Polar Biol (1998) 19: 63–76

ORIGINAL PAPER

K.N. Kosobokova · H. Hanssen · H.-J. Hirche
K. Knickmeier

Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993

Received: 25 March 1997 / Accepted: 18 July 1997

Abstract Zooplankton composition and distribution were investigated on the Laptev Sea shelf, over the continental slope and in the adjacent deep Nansen Basin during the joint German-Russian expedition "Arctic 93" with RV *Polarstern* and *Ivan Kireyev* in August/September 1993. In the shelf area biomass decreased from west to east with the lowest values in the area influenced by the Lena river runoff. A gradual increase of biomass from the shallow to the deep area correlated with water depth. Total biomass ranged between 0.1 and 1.5 g m^{-2} on the shelf and 4.7 and 7.9 g m^{-2} in the adjacent Nansen Basin. On the shelf *Calanus glacialis/finmarchicus* dominated overall. The contribution of brackish-water taxa was low in the west, where high salinity and southward currents from the Arctic Basin supported a marine neritic community, but on the southern and eastern Laptev shelf, in the areas of freshwater influence, brackish-water taxa contributed up to 27% of the total biomass. On the slope and in deep areas a few large Arctic copepod species, *Calanus glacialis*, *C. hyperboreus* and *Metridia longa*, composed the bulk of biomass and determined the pattern of its vertical distribution. The export of *Calanus* species from the Nansen Basin onto the Laptev shelf appears to be of great importance for the shelf communities. In turn, the eastern outer shelf and slope area of the Laptev Sea are thought to have a pronounced effect on the deep basin, modifying the populations entering the central Arctic.

K.N. Kosobokova
P.P. Shirshov Institute of Oceanology, Russian Acad. Sci.,
Krasikova, 23, 117218, Moscow, Russia

H. Hanssen · K. Knickmeier
Institut für Polarökologie, Universität Kiel,
Wischhofstrasse 1–3 Gebäude 12,
D-24148 Kiel, Germany

H.-J. Hirche (✉)
Alfred-Wegener-Institut für Polar- und Meeresforschung,
Columbusstrasse 1, D-27515 Bremerhaven, Germany

Introduction

Plankton communities in the Arctic Ocean are generally shaped by the strong seasonality in light regime and ice cover, and the advection of waters from adjacent seas. One-third of the total area is covered by shallow wide marginal seas with seasonally ice-free regions and polynyas. These neritic waters are of major importance with respect to biological production (Subba Rao and Platt 1984), sea ice (Eicken et al. 1997) and water mass formation (Rudels and Quadfasel 1991) in the Arctic Ocean.

The Laptev Sea is one of the very shallow Siberian shelf seas widely connected with the Arctic Basin. According to the geographical definition of Treshnikov (1985), the Laptev Sea also includes the eastern part of the Nansen Basin, and, therefore its northern geographical boundary passes over the sea bed with depths exceeding 2,000 m. A steep continental slope separates the shallow southern part from this deep northern area. Mean depths over 75% of the Laptev Sea area are between 15 and 25 m. Near the New Siberian Islands the shallow area extends up to 600 km from the Arctic coast (Timokhov 1994).

The southern part of the neritic zone is strongly influenced by freshwater input from the large Siberian rivers Khatanga and Lena, whereas the Atlantic water, advected to the continental slope and the oceanic part of the Laptev Sea (Schauer et al. 1997), does not penetrate onto the shallow shelf.

Pelagic communities, shaped by freshwater influence or the advection of warm and saline Atlantic water, are supposed to have different characteristics. This, in turn, suggests specific patterns of transformation of organic matter in the pelagic communities of the shallow sea and adjacent deep Nansen Basin and different energy and matter fluxes. Biological productivity has been little investigated and, consequently, very little is known about the Laptev Sea plankton.

The first zooplankton collections were obtained almost 100 years ago in two locations in the deep northern

Laptev Sea during the drift expedition of "*Fram*" (Sars 1900). Later, Linko (1913) reported on several plankton species obtained during the Russian Polar Expedition 1900–1903 near the New Siberian Islands, and Virketis (1932) reported on zooplankton composition in the southeastern part of Tiksi Bay, the region strongly influenced by the Lena river. Some data on plankton biomass in the shallow Laptev Sea were provided by Jaschnov (1940), and on zooplankton composition and abundance near the New Siberian Islands by Pavshtiks (1990). Sirenko et al. (1996) described near-bottom fauna collected in the northern Laptev Sea in 1993; however, the greater part of the Laptev Sea, especially the northern area, has not been covered by previous investigations.

The present study has investigated zooplankton composition and distribution from the wide shallow shelf of the Laptev Sea over the slope region to the deep adjacent Nansen Basin to provide the background for further assessments of productivity and organic matter fluxes. The main goals of the study were: (1) to describe the faunal composition, abundance and biomass of zooplankton in the different regions; and (2) to analyse patterns of vertical and horizontal distribution of biomass in the shallow and deep regions.

Materials and methods

Zooplankton was collected during the joint expedition "Arctic '93" with RV *Polarstern* (ARK IX/4) and *Ivan Kireyev* (TRANSDRIFT I) between 10 August and 22 September 1993 (Table 1, Fig. 1). Samples were taken from four latitudinal transects (H, G, F and E) extending from the Laptev shelf over the continental slope into the adjacent eastern Nansen Basin. In the deep and slope zones five depth strata were sampled from the bottom or 1500 m to the surface by vertical hauls with a multinet (Hydrobios, Kiel, 0.25-m^2 mouth opening, 150-μm mesh). Regular depth intervals on the outer shelf and deep stations were 0–10–25–50–100–200 m and 0–25–50–200–500–1500 m (or bottom) respectively. On the shallow shelf a multinet with 300-μm mesh was used to sample the layers 0–10–20–30–40 m.

In order to characterise the different regions, the 32 stations were grouped according to depth. Stations located at depths < 100 m were regarded as shelf zone stations. Stations at depths between 100 and 1000 m and those deeper than 1000 m were pooled to represent continental slope and deep Laptev Sea stations, respectively.

Samples were preserved in 4% borax-buffered formalin. All zooplankton organisms from a sample were sorted to main taxonomic groups, and copepods to species and stages level. Rare organisms were counted from the whole sample, while abundant organisms were counted from an aliquot (down to 1:32) of a sample.

Calanus finmarchicus and *C. glacialis* copepodite stages IV–VI were separated by prosome length according to Tande et al. (1985): CIV > 2.3 mm, CV > 3.0 mm and females > 3.2 mm were determined as *C. glacialis*. Frequency distribution of the prosome lengths of copepodite stages IV–VI obtained during the present study resembled the bimodal distribution found by Tande et al. 1985 and Hirche and Mumm 1992.

Dry mass was calculated using length-mass relationships and mean individual dry mass for each species derived from the literature (Table 2). Length measurements were performed using an image-analysing system. When neither length-mass relationship nor mean individual dry mass was available, length-mass relationships of species similar in shape were applied. Cnidarians, larvaceans, echinoderm larvae, nudibranchians and polychaetes were of minor importance in terms of biomass and were excluded from our calculations.

At 17 stations the upper 100-m water layer was sampled using a bongo net with 200-μm mesh size. The samples were frozen and dry mass was measured gravimetrically after drying at 70°C. These data were used for comparison with the calculated zooplankton dry mass from the multinet samples from the same stations.

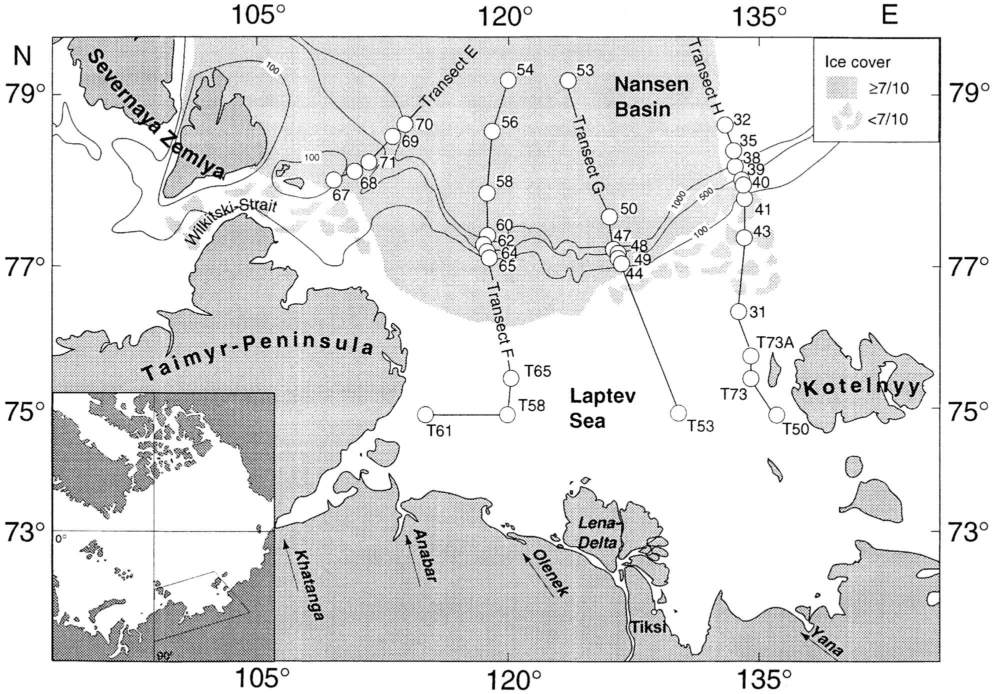


Fig. 1 Station locations in the Laptev Sea and adjacent Nansen Basin. *Polarstern* stations (#) and *Ivan Kireyev* stations (T#)

