their developmental stages. Small copepods are important links in marine food webs, serving as major grazers of phytoplankton, as components of the microbial loop, and as prey for ichthyoplankton and other larger pelagic carnivores (Turner, 2004).

Because zooplankters link primary producers and higher trophic levels predators, they can reflect the influences of both bottom-up (productivity) and top-down (predation and grazing pressure) population control. As in our study, Thibault et al. (1999) found only a few predatory forms in the Arctic Ocean, although their relative importance becomes greater during the winter when the herbivores and omnivores descend to depth (Søreide et al., 2003). The dominant zooplankton predator in our study, both in numbers and biomass, was *Eukrohnia hamata* (Chaetognatha), which is regarded as oceanic species. The species also constituted up to 13% of the total zooplankton biomass in the deep waters of the Laptev Sea (Kosobokova et al., 1998). Chaetognatha are sensitive to climatic shifts, and are good indicators of changes in water temperature (Southward, 1980). Baier and Terazaki (2005) pointed out that the effect of chaetognath predation on the copepod community of the Bering Sea depends on which copepod species is predominant and its susceptibility to cumulative predation effects, as well as on daily predation impact, both of which varied between years with different climatic conditions. According to Gislason and Astthorsson (1998), extensive predation by chaetognaths may have contributed to decline of zooplankton stocks also in subarctic waters north of Iceland in mid-July.

The vertical distribution pattern of zooplankton in Fram Strait, with herbivores dominating in the upper layer (0–20 m) and omnivores in the deeper layer (20–50 m), basically confirms the traditional view of planktonic trophic structure. The maximum concentration of predators in the surface layer during spring, and deeper in autumn is probably related to the decreasing food availability following the seasonal ontogenetic migration of *Calanus* into deeper waters.

If the predicted increase in Northern Hemisphere temperature continues, a marked change in the

organization of the pelagic ecosystem from phytoplankton to fish can be expected, with a possible impact on biochemical cycles, especially carbon sequestration by the ocean (e.g., Beaugrand and Reid, 2003). The shelf seas of the Eurasian Arctic are known to be important in the oceanic carbon cycle, in part due to the structure of lower trophic levels in this region. The size and species composition of plankton communities influence the vertical carbon flux in a marine food web (Boyd and Newton, 1995), mainly through modification of sinking particles (faecal pellets) and retention within the pelagic system (Wassmann, 1989). For example, a pelagic food web model of Disco Bay constructed by Hansen et al. (2003) showed that climate warming led to an earlier ice break-up, and to enhanced primary productivity from an early spring bloom with reduced grazing by large copepods (*Calanus* spp.). This resulted in a protozoan-dominated microbial food web, and transfer of primary production through ciliates and/or dinoflagellates before ingestion by copepods. In such a situation, the vertical carbon flux was reduced compared to a more normal situation with a timing match between primary productivity and ascent from hibernation by large *Calanus* grazers (Pedersen et al., 2005). There is now an increasing recognition of the importance of functional components of zooplankton community structure for examining ecosystem change, rather than the conventional total biomass-based approach. We hope that our study may initiate an important discussion on changes in zooplankton trophic structure and possible implications in a scenario of a warming Arctic.

## 5. Conclusions

Our study confirmed significantly higher abundance and biomass in the shelf area in comparison with deeper localities of Fram Strait. The increase of mesozooplankton biomass from spring-bloom to post-bloom is in accordance with the general pattern of the seasonal plankton cycle in Arctic. We further confirm the existence of large and productive areas with high zooplankton biomass strongly influenced by the large-scale current system in Fram Strait. Recent work by Cottier et al. (2005) has shown that the coastal waters off western Spitsbergen are susceptible to massive and rapid shifts in the balance between ‘Atlantic’ (warm and salty) and ‘Arctic’ (cold and fresh) regimes.

Atlantic inflow from the Norwegian Sea transports large amounts of Atlantic origin zooplankton, such as *C. finmarchicus*, *Themisto abyssorum*, *Thysanoessa inermis* and *T. longicaudata*, into Fram Strait. On the other hand, the Transpolar Drift brings typically arctic zooplankton, such as *C. hyperboreus*, from deeper water masses of the Arctic Ocean into Fram Strait. Upwelling coupled with seasonal vertical movements by organisms up from the Spitsbergen shelf slope introduce these zooplankters from deeper water masses onto the shelf and shelf break (Falk-Petersen et al., 2006). The northward coastal current (South Cape Current) on the Spitsbergen shelf and local wind driven currents in the Northern Barents Sea advect arctic shelf species, such as *C. glacialis*, into Fram Strait.