Table 1 Station data of the expedition ARCTIC 93. [*Polarstern* stations (#) and *Ivan Kireyev* stations (T#). *D* daylight; *T* twilight and *N* night]

	Station	Date	Latitude (N)	Longitude (E)	Depth (m)	Ice (%)	Light*
Transect H	32	02.09.93	78°43′	132°21′	2975	0	D
	35	04.09.93	78°23′	133°04′	2062	0	T
	38	05.09.93	78°10′	133°25′	982	0–10	D
	39	05.09.93	78°06′	133°31′	514	0	T–N
	40	05.09.93	78°04′	133°33′	243	0	D
	41	06.09.93	77°54′	133°34′	72	0–10	D
	43	06.09.93	77°24′	133°35′	53	30–50	N
	31	01.09.93	76°30′	133°20′	38	0	D
	T-73A	02.09.93	75°50′	134°34′	46	0	D
	T-73	09.09.93	75°21′	135°10′	43	0	D
	T-50	03.09.93	75°00′	136°01′	30	0	T
Transect G	53	12.09.93	79°15′	122°53′	3244	90–100	D
	50	10.09.93	77°44′	125°46′	1990	90	D
	47	08.09.93	77°11′	126°14′	990	90	N
	48	09.09.93	77°08′	126°23′	544	70–80	D
	49	09.09.93	77°06′	126°19′	200	90	N
	44	07.09.93	77°02′	126°24′	93	60	D
	T-53	04.09.93	74°58′	129°46′	40	0	T
Transect F	54	13.09.93	79°11′	119°54′	3071	70–80	T
	56	14.09.93	78°40′	118°44′	2618	90–100	N
	58	15.09.93	78°00′	118°34′	1930	80–90	T
	60	16.09.93	77°34′	118°26′	1181	90	D
	62	17.09.93	77°24′	118°11′	554	80–90	N
	64	18.09.93	77°16′	118°32′	230	80	D
	65	18.09.93	77°11′	118°44′	106	80–90	N
	T-65	06.09.93	75°28′	119°57′	43	0	N
	T-58	05.09.93	75°01′	119°52′	33	0	N
	T-61	10.08.93	75°00′	114°33′	42	0	T
Transect E	70	21.09.93	78°45′	112°42′	1141	100	N
	69	21.09.93	78°42′	112°32′	518	100	D
	71	22.09.93	78°35′	111°22′	235	100	D
	68	20.09.93	78°28′	110°49′	101	90–100	N
	67	20.09.93	78°16′	109°15′	51	70	D

Results

Hydrography

In summer the water temperature and salinity distribution in the surface layer of the Laptev Sea are governed by ice conditions, river runoff and advection of water masses from the adjacent areas (Timokhov 1994). In the shallow part a counter-clockwise circulation has been observed (Haas et al. 1995). Water masses from the Kara Sea and the Nansen Basin enter the Laptev Sea to the west and follow the coastline eastwards up to the Lena Delta. In the eastern shallow sea, currents are directed to the northeast. The western part of the Laptev Sea, influenced by the Nansen Basin waters, is colder and more saline than the eastern part, which is affected by warm river water.

During the period of our investigation the shelf waters of the Laptev Sea were clearly stratified. The surface layer was warm and less saline compared to the cold saline waters beneath the pycnocline at 10- to 15-m depth. The eastern Laptev Sea was strongly stratified by the input of warm freshwater from the river Lena, with temperatures of +1.8 to +2.6°C and salinities of 17–18 in the surface layer and −1.7 to −0.7°C and salinities of 25–27 under the pycnocline (Fig. 2). In the western shallow area the pycnocline was less pronounced. The surface salinities were higher, about 22, and temperatures were below +1.5°C.

In the slope region and in the northern deep Laptev Sea, our sampling covered the Polar Surface Water (0–50 m, $t < -1.7°C$, $S < 33.0$), the Halocline (50–200 m, $t = -1.7$ to $-0.5°C$, $S = 33.0–34.5$), the Atlantic Intermediate Water (200–1000 m, $t = 0.5–1.0°C$, $S > 34.5$) and the transition to the Polar Deep Water (>1000 m, $t = -0.5$ to $-1°C$, $S > 34.9$) (Fig. 6 in Schauer et al. 1997).

Ice cover

Reduced ice cover in the Laptev Sea lasts about 3 months. Ice-free regions become more extensive in the eastern part, because cyclonic winds result in ice drift out of the eastern area and input of sea ice into the western part, east of Severnaja Zemlja. In addition the Lena river runoff supports early melting in the eastern Laptev Sea (Eicken et al. 1997).

Table 2 List of species and their occurrence in the shallow, slope and deep region of the Laptev Sea. * = found in the Laptev Sea for the first time, ● = neritic species, ▼ = brackish-water species. Citations for dry weight calculation are indicated in brackets when the values were taken from other species similar in size and shape: 1 = Båmstedt 1981, 2 = Båmstedt et al. 1990, 3 = Conover & Huntley 1991, 4 = W Hagen unpubl., 5 = H Hanssen unpubl., 6 = Hirche et al. 1994, 7 = Kosobokova 1980, 8 = Mizdalski 1988, 9 = Mumm 1991, 10 = Norrbin & Båmstedt 1984, 11 = Richter 1994, 12 = C Richter unpubl.

	Taxa	Shallow	Slope	Deep	Citations for dry mass calculation
	Copepoda				
●	*Acartia longiremis* (Lilljeborg)	×	×		(5)
	Aetideopsis armata Boeck		×		(12)
	Aetideopsis minor (Wolfenden)		×	×	12
*	*Aetideopsis rostrata* G.O. Sars		×	×	12
	Augaptilus glacialis G.O. Sars			×	(12)
	Calanus finmarchicus (Gunnerus)	×	×	×	5, 9
	Calanus glacialis Jaschnov	×	×	×	5, 9
	Calanus hyperboreus Krøyer	×	×	×	4, 6
	Chiridius obtusifrons G.O. Sars		×	×	12
▼	*Drepanopus bungei* G.O. Sars	×	×		(5)
	Eurytemora richingsii (Heron & Damkaer)	×			–
	Gaetanus brevispinus (G.O. Sars)		×	×	12
	Gaetanus tenuispinus (G.O. Sars)		×	×	12
	Haloptilus acutifrons (Giesbrecht)		×	×	(12)
	Heterorhabdus compactus (G.O. Sars)		×	×	–
	Heterorhabdus norvegicus (Boeck)		×	×	12
	Jaschnovia brevis (Farran)	×	×		(5)
▼	*Jaschnovia tolli* (Linko)	×	×		(5)
▼	*Limnocalanus grimaldii* De-Guerne	×			(3, 4, 7, 12)
	Lubbockia glacialis G.O. Sars		×	×	–
	Metridia longa (Lubbock)	×	×	×	2, 3, 4, 7, 12
	Microcalanus pygmaeus (G.O. Sars)	×	×	×	11
	Microsetella norvegica (Boeck)		×	×	–
	Mormonilla minor Giesbrecht		×	×	–
*	*Oithona atlantica* Farran	×	×	×	–
	Oithona similis Claus	×	×	×	2, 9
	Oncae borealis G.O. Sars	×	×	×	11
*	*Oncaea minuta Giesbrecht*			×	–
*	*Oncaea notopus* (Giesbrecht)		×	×	–
*	*Paraeuchaeta barbata* (Brady)			×	4
*	*Paraeuchaeta glacialis* (Hansen)		×	×	4
	Paraeuchaeta norvegica (Boeck)		×	×	4
*	*Paraeuchaeta polaris* Brodsky			×	(4)
*	*Pseudaugaptilus polaris* Brodsky			×	(4, 11)
●	*Pseudocalanus acuspes* (Giesbrecht)	×	×		(9, 5)
▼	*Pseudocalanus major* G.O. Sars	×	×	×	(9, 5)
●	*Pseudocalanus minutus* (Krøyer 1845)	×	×	×	(9, 5)
*	*Pseudochirella spectabilis* Sars			×	(1, 4, 10, 11)
*	*Scaphocalanus brevicornis* (G.O. Sars)		×	×	12
	Scaphocalanus magnus (T. Scott)		×	×	4, 12
*	*Scaphocalanus polaris* Brodsky			×	–
*	*Scolecithricella minor* var. occidentalis (Brodsky)	×	×	×	8
*	*Spinocalanus abyssalis* Giesbrecht			×	–
*	*Spinocalanus antarcticus* Wolfenden		×	×	–
*	*Spinocalanus elongatus* Brodsky			×	–
	Spinocalanus longicornis G.O. Sars	×	×	×	8
*	*Spinocalanus longispinus* Brodsky		×	×	–
	Temorites brevis G.O. Sars		×	×	(5)
*	*Tharybis groenlandicus* (Tupitzky)			×	(5)
	Tisbe furcata (Baird)		×	×	–
	Undinella oblonga G.O. Sars			×	(12)
*	*Xanthocalanus borealis* G.O. Sars		×		(1, 4, 10)
*	*Xanthocalanus profundus* G.O. Sars			×	(5)
	Hydromedusae				
	Aglantha digitale (O.F. Müller)	×	×	×	–
	Aeginopsis laurentii Brandt	×	×	×	–
*	*Botrynema ellinorae* Kramp		×	×	–
●	*Catablema vesicarium* Agassiz	×			–
●	*Eumedusa birulai*	×			–

Table 2 (Continued)

	Taxa	Shallow	Slope	Deep	Citations for dry mass calculation
●	*Euphysa flammea* (Linko)	×	×		–
●	*Halitholus yoldia-arcticae* Birula	×			–
	Homoeonema platygonon Maas		×	×	–
●	*Obelia* spp.	×			–
*	*Paragotoea elegans* Margulis			×	–
	Plotocnide borealis Wagner	×	×		–
●	*Sarsia princeps* (Haeckel)	×			–
*	*Yakovia polinae* Margulis			×	–
	Scyphomedusae				
*	*Atolla tenella* Hartlaub			×	–
	Siphonophora	×	×		–
	Dimophyes arctica (Chun)			×	
	Ctenophora				
	Bolinopsis infundibulum (O.F. Müller)			×	–
	Beroe cucumis Fabricius			×	–
	Mertensia ovum (Fabricius)			×	–
	Pleurobrachia pileus O.F. Müller	×	×	×	–
	Nermertini				
	Pilidium larvae	×			–
	Polychaeta	×	×	×	–
	Bivalvia				
	Veliger larvae	×	×		–
	Pteropoda				
	Clione limacina Phipps	×	×	×	–
	Limacina helicina Phipps	×	×		–
	Ostracoda				
	Conchoecia sp.	×	×	×	9
	Cirripedia				
	nauplii	×	×		–
	Cypris larvae	×	×		–
	Mysidacea				
	Mysis oculata (Fabricius)	×	×		–
	Amphipoda	×			
	Apherusa glacialis (Nansen)			×	9
	Cyclocaris guilelmi Chevreux			×	9
	Onisimus glacialis (G.O. Sars)	×	×	×	9
	Parathemisto abyssorum Boeck	×	×	×	9
	Parathemisto libellula (Mandt)			×	9
	Lanceola clausi Sovallius			×	9
	Euphausiacea				
	Furcilia larvae	×	×		9
	Thysanoessa inermis (Krøyer)		×		9
	Thysanoessa longicaudata (Krøyer)		×	×	9
	Thysanoessa raschii (M. Sars)		×		9
	Cumacea	×			(9)
	Decapoda	×	×		(9)
	Hymenodora glacialis (Buchholz)		×	×	(9)
	Chaetognatha				
	Eukrohnia hamata (Moebius)		×	×	9
●	*Sagitta elegans* Verrill	×	×	×	9
*	*Sagitta maxima*			×	
	Appendicularia				
	Oikopleura vanhoeffeni Lohmann	×	×	×	–
	Fritillaria borealis Lohmann	×	×	×	–
	Echinodermata				
	Bipinnaria	×			–
	Ophioplutei	×			–

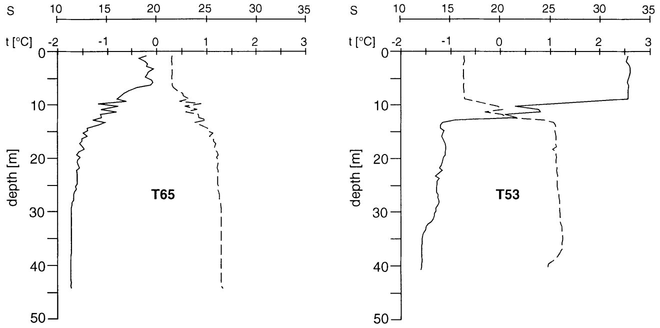


Fig. 2 Temperature and salinity, vertical profiles at st. T65 in the western and st. T53 in the eastern part of the shallow Laptev Sea (M.K. Schmid unpublished data)

In 1993 the ice cover opened first in the eastern shelf area in late May. By early August the ice cover on the shelf and over the slope of the western sea was reduced to 10–60%, while the eastern Laptev Sea for the most part was already ice free. From mid-August to the beginning of September the western part was again completely covered by ice due to northeasterly winds, before the shelf areas again became ice free.

All plankton stations in the shallow Laptev Sea were taken in the ice-free region, while the slope and deep stations west of 130°E were located in the region covered by ice (≥ 70% cover, Table 1). On the eastern transect (H), ice cover did not exceed 50%, and most stations were in the ice-free region, some of them located directly at the ice edge (Fig. 1).

Faunal composition of zooplankton

A total of 53 copepod species (44 calanoids, 7 cyclopoids and 2 harpacticoids) and 18 other taxa from 8 phyla were identified (Table 2). A copepod (*Eurytemora richingsi*) was found in the Laptev Sea for the first time (st. 31, 20–30 m). Heron and Damkaer (1976) described this species as a new Arctic deep-water copepod from depths of 350–1000 m in the Canadian Basin. However, in the present collections, as well as in plankton samples obtained during the expedition ARK XI/1 in 1995, this species (CV, adult females and males) was found only in the eastern part of the Laptev Sea and exceptionally in the upper water layers above 30 m (K.N. Kosobokova, unpublished data). Several specimens of *E. richingsi* were also present in under-ice samples collected on ARK IX/4 with a pump (I. Werner, personal communication), indicating that the species apparently belongs to the epipelagic or sympagic fauna.

Species numbers were lowest in the shallow region (Table 2), where 19 species of Copepoda, 9 Hydromedusae, 1 Ctenophora, 2 Pteropoda, 1 Mysidacea, 2 Amphipoda, 1 Chaetognatha, 2 Appendicularia and 10 other taxa were found. Most zooplankton species found in the shallow region have already been found there earlier (Linko 1913; Virketis 1932; Markhaseva 1984; Pavshtiks 1990). In the deep region, 44 Copepoda, 6 Hydromedusae, 1 Scyphomedusae, 2 Syphonophora, 4 Ctenophora, 2 Pteropoda, 6 Amphipoda, 3 Euphausiacea, 1 Decapoda, 3 Chaetognatha and 2 Appendicularia were identified (Table 2).

Zooplankton abundance

Zooplankton abundance was clearly dominated by copepods over the entire area studied. However, the contribution of the other groups was higher in the shallow zone (20% compared to 4% in the deep-sea zone, Table 3) due to the presence of meroplanktic larvae and larvaceans. *Pseudocalanus* spp., *Oithona similis* and *Calanus glacialis* dominated among copepods in the shallow area. In the areas of the Lena river plume in the eastern part and the Khatanga river influence in the central southern part of the shallow Laptev Sea, the brackish-water species *Drepanopus bungei*, *Limnocalanus grimaldii*, and *Pseudocalanus major* were abundant. Over the continental slope and in the deep basin *O. similis* was the most abundant species, followed by *Oncaea borealis*, *Microcalanus pygmaeus*, copepod nauplii and *Metridia longa*. In the deep sea the relative abundance of *Oithona similis* decreased compared to the slope zone, while the share of the deeper living *Oncaea* spp., *Microcalanus pygmaeus* and *Metridia longa* increased (Table 3).

In the shallow Laptev Sea zooplankton abundance did not reveal any distinctive vertical pattern. At most stations in the western part zooplankton was distributed evenly. At some locations a slight maximum in the surface layer and a slow decrease of abundance with depth were observed, whilst at others the highest abundance was found in the near-bottom layer (Fig. 3). Maximum values ranged between 900 and 5,000 ind. m^{-3}. In the eastern sea the same patterns of vertical distribution were observed with maximum values ranging between 1,200 and 1,600 ind. m^{-3}. An exceptionally high abundance of 8,500 ind. m^{-3} was found in 0–10 m at st. 41 in the marginal ice zone. At three stations (T53, T73, T73A) located in the area of the Lena river plume, abundance was <25 ind. m^{-3}.

In both the slope and the deep-sea regions, abundance demonstrated a pronounced vertical pattern. A considerable part of the zooplankton was concentrated in the upper 50 m with up to 600–4,800 ind. m^{-3} occupying the upper 0–25 m. A considerable decrease in abundance was observed below 50 m. Below 200 m abundance seldom exceeded 100 ind. m^{-3}.