Our seasonal sampling revealed mean zooplankton abundance and biomass 2-times higher in August than in May. The dominance of different trophic groups of Fram Strait zooplankton varied between stations/seasons with herbivores being numerically dominant in spring and omnivores in autumn. The higher abundance of predators in August was also distinctive. Herbivores dominated the surface waters (0–20 m) of most of stations in both sampling periods, whereas omnivores were concentrated deeper (between 20 and 50 m). Maximum abundance of predators was found at the surface water layer (<20 m) in spring and deeper (20–100 m) in autumn. The observed trophic structure is strongly modified by biological factors, such as growth, life cycle, diel vertical migration, ontogenetic seasonal migration and feeding patterns of particular zooplankters (Mackas and Tsuda, 1999; Blachowiak-Samolyk et al., 2006; Cottier et al., 2006; Willis et al., 2006).

Future attempts to predict changes in the Arctic marine pelagic ecosystem on the basis of climate scenarios will require focusing major effort on biological–physical modelling and large-scale plankton population ecology. It is essential to maintain the long-term monitoring programmes to determine whether climate–plankton connections observed during several recent decades will persist in the future or will be overruled by other mechanisms and/or human-induced perturbations.

### Acknowledgments

This study was part of the OTI project (150356-720) funded by the Norwegian Research Council. The authors thank E.N. Hegseth and A. Sundfjord

who kindly provided us with unpublished chlorophyll-*a* and hydrographical data. We are indebted to our friends L. Stempniewicz and J. Wiktor for their suggestions on an earlier version of the manuscript. Our particular thanks go to our anonymous reviewers for many relevant comments, which improved the manuscript. This paper was first presented in the GLOBEC-ESSAS Symposium on “Effects of climate variability on sub-arctic marine ecosystems”, hosted by PICES in Victoria, BC, May 2005.

### References

- Aagaard, K., 1982. Inflow from the Atlantic Ocean in the Polar Basin. In: Rey, L. (Ed.), The Arctic Ocean. Comité Arctique International, Monaco, pp. 69–82.
- Allredge, A., Madin, L.P., 1982. Pelagic tunicates: unique herbivores in the marine plankton. *Bioscience* 32, 655–663.
- Arashkevich, E., Wassmann, P., Pasternak, A., Wexels Riser, C., 2002. Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. *Journal of Marine Systems* 38, 125–145.
- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Van Keuren, D., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Research I* 50, 1235–1261.
- Auel, H., Hagen, W., 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Marine Biology* 140, 1013–1021.
- Baier, C.T., Terazaki, M., 2005. Interannual variability in a predator–prey interaction: climate, chaetognaths and copepods in the southeastern Bering Sea. *Journal of Plankton Research* 27, 1113–1125.
- Beaugrand, G., Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* 9, 801–817.
- Berestovskij, E.G., Anisimova, N.A., Denisenko, C.G., Luppowa, E.N., Savinov, V.M., Timofeev, C.F., 1989. Relationship Between Size and Body Mass of Some Invertebrates and Fish of the North-East Atlantic. Academy of Sciences of the USSR, Murman Marine Biological Institute, Apatity.
- Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S., Thybo Mouritsen, L., 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series* 308, 101–116.
- Boyd, P., Newton, P., 1995. Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. *Deep-Sea Research I* 42, 619–639.
- Clark, R.A., Frid, C.L.J., Nicholas, K.R., 2003. Long-term, predation-based control of the central-west North Sea zooplankton. *ICES Journal of Marine Science* 60, 187–197.
- Conover, R.J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167, 127–142.