Zooplankton biomass

Copepods were the most important taxonomic group also in terms of biomass (Table 4a,b), followed by chaetognaths. *Calanus glacialis*, *C. finmarchicus* and small calanoids (mainly *Pseudocalanus* spp.) dominated in the

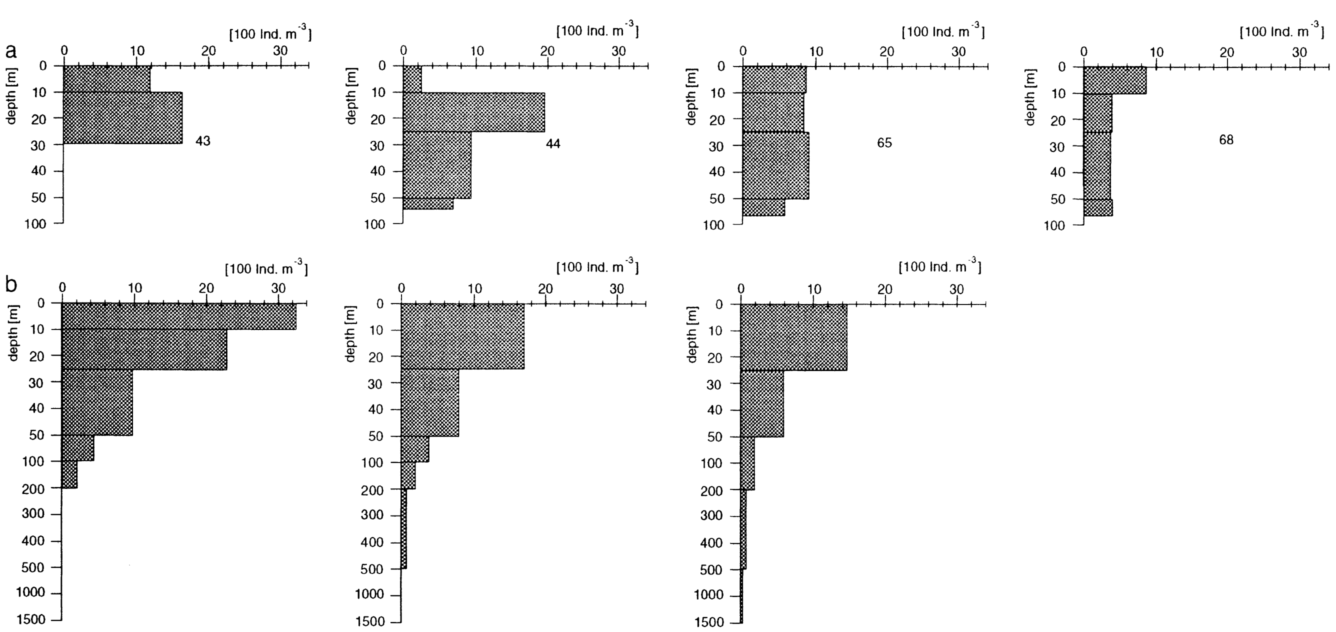


Fig. 3a,b Vertical distribution of zooplankton abundance in the Laptev Sea. **a** Examples for four shallow stations and **b** mean abundance profiles for stations located at 200-m, 500-m, and > 500-m depth

shelf zone (Table 4a). Over the continental slope *C. glacialis* was still the most important species followed by two other large Arctic copepods, *C. hyperboreus* and *Metridia longa*, and the boreal *C. finmarchicus*. At the deep-sea stations the three *Calanus* species and *Metridia longa* again dominated biomass. However, there, *C. hyperboreus* contributed more than *C. glacialis* (Table 4a).

The different mesh sizes used lead to an underestimation of small organisms on most of the shallow stations, which could not be quantified. However, biomass on the shallow stations outside the area of the Lena outflow was, independently of the mesh size, clearly dominated by the large copepod *C. glacialis*. Further the biomass values on the shallow stations match most of those from the surface layer in the deep region (Fig. 4). Therefore the total

Table 3 Mesozooplankton abundance composition (%) in the shallow Laptev Sea, the continental slope and the deep area

Species	Shallow Laptev Sea (< 100 m)				Continental slope (100–1000 m)				Deep Laptev Sea (> 1000 m)			
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Aetideidae	0.15	0.00	1.46	0.38	0.48	0.09	1.24	0.38	0.63	0.34	1.15	0.28
Calanus finm./glac. CI–III	2.46	0.12	11.00	2.93	1.16	0.02	5.10	2.07	0.08	0.00	0.60	0.19
Calanus finmarchicus CIV–VI	1.93	0.10	4.24	1.49	1.07	0.10	2.26	0.71	0.85	0.23	1.63	0.47
Calanus glacialis CIV–VI	6.60	0.96	19.33	6.06	2.25	0.86	3.82	1.19	1.36	0.73	2.13	0.44
Calanus hyperboreus CII–VI	0.35	0.00	1.72	0.46	0.66	0.18	2.18	0.60	1.71	0.84	3.69	0.91
Drepanopus bungei	3.77	0.00	46.65	12.36	0.06	0.00	0.20	0.07	0.00	0.00	0.00	0.00
Limnocalanus grimaldii	1.01	0.00	9.25	2.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metridia longa	0.85	0.00	2.84	0.95	7.85	3.64	14.60	3.93	11.25	5.34	19.48	5.17
Microcalanus pygmaeus	1.76	0.00	9.59	2.85	9.92	4.48	12.69	2.81	15.00	4.76	20.97	5.15
Pareuchaeta spp.	0.02	0.00	0.15	0.04	0.23	0.07	0.62	0.17	0.37	0.23	0.61	0.13
Pseudocalanus spp.	28.97	2.15	60.26	19.35	6.16	0.34	11.91	5.14	0.89	0.02	3.47	1.17
Oithona similis	21.74	0.16	60.17	23.38	39.50	25.69	66.19	14.13	31.98	21.26	42.76	7.24
Oncaea spp.	2.40	0.00	12.37	3.93	12.98	5.82	20.73	4.70	16.24	11.09	23.91	4.59
Other copepods	1.90	0.10	5.95	2.13	1.35	0.33	2.52	0.86	5.26	2.47	13.95	4.27
copepod nauplii	6.99	0.00	36.65	9.83	10.25	5.42	15.49	3.82	9.30	5.05	23.40	5.93
Ostracoda	0.01	0.00	0.04	0.01	0.89	0.04	2.47	0.74	2.02	1.14	3.62	0.78
Other crustacea	0.46	0.01	1.63	0.57	0.08	0.04	0.12	0.03	0.07	0.03	0.17	0.05
Eukrohnia hamata	0.01	0.00	0.09	0.03	0.53	0.09	1.25	0.38	1.44	0.22	3.30	1.22
Sagitta elegans	2.27	0.07	8.44	2.79	0.06	0.00	0.13	0.04	0.00	0.00	0.00	0.00
Others	16.33	1.09	47.80	16.29	4.52	1.04	9.59	3.08	1.53	0.79	2.88	0.81
Total copepods	80.91	49.42	98.64	17.40	93.93	88.45	97.27	3.23	94.94	91.91	97.37	1.88
Other crustacea	0.47	0.01	1.63	0.56	0.96	0.17	2.57	0.75	2.09	1.17	3.65	0.77
Others	18.62	1.35	50.27	17.18	5.11	1.51	10.35	3.18	2.97	1.01	5.15	1.59

Table 4 Composition of mesozooplankton dry mass (%) in the shallow Laptev Sea, the continental slope and the deep area for the total sampled depth and for the upper 50 m

Taxa	Shallow Laptev Sea (< 100 m)				Continental slope (100–1000 m)				Deep Laptev Sea (> 1000 m)			
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Total sampled depths												
Aetideidae	0.1	< 0.1	1.4	0.4	0.8	< 0.1	1.5	0.6	1.3	0.6	2.7	0.6
Calanus finm./glac. CI–III	3.2	0.2	13.3	4	2.2	< 0.1	10.7	3.6	0.2	< 0.1	0.8	0.3
Calanus finmarchicus CIV–VI	6.7	1.2	33.1	8.8	8.5	0.6	21.9	5.8	4.2	1.2	7.1	1.8
***Calanus glacialis* CIV–VI**	**60.7**	41	82.2	13.9	**41.4**	12.5	67.9	15.9	**18.9**	13.1	26.6	5.3
***Calanus hyperboreus* CII–VI**	4	< 0.1	20.3	5.8	**10.3**	2.3	34.5	8.2	**27.8**	16.4	41.2	9.9
Drepanopus bungei	1	< 0.1	12.3	3.5	< 0.1	< 0.1	0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Limnocalanus grimaldii	2.4	< 0.1	11.8	4.4	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Metridia longa	1.9	< 0.1	6.5	2	**10.7**	3.6	23.7	5.8	**16.5**	11.2	26.1	4.3
Pareuchaeta spp.	0.2	< 0.1	1.2	0.4	3.2	0.3	7.3	2.2	4.3	1.7	7.8	1.9
Pseudocalanus spp.	6.4	0.7	22.1	5.4	2.6	0.1	20.8	5.5	0.1	< 0.1	0.3	0.1
Oithona similis	2.8	< 0.1	10	3.8	4.4	1.7	8.9	2.2	2.2	0.8	3.8	0.9
Other copepods	1	< 0.1	3.3	1.2	3.9	1.7	6.7	1.6	5.4	4.1	7.4	1.2
Ostracoda	< 0.1	< 0.1	0.5	0.1	1.5	< 0.1	3.6	1.4	3.2	1.7	5.3	1.1
Other crustacea	2.9	< 0.1	16	4.8	1.3	< 0.1	8.7	2.4	2.8	0.1	5.4	1.5
Eukrohnia hamata	< 0.1	< 0.1	0.4	0.1	7.7	< 0.1	41.2	10.9	**13.2**	6.5	19.2	4.6
Sagitta elegans	6.5	0.3	25.7	8.2	1.6	< 0.1	4.4	1.3	< 0.1	< 0.1	< 0.1	< 0.1
Others	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Total copepods	90.6	73.4	99.5	9.8	88	54.7	98.1	11.4	80.9	73.1	89.2	5
Other crustacea	2.9	< 0.1	16	4.8	2.8	< 0.1	8.8	2.8	5.9	4.1	8.8	1.8
Others	6.5	0.4	25.7	8.2	9.2	1.9	41.2	10.5	13.2	6.5	19.2	4.6
Upper 50 m												
Aetideidae	0.1	< 0.1	1.4	0.4	0.1	< 0.1	0.5	0.2	0.3	< 0.1	1.5	0.5
Calanus finm./glac. CI–III	3.5	0.2	13.3	4.1	4.8	< 0.1	23.6	7.8	0.5	< 0.1	4.4	1.4
Calanus finmarchicus CIV–VI	6.7	1.2	33.1	8.8	9.4	0.8	23	6.6	4.3	1.3	9.4	2.6
***Calanus glacialis* CIV–VI**	**58.6**	22.2	82.2	17.5	**43.1**	15.6	70.2	19.3	**39.1**	25.8	62.5	13.4
***Calanus hyperboreus* CII–VI**	5.6	< 0.1	38.9	10.8	**10.7**	0.5	35.2	11.3	**14.8**	2.1	39.1	13.4
Drepanopus bungei	1	< 0.1	12.3	3.5	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Limnocalanus grimaldii	2.4	< 0.1	11.8	4.4	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Metridia longa	1.4	< 0.1	4.1	1.4	**8**	0.3	26.4	9.1	**12.9**	1	30.9	8.9
Pareuchaeta spp.	0.2	< 0.1	1.2	0.4	3	< 0.1	9.9	3.6	3.8	1	11.3	3.1
Pseudocalanus spp.	6.7	0.7	22.1	5.5	3.4	0.1	15.7	4.4	0.4	< 0.1	1.1	0.4
Oithona similis	3.3	< 0.1	15.8	5	8.5	3.2	15.9	4.6	7.6	2.2	14.3	4.4
Other copepods	1.1	< 0.1	4.4	1.4	2.9	0.4	8	2.4	2.1	0.9	5.2	1.2
Ostracoda	< 0.1	< 0.1	0.1	< 0.1	0.2	< 0.1	1.2	0.4	1.2	0.1	2.3	0.8
Other crustacea	2.9	< 0.1	16	4.8	0.5	< 0.1	2.5	1	0.6	< 0.1	3.6	1.1
Eukrohnia hamata	< 0.1	< 0.1	0.4	0.1	1.7	< 0.1	6	2	**12.4**	2.9	27.2	8.4
Sagitta elegans	6.5	0.5	25.7	8.2	3.6	< 0.1	15.1	4.6	< 0.1	< 0.1	< 0.1	< 0.1
Others	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Total copepods	90.6	73.4	99.5	9.8	94	79.8	99.2	5.6	85.8	71.5	96.4	8.7
Other crustacea	2.9	< 0.1	16	4.8	0.8	< 0.1	2.7	1.1	1.9	0.7	3.7	1
Others	6.5	0.5	25.7	8.1	5.3	0.5	20.1	5.6	12.4	2.9	27.2	8.4

biomass values will not be severely affected by the methodological restraint of different mesh sizes.

The principal role of the dominant copepod species in the shallow and slope regions did not differ much, when biomass composition in the entire water column (Table 4a) was compared with that in the upper 50 m (Table 4b). However, data for the deep region indicated that in oceanic waters *Calanus glacialis* dominated in the upper layer, while *C. hyperboreus* and *Metridia longa* contributed more to the zooplankton biomass below 50 m.

The neritic chaetognath, *Sagitta elegans*, dominated in the shallow region, composing 6.5% of the total biomass, and an oceanic species, *Eukrohnia hamata*, dominated in the deep-sea region (13.2% of the total biomass). Ostracods were almost absent in the shallow sea, while in the deep area they represented 3.2% of the total biomass. Other groups (Amphipoda, Euphausiacea, Pteropoda, Polychaeta) were of minor importance.

The distribution of total zooplankton biomass over the shelf area demonstrated a pronounced decrease from west to east. Lowest values were observed in the area influenced by the Lena river runoff (Fig. 4), where lowest abundances were found. A gradual increase in biomass along the transects correlated with increasing water depth. In the shelf zone total biomass ranged between 0.1 and 1.5 g m^{-2}, while in the adjacent Nansen Basin it reached 4.7–7.9 g m^{-2} (Fig. 4).

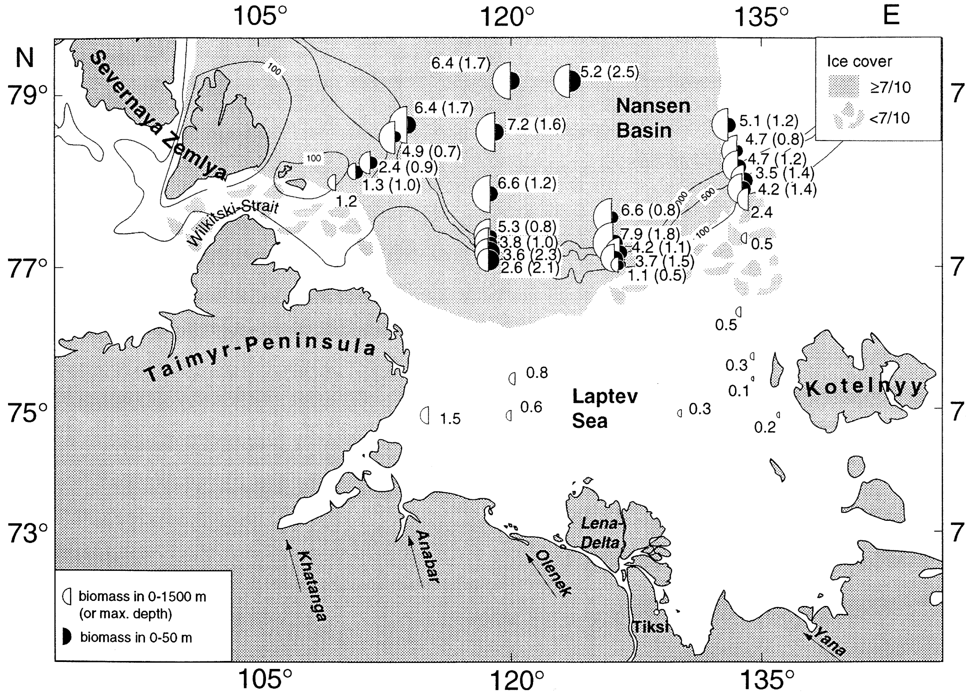


Fig. 4 Distribution of total zooplankton biomass [g m^{-2}] in 0–1500 m or maximum depth in the Laptev Sea. Values of total biomass in the layer 0–50 m in parentheses

The vertical distribution of zooplankton biomass on the shallow shelf was related to the hydrographic stratification, which was mainly determined by the vertical distribution of temperature. Generally, the bulk of biomass was concentrated in the deepest layer with the lowest temperature, while in the relatively warm surface layer a biomass minimum was observed (Fig. 5). The position of the biomass maximum was determined mostly by the vertical distribution of *Calanus glacialis* and *Pseudocalanus* spp. Their preference for cold water was evident in the area of the Lena outflow where warm river water was advected and surface temperatures were 2–3°C higher compared to other shelf stations.

In the slope and deep regions, as well as on the outer shelf, up to one-third of the total zooplankton biomass (0.8 and 2.5 g m^{-2}) was concentrated in the 0- to 50-m horizon. The biomass maximum within the upper 50 m was related to the vertical distribution of *Calanus glacialis*, *C. hyperboreus*, *C. finmarchicus* and *Metridia longa*. Biomass decreased exponentially with depth (Fig. 5). There were no pronounced differences between the western and eastern deep-sea area, either in total biomass (0–50 m or 0–1500 m) or in the vertical distribution of biomass (Fig. 5).

Calculated and measured values of total biomass (0–100 m) were similar at the shallow stations (Table 5), although at the deepest stations they were consistently lower (13% on average), but these differences were not statistically significant. The underestimation of calculated zooplankton biomass in the deep region is possibly caused by the application of individual dry mass from different Arctic regions for the biomass-important species (Table 2).

Stage composition of the dominant copepod species on slope and deep stations

The populations of both *Calanus glacialis* and *C. hyperboreus* during the period investigated seem to represent two year-classes. The proportion of young and late stages of both species differed in the ice-covered (transects E, F, G) and ice-free areas (transect H). *C. glacialis* CI–CIII were almost absent in the ice-covered area, which indicates that reproduction hardly took place or failed in this region (Table 6). In contrast, in the polynya area in the eastern Laptev Sea, young copepodites of *C. glacialis* composed more than 30% of the population. The proportion of young stages of *C. glacialis*, as well as of *C. hyperboreus* and *Metridia longa*, were highest in the eastern ice-free area (Table 6). The population of *C. finmarchicus* on the slope and in the deep Laptev Sea consisted only of CIV, CV and adult females.