- Cottier, F.R., MacLachlan, S., Howe, J., 2005. Rapid shifts in Arctic marine climate: observations and archives in a Spitsbergen fjord. *Ocean Challenge* 14, 16–23.
- Cottier, F.R., Falk-Petersen, S., Tarling, G., Wold, A., 2006. Synchronous vertical migration of *Calanus finmarchicus* in an Arctic fjord. *Limnology and Oceanography* 51, 2586–2599.
- Cushing, D.H., 1975. *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge, 287pp.
- Daase, M., Eiane, K., 2007. Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. *Polar Biology* 30, 969–981.
- Diel, S., 1991. On the life history of dominant copepod species (*Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, *Metridia longa*) in the Fram Strait. *Reports on Polar Research* 88, 1–113.
- Drinkwater, K.F., 2006. The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography* 68, 134–151.
- Falk-Petersen, S., Hop, H., Budgell, W.P., Hegseth, E.N., Korsnes, R., Løyning, T.B., Ørbæk, J.B., Kawamura, T., Shirasawa, K., 2000. Physical and ecological processes in the Marginal Ice Zone of the northern Barents Sea during the summer melt periods. *Journal of Marine Systems* 27, 131–159.
- Falk-Petersen, S., Timofeev, S., Pavlov, V., Sargent, J.R., 2006. Climate variability and the effect on arctic food chains. The role of *Calanus*. In: Ørbæk, et al. (Eds.), *Arctic–Alpine Ecosystems and People in a Changing Environment*. Monograph. Springer, Berlin.
- Gislason, A., Astthorsson, O.S., 1998. Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland. *Polar Biology* 20, 85–94.
- Grainger, E.H., 1961. The Copepods *Calanus glacialis* Jaschnov and *Calanus finmarchicus* (Gunnerus) in Canadian Arctic–Subarctic waters. *Journal of Fisheries Research Board of Canada* 18, “*Calanus*” Series 21, 663–678.
- Hanssen, H., 1997. Mesozooplankton of the Laptev Sea and the adjacent eastern Nansen Basin—distribution and community structure in late summer. *Reports on Polar Research* 229, 1–131.
- Hansen, B.W., Nielsen, T.G., Levinsen, H., 1999. Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. III. Mesozooplankton. *Aquatic Microbial Ecology* 16, 233–249.
- Hansen, A.S., Nielsen, T.G., Levinsen, H., Madsen, S.D., Thingstad, T.F., Hansen, B.W., 2003. Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: a dynamic model approach. *Deep-Sea Research I* 50, 171–187.
- Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M., 2000. *ICES Zooplankton Methodology Manual*. Academic Press, New York, 684pp.
- Hassel, A., 1986. Seasonal changes in zooplankton composition in the Barents Sea, with special attention to *Calanus* spp. (Copepoda). *Journal of Plankton Research* 8, 329–339.
- Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 337–344.
- Hirche, H.-J., 1991. Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biology* 11, 351–362.
- Hirche, H.-J., 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Marine Biology* 128, 607–618.
- Hirche, H.-J., Mumm, N., 1992. Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep Sea Research* 39 (Suppl. 2), S485–S505.
- Hirche, H.-J., Baumann, M.E.M., Kattner, G., Gradinger, R., 1991. Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea. *Journal of Marine Systems* 2, 477–494.
- Hopkins, T.L., 1969a. Zooplankton biomass related to hydrography along the drift track of Arlis II in the Arctic Basin and the east Greenland Current. *Journal of the Fisheries Research Board of Canada* 26, 305–310.
- Hopkins, T.L., 1969b. Zooplankton standing crop in the Arctic Basin. *Limnology and Oceanography* 14, 80–85.
- Karnovsky, N.J., Kwasniewski, S., Weslawski, J.M., Walkusz, W., Beszczynska-Möller, A., 2003. Foraging behavior of little auks in a heterogeneous environment. *Marine Ecology Progress Series* 253, 289–303.
- Kosobokova, K.N., 1982. Composition and distribution of the biomass of zooplankton in the central Arctic Basin. *Oceanology* 22, 744–750.
- Kosobokova, K., Hirche, H.-J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Research I* 47, 2029–2060.
- Kosobokova, K.N., 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 Biology* 19, 63–76.
- Longhurst, A.R., 1985. The structure and evolution of plankton communities. *Progress in Oceanography* 15, 1–35.
- Mackas, D.L., Tsuda, A., 1999. Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. *Progress in Oceanography* 43, 335–363.
- Maslowski, W., Marble, D., Walczowski, W., Schauer, U., Clement, J.L., Semtner, A., 2004. On climatological mass, heat, and salt transport through the Barents Sea and Fram strait from pan-Arctic coupled ice-ocean model simulation. *Journal of Geophysics Research* 109, C03032.
- Mauchline, J., 1998. The biology of calanoid copepods. *Advances in Marine Biology*, 33.
- Minoda, T., 1967. Seasonal distribution of Copepoda in the Arctic Ocean from June to December, 1964. *Records of Oceanographic Works in Japan* 9, 161–168.
- Morison, J., 1991. Seasonal variations in the West Spitsbergen current estimated from bottom pressure measurements. *Journal of Geophysics Research* 96 (C3), 18381–18395.
- Mumm, N., 1991. On the summer distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. *Reports on Polar Research* 92, 146.
- Mumm, N., 1993. Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. *Polar Biology* 13, 451–461.
- 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 Biology* 20, 189–197.
- Nansen, F., 1902. *Oceanography of the North Polar basin*. The Norwegian North Polar Expedition 1893–1896. *Scientific Results*, vol. 9 (3). Greenwood Press, New York, 427pp.
- Nielsen, T.G., Hansen, B., 1995. Plankton community structure and carbon cycling on the western coast of Greenland during