Discussion

Different zooplankton communities host the shallow shelf area and the adjacent deep Nansen Basin. The relatively narrow continental slope represents a sharp boundary and a zone of mixing of the shallow-and deep-water communities. The number of species increased from the shelf to the north. The shelf fauna is characterised by marine neritic, brackish-water, and ubiquitous taxa of the upper layer of the oceanic region (Table 2). The presence of brackish-water species seems to be typical for the outer shelves of the Kara, Laptev and East Siberian Seas, which are strongly influenced by river runoff (Jaschnov 1940; Pavshtiks 1990; Vinogradov et al. 1994). At the continental slope neritic, ubiquitous and oceanic taxa were found, but not true deep-water species (Table 2). The adjacent Nansen Basin is inhabited by many meso- and bathypelagic taxa of the open ocean community. Several copepod and hydromedusan

Table 5 Mesozooplankton dry mass (g m^{-2}). Comparison of calculated and measured values for the upper 100 m

		Station No.							
Shallow Laptev Sea (< 100 m)		41	43	T53					
DM calculated	(max. depth–0 m)	2.42	0.54	0.28					
DM calculated	(max.100–0 m)	2.42	0.54	0.28					
DM measured	(max.100–0 m)	2.93	0.85	0.23					
Calculated/measured	(100–0 m)	0.83	0.64	1.19					
Continental slope (100–1000 m)		38	39	40	47	62	64	65	
DM calculated	(max. depth–0 m)	4.71	3.51	4.22	7.90	3.79	3.61	2.60	
DM calculated	(100–0 m)	1.94	2.54	3.07	2.23	1.62	2.79	2.60	
DM measured	(100–0 m)	2.61	1.89	1.94	3.54	0.68	1.66	2.36	
Calculated/measured	(100–0 m)	0.74	1.34	1.59	0.63	2.40	1.68	1.10	
Deep Laptev Sea (> 1000 m)		32	35	53	54	56	58	60	70
DM calculated	(max. depth–0 m)	5.05	4.72	5.20	6.43	7.15	6.57	5.25	6.36
DM calculated	(100–0 m)	1.84	1.46	2.87	2.27	2.25	1.90	2.13	2.33
DM measured	(100–0 m)	2.17	2.27	2.89	3.13	2.79	2.39	3.13	3.00
Calculated/measured	(100–0 m)	0.85	0.64	0.99	0.73	0.81	0.80	0.68	0.78

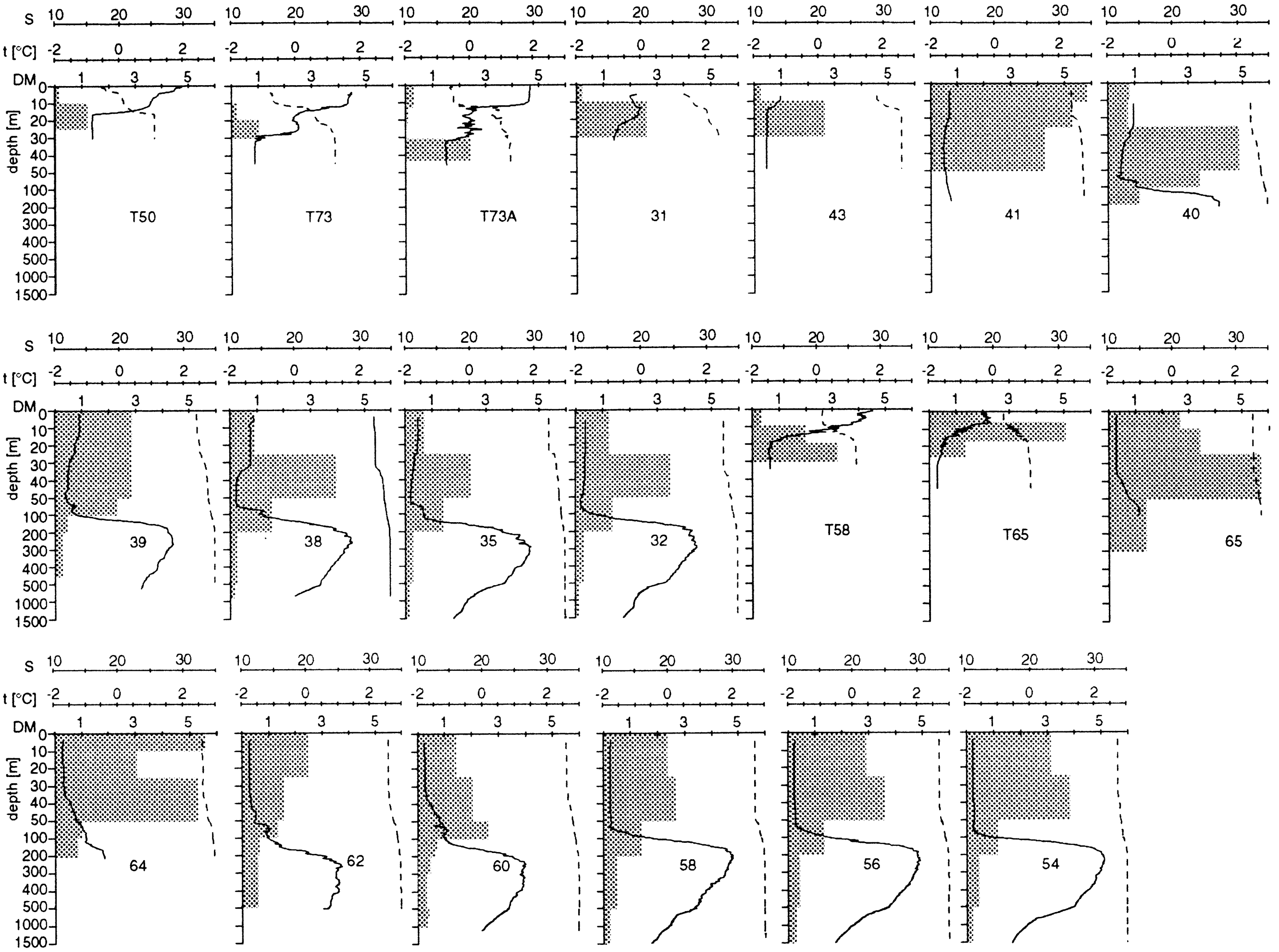


Fig. 5 Vertical distribution of zooplankton biomass [g 100 m^{-3}], temperature and salinity on transects F and H in the Laptev Sea

Table 6 Mean stage composition (%) of the dominant copepod species in the deep Laptev Sea and the adjacent Nansen Basin, August–September 1993

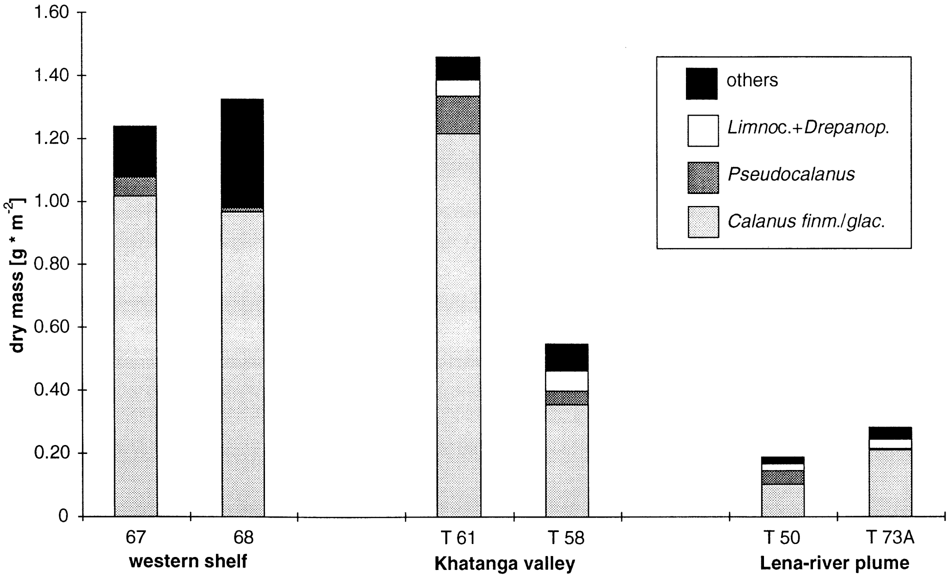
Species	Stage composition [%]						
	CI	CII	CIII	CIV	CV	♀	♂
Ice-covered region							
Calanus glacialis	0.1	0.8	0.6	9.2	42.5	46.5	0.2
C. hyperboreus	0.0	0.0	4.1	38.2	43.9	13.7	0.0
C. finmarchicus	0.0	0.0	0.0	0.1	63.8	36.1	0.0
Metridia longa	2.8	2.3	32.5	36.2	7.5	14.2	4.3
Open water							
C. glacialis	3.4	11.8	17.0	5.6	42.4	19.5	0.3
C. hyperboreus	0.0	1.6	11.0	43.6	30.8	12.9	0.07
C. finmarchicus	0.0	0.0	0.0	0.0	56.2	43.7	0.1
M. longa	9.4	5.0	29.0	31.5	9.2	12.0	3.6

species well-known from the central Arctic Ocean (Harding 1966; Huges 1968; Kosobokova 1981) were found in this region for the first time (Table 2).

The composition of zooplankton biomass varied between the communities. On the shelf *Calanus* species dominated (Fig. 6). The contribution of brackish-water taxa was low in the west, where high salinity and southward currents from the Arctic Basin supported a marine neritic community (Fig. 6) while only a few individuals of the brackish-water taxa were advected from the immediate coastline and from the eastern Kara Sea via Wilkitski Strait. In the southern and eastern Laptev Sea brackish-water taxa were more important in terms of biomass (Fig. 6), but nowhere exceeded 27% due to the low mass of the numerous brackish-water copepod *Drepanopus bungei* and relatively low abundance of the larger *Limnocalanus grimaldii* (Table 3). Another large brackish-water copepod, *Jaschnovia tolli*, which accounted for more than half of the biomass in the eastern area in earlier studies (Pavshtiks 1990), was rare during summer 1993.

In the slope and deep area the relative composition of the zooplankton biomass was very similar to that in the central Arctic Basin (Kosobokova 1982; Mumm 1993). Oceanic and ubiquitous taxa dominated the biomass, while the portion of marine neritic and brackish-water species decreased dramatically towards the deep basin. Copepods dominated overwhelmingly while among other groups only chaetognaths and ostracods were noteworthy (Table 4). A few large copepod species, *Calanus glacialis*, *C. hyperboreus* and *Metridia longa*, composed the bulk of biomass, although sometimes the North Atlantic species *C. finmarchicus* was also noticeable. The first three species are considered to be of true Arctic origin (Gran 1902; Grainger 1961; Grice 1962; Jaschnov 1970) and are known to determine the horizontal and vertical pattern of biomass distribution in the Arctic Basin and adjacent polar regions, building up to >80% of zooplankton biomass (Kosobokova 1982; Smith 1988; Diel 1991; Hirche 1991). Differences in their population structure between the ice-covered western and ice-free eastern deep regions (Table 6) suggest different ways of recruitment. In the west the populations of *C. glacialis*, Metridia longa and *C. hyperboreus* consisted mainly of overwintering stages. The almost complete absence of young copepodites suggests reproductive failure prior to collection, probably due to food limitation as in this ice-covered western area very low phytoplankton concentrations were registered (Springer 1994). In the east a permanent summer polynya (Reimnitz et al. 1995; Eicken et al. 1997) allowed for a relatively high primary production, which supported successful reproduction of *C. glacialis* and *Metridia longa*, as indicated by the occurrence of young stages and egg production experiments (Kosobokova 1994). *C. hyperboreus* usually reproduces in winter in the absence of food (Pavshtiks 1976; Hirche 1997). In this species the increased number of young copepodites may be indicative of better food conditions during their de-

Fig. 6 Composition of zooplankton biomass in the western, central (Khatanga Valley) and eastern Lena river plume shelf area



velopment in this area. These observations illustrate the great importance of the summer polynya for the annual recruitment. Due to their low mass, however, the young copepodites did not affect the distribution of total biomass.

The occurrence of the North Atlantic species *Calanus finmarchicus* in the Kara and Laptev Seas is attributed to advection of water masses of Atlantic origin (Jaschnov 1966). According to Jaschnov (1970), the Laptev Sea is an expatriation area where no reproduction takes place. During the present study this species reached its highest abundance and biomass to the north of the shelf break (Table 4), where it was represented almost exclusively by CV and adult females. Its maximum biomass was 6 times, and its average biomass 10 times lower than on the northern Barents Sea shelf, where it can compose up to 44% of the total biomass (Mumm 1993). Due to difficulties in distinguishing between the young copepodites of *Calanus glacialis/finmarchicus*, we cannot totally exclude the occurrence of *C. finmarchicus* CI–CII in the shallow coastal area. However, few, if any young copepodites were in the size range of *C. finmarchicus*. The present data confirm that the stock of *C. finmarchicus* undergoes a drastic decrease on its route around the perimeter of the Eurasian Basin (Hirche and Mumm 1992).

The vertical distribution pattern of zooplankton biomass, both on the shelf and in the deep areas, was determined by the large copepod species. In the shelf area mostly young *Calanus glacialis/finmarchicus* exhibited the pattern initially found in the Laptev Sea by Jaschnov (1940). He reported that in the Lena and Khatanga plumes the low saline and warm modified riverine waters spread over the more saline and cold oceanic waters. Biomass was confined mainly to the near-bottom layer, where *C. glacialis* and *Pseudocalanus* species were concentrated (Jaschnov 1940), while the surface layer was very poor. Similar patterns have been observed recently by Vinogradov et al. (1994), also in the Kara Sea for the plumes of the Yenisey and Ob rivers.

On the slope and in deep areas the vertical distribution of biomass was typical for the Arctic summer season with a pronounced maximum in the surface layer (Fig. 5) and a rapid decrease below 50 m (Kosobokova 1982; Kosobokova et al. 1995). The Arctic species *Calanus glacialis* and *C. hyperboreus* were concentrated close to the surface, typical for the summer phase of the seasonal vertical distribution (Pavshtiks 1976, 1977; Dawson 1978; Kosobokova 1981, 1982; Geynrikh et al. 1983; Hirche 1997). In contrast, *Metridia longa* and *C. finmarchicus* occupied the layers between 50 and 300 m.

Regional differences were found in the distribution of zooplankton biomass on the Laptev shelf. The gradual decrease from west to east was mostly related to the decreasing abundance of *Calanus* species in the waters influenced by the Lena river outflow (Fig. 6). Total biomass on the western Laptev shelf compared well with summer values in the coastal regions of the White Sea (Pertzova 1970, 1980; Pertzova and Prygunkova 1995) and the eastern Kara Sea (Vinogradov et al. 1994) (Table 7) in areas of comparable depth. However, as these shelves are deeper on average than the Laptev shelf and their deeper parts are inhabited by assemblages of several large-sized species, the zooplankton standing stocks there are higher compared to the Laptev Sea (Vinogradov et al. 1994; Pertzova and Prygunkova 1995). Thus the highest zooplankton biomass is reported for the Barents Sea, the deepest among the Eurasian Arctic shelf seas (Jaschnov 1940; Slagstad and Tande 1990; Mumm 1993; Hansen et al. 1996), while the zooplankton stock in the shallow Laptev Sea is considerably lower (Table 7). This may indicate that the Laptev shelf is less productive, contrasting with the general assumption that nutrient input by river runoff, resuspension of organic matter from the sediments, and temporal enrichment of the pelagic fauna by meroplanktic larvae are prerequisites for enhanced biological production in marginal seas (Smetacek et al. 1987). In the Laptev Sea the severe Arctic climate is superimposed on the specific hydrography and topography, and may make environmental conditions unfavourable for the large zooplankton organisms over at least half of the shallow area. Dominant small-sized neritic species with shorter generation times and higher metabolic rates could be supposed to compensate for the lack of secondary

Table 7 Biomass of zooplankton (dry mass) for Eurasian arctic seas

Region	Maximum depth (m)	Biomass (mg m^{-3})	Total biomass (g m^{-2})	Mesh (µm)	Source
Laptev Sea					
Western area	50	23	1.2	150	Present study
Central area (Khatanga river-plume)	30–40	18.0–36.0	0.6–1.5	300	Present study
Eastern area (Lena river-plume)	30–50	2.0–13.0	0.1–0.5	300	Present study
Central and eastern areas	30–40	9.0–24.0	0.32–0.84	320	Jaschnov 1940
Coastal waters around the New Siberian Islands	5–16	20.0–196.0	0.1–3.1	176	Pavshtiks 1990
White Sea					
Kandalaksha Bay, coastal zone	40–50	24.0–60.0	1.2–2.4	176	Pertzova 1970
Onega Bay	30–40	12.0–18.0	0.4–0.6	176	Pertzova and Prygunkova 1995
Kandalaksha Bay	300	11	3.3	176	Pertzova and Prygunkova 1995
Kara Sea					
Eastern part, Yenisey estuary	25–50	2.8–21.6	0.04–0.35	180	Vinogradov et al. 1994

production by the large species. However, a very short productive season and low temperatures in summer do not allow small-sized neritic species to produce more than one generation per year, which prevents a higher turnover of primary production. This may explain the rather low zooplankton biomass over the vast shallow area, and especially in the eastern part influenced by river runoff.

The low zooplankton stock on the ice-free Laptev shelf in summer is in great contrast to the relatively high biomass in the adjacent ice-covered Nansen Basin. There the zooplankton stock was very close to values observed near the shelf edge of the western Nansen Basin (Mumm 1993; Auel 1995), but 4–5 times higher than in the inner Nansen Basin (Mumm 1993). Apparently, high zooplankton stocks in the Nansen Basin are confined to the margin of the Eurasian Basin, where the Atlantic water inflow is concentrated (Hirche and Mumm 1992; Schauer et al. 1997). The zooplankton community of the Nansen Basin adjacent to the Laptev Sea thus depends on the advection of Atlantic waters. This community is of great importance for the shelf communities through export of, for example, *Calanus* species onto the Laptev shelf. In turn, the eastern outer shelf and slope area of the Laptev Sea has a pronounced effect on the deep basin, as it seems to be a major nursery ground for the large Arctic copepods, modifying the populations entering the central Arctic Ocean.