- and after the sedimentation of a diatom bloom. Marine Ecology Progress Series 125, 239–257.
- Paffenhoefer, G.-A., 1988. Feeding rates and behavior of zooplankton. Bulletin of Marine Science 43, 430–445.
- Paffenhoefer, G.-A., 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). Journal of Plankton Research 15, 37–55.
- Pedersen, S.A., Ribergaard, M.H., Simonsen, C.S., 2005. Micro- and mesozooplankton in Southwest Greenland waters in relation to environmental factors. Journal of Marine Systems 56, 85–112.
- Percy, J.A., 1989. Abundance, biomass, and size frequency distribution of an arctic ctenophore, *Mertensia ovum* (Fabricius) from Frobisher Bay, Canada. Sarsia 74, 95–105.
- Quadfasel, D., Gascard, J.-C., Kolermann, K.-P., 1987. Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. Journal of Geophysical Research 92, 6719–6728.
- Richter, C., 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Reports on Polar Research 154, 1–90.
- Sars, G.O., 1900. Crustacea. In: Nansen, F. (Ed.), Norwegian North Polar Expedition 1893–1896. Scientific Results 1, 1–137.
- Schauer, U., Fahrbach, E., Østerhus, S., Rohardt, G., 2004. Arctic warming through the Fram Strait: oceanic heat transport from 3 years of measurements. Journal of Geophysical Research 109, C06026.
- Seiler, D., Brandt, A., 1997. Seasonal occurrence of planktic Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biology 17, 337–349.
- Smidt, E.L.B., 1979. Annual cycles of primary production and of zooplankton at Southwest Greenland. Greenland Bio-Science 1, 52.
- Smith, S.L., 1988. Copepods in Fram Strait in summer: distribution, feeding and metabolism. Journal of Marine Research 46, 145–181.
- Smith, S.L., 1990. Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. Marine Biology 106, 59–69.
- Smith, S.L., Smith, W.O., Codispoti, L.A., Wilson, D.L., 1985. Biological observations in the marginal ice zone of the East Greenland Sea. Journal of Marine Research 43, 693–717.
- Søreide, J.E., Hop, H., Falk-Petersen, S., Gulliksen, B., Hansen, E., 2003. Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring. Marine Ecology Progress Series 263, 43–64.
- Southward, A.J., 1980. The Western English channel—an inconsistent ecosystem. Nature 285, 361–366.
- Thibault, D., Head, E.J.H., Wheeler, P.A., 1999. Mesozooplankton in the Arctic Ocean in summer. Deep-Sea Research I 46, 1391–1415.
- Turner, J.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies 2, 255–266.
- Turner, J.T., Levinsen, H., Nielsen, G., Hansen, B.W., 2001. Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Marine Ecology Progress Series 221, 209–219.
- Uye, S., 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. Journal of the Oceanographical Society of Japan 38, 149–158.
- Vinje, T.E., 1985. Sea ice distribution 1971–80. Norsk Polarinstittutt Skrifter, 179D, Oslo.
- Wassmann, P., 1989. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiologia 363, 29–57.
- Weslawski, J.M., Kwasniewski, S., 1990. The consequences of climatic fluctuations for the food web in Svalbard coastal waters. In: Barnes, M., Gibson, R.N. (Eds.), Trophic Relationships in the Marine Environment. In: Proceedings of 24th European Marine Biology Symposium. Aberdeen University Press, pp. 281–295.
- Willis, K., Cottier, F., Kwasniewski, S., Word, A., Falk-Petersen, S., 2006. The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). Journal of Marine Systems 61, 39–54.