Acknowledgements We are grateful to crews and captains of RV "*Polarstern*"and RV *Ivan Kireyev* for their support. We thank Drs. Sergej Timofeev and Michael K. Schmid for help with collecting samples and Drs. Claudio Richter and Slavomir Kwasniewski for support during sorting of the material. Drs. Ursula Schauer and M.K. Schmid kindly provided us with hydrographical data. We are indebted to the GEOMAR Institute, especially Dr. Heidemarie Kassens for organising the "TRANSDRIFT I" expedition (BMBF-Project FKZ525400OG0517). This study was partially supported by the *Russian Foundation for Basic Research* (K.N. Kosobokova: RFFI Project 95-05-15424), the *Deutsche Forschungsgemeinschaft* DFG (K.N. Kosobokova: 436 RUS 17/57/96) and the *Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie* BMBF (H. Hanssen and K. Knickmeier: Project 03PL009A9). This is publication no. 1272 of the Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven.

References

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

Conover RJ, Huntley M (1991) Copepods in ice-covered seas-distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J Mar Sys 2:1–41

Dawson JK (1978) Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. Limnol Oceanogr 23:950–957

Diel S (1991) On the life history of dominant copepod species (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, Metridia longa) in the Fram Strait. Rep Polar Res 88:1–113

Eicken H, Reimnitz E, Alexandrov V, Martin T, Kassens H, Viehoff T (1997) Sea ice processes in the Laptev Sea and their importance for sediment transport. Cont Shelf Res 17:205–233

Geynrikh AK, Kosobokova KN, Rudyakov YA (1983) Seasonal variations in the vertical distribution of some prolific copepods of the Arctic Basin. Can Transl Fish Aquat Sci 4925:1–22

Grainger EH (1961) The copepods *Calanus glacialis* Jaschnov and *Calanus finmarchicus* (Gunnerus) in Canadian arctic-subarctic waters. J Fish Res Board Can 18:663–677

Gran HH (1902) Das Plankton des norwegischen Nordmeeres, von biologischen und hydrographischen Gesichtspunkten behandelt. Rep Norw Fish Invest 2:1–222

Grice GD (1962) Copepods collected by the nuclear submarine Seadragon on a cruise to and from the North Pole, with remarks on their geographic distribution. J Mar Res 20:97–108

Haas E, Antonow M, Shipboard Scientific Party (1995) Movement of Laptev Sea shelf waters during the Transdrift II Expedition. Rep Polar Res 176:121–134

Hansen B, Christiansen S, Pedersen G (1996) Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: carbon flow and structure of the grazer food chain. Polar Biol 16:115–128

Harding GCH (1966) Zooplankton distribution in the Arctic Ocean with notes on life cycles. MSc Thesis, McGill University

Heron GA, Damkaer DM (1976) *Eurytemora richingsi*, a new species of deep-water calanoid copepod from the Arctic Ocean. Proc Biol Soc Wash 80:127–136

Hirche HJ (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. Polar Biol 11:351–362

Hirche HJ (1997) Life cycle of *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128:607–618

Hirche HJ, 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 summer. Polar Biol 14:491–503

Hirche HJ, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. Deep Sea Res 39:S485–S505

Huges KH (1968) Seasonal vertical distribution of copepods in the Arctic water in the Canadian Basin of the North Polar Sea. MSc Thesis, University of Washington

Jaschnov VA (1940) Plankton productivity of the northern seas of the USSR (in Russian). Moskovskoe Obchsestvo Ispytatelei Prirody Press, Moscow

Jaschnov VA (1966) Water masses and plankton. 4. *Calanus finmarchicus* and *Dimophyes arctica* as indicators of atlantic waters in the Polar Basin (in Russian). Oceanology 6:493–503

Jaschnov VA (1970) Distribution of *Calanus* species in the seas of the northern hemisphere. Int Rev Ges Hydrobiol 55:197–212

Kosobokova KN (1980) Caloric value of some zooplankton representatives from the central Arctic Basin and the White Sea. Oceanology 22:744–750

Kosobokova KN (1981) Zooplankton of the central Arctic Basin (in Russian). PhD Thesis, Moscow

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

Kosobokova KN (1994) Egg production of dominant copepod species. In: Fütterer DK (ed) The Expedition ARCTIC 93 Leg ARK IX/4 of RV "Polarstern". Rep Polar Res 149:90–94

Kosobokova KN, Hanssen H, Markhaseva EL, Petryashov VV, Pintchuk A (1995) Composition and distribution of summer zooplankton in the Laptev Sea. In: Kassens H, Piepenburg D, Thiede J, Timokhov L, Hubberten HW, Priamikov SM (eds) Russian-German Cooperation: Laptev Sea System. Rep Polar Res 176:192–199

Linko AK (1913) Zooplankton of the Siberian ice ocean after collections of the Russian Polar Expedition 1900–1903 (in Russian). Zap Imp Akad Nauk St. Petersb 29:1–54

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

Mizdalski E (1988) Weight and lengths data of zooplankton in the Weddell Sea in austral spring 1986 (ANT V/3). Rep Polar Res 55:1–72

Mumm N (1991) Zur sommerlichen Verteilung des Mesozooplanktons im Nansen Basin, Nordpolarmeer. Rep Polar Res 92: 1–173

Mumm N (1993) Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. Polar Biol 13:451–461

Norrbin MF, Båmstedt U (1984) Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. – A comparison of energetic strategies in marine organism groups. Ophelia 23:47–64

Pavshtiks EA (1976) Biological seasons and a life span of *Calanus hyperboreus* Kroyer in the Central Arctic (in Russian). Nat Econ North 4:121–127

Pavshtiks EA (1977) Seasonal changes in the stage composition of the populations of calanoid copepods in the Arctic Basin (in Russian). Issled Fauny Morei, Nauk St. Petersb 19:56–73

Pavshtiks EA (1990) Composition and quantitative distribution of the zooplankton near New Siberian islands. In: Golikov AN (ed) Ecosystems of the new Siberian shoal and the fauna of the Laptev Sea (in Russian). Explor fauna Seas 37:89–104

Pertzova NM (1970) Zooplankton of the Kandalaksha Bay of the White Sea (in Russian). Biol White Sea 3:34–45

Pertzova NM (1980) Distribution of zooplankton in the Basin and the Kandalaksha Bay of the White Sea (in Russian). Biol White Sea 5:49–68

Pertzova NM, Prygunkova RV (1995) Zooplankton In: Golikov (ed) The biology of the White Sea. Issled Fauny Morei Nauk St. Petersb pp 35–56

Reimnitz E, Eicken H, Martin T (1995) Multiyear fast ice along the Taymyr Peninsula, Siberia. Arctic 48:359–367

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Rep Polar Res 154:1–87

Rudels B, Quadfasel D (1991) Convection and deep water formation in the Arctic Ocean-Greenland Sea system. J Mar Systems 2:435–450

Sars GO (1900) Crustacea. In: Nansen F (ed) Norwegian North Polar Expedition 1893–1896. Sci Res 1:1–137

Schauer U, Muench R, Rudels B (1997) The impact of eastern Arctic shelf waters on the Nansen Basin intermediate layers. J Geophys Res 102:3371–3382

Sirenko BI, Markhaseva EL, Buzhinskaya GN, Golikov AA, Menshutkina TV, Petryashov VV, Semenova TN, Stepanjants SD, Vassilenko SV (1996) Preliminary data on suprabenthic invertebrates collected during the RV Polarstern cruise in the Laptev Sea. Polar Biol 16:345–352

Slagstad D, Tande KS (1990) Growth and production dynamics of *Calanus glacialis* in an arctic pelagic food web. Mar Ecol Prog Ser 63:189–199

Smetacek VS, Bodungen B von, Bröckel K von, Knoppers B, Martens P, Peinert R, Pollehne F, Stegmann P, Zeitschel B (1987) The pelagic system. In: Rumohr J, Walger E, Zeitschel B (eds) Seawater-sediment interactions in coastal waters. Springer, Berlin Heidelberg New York, pp 32–68

Smith SL (1988) Copepods in Fram Strait in summer: distribution, feeding and metabolism. J Mar Res 46:145–181

Springer K (1994) Phytoplankton and particle flux. In: Fütterer DK (ed) The Expedition ARCTIC '93 Leg ARK IX/4 of RV "Polarstern". Rep Polar Res 149:79–83

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

Tande KS, Hassel A, Slagstad D (1985) Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwestern part of the Barents Sea. In: Gray FS, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, Chichester, pp 141–155

Timokhov LA (1994) Regional characteristics of the Laptev and the East Siberian Seas: climate, topography, ice phases, thermohaline regime, circulation. In: Kassens H, Hubberten HW, Pryamikov SM, Stein R (eds) Russian-German cooperation in the Siberian shelf seas: geo-system Laptev Sea. Rep Polar Res 144:15–31

Treshnikov AF (1985) Arctic Atlas (in Russian) Main Department of Geodesy and Cartography under the Council of Ministers of the USSR, Moscow

Vinogradov ME, Shushkina EA, Lebedeva LP, Gagarin VI (1994) Mesoplankton in the eastern part of the Kara Sea and Ob and Yenisei rivers estuaries (in Russian). Oceanology 34:716–723

Virketis MA (1932) Some data on the zooplankton of the southeastern part of the Laptev Sea (in Russian). Issled Morei SSSR 15:105–125