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Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises

Abstract Mesozooplankton collected during five summer expeditions to the Arctic Ocean between 1987 and 1991 was analysed for regional patterns in biomass and species distribution, distinguishing between an epipelagic (0–100 m) and a deeper (0–500 m) layer. A total of 58 stations was sampled mainly in the Nansen, Amundsen and Makarov Basins of the central Arctic Ocean and in areas of the Greenland Sea, West Spitsbergen Current and Barents Sea. Results from the different expeditions were combined to create a transect extending from the Fram Strait across the Eurasian Basin into the Makarov Basin. Mesozooplankton dry mass in the upper 500 m decreased from 8.4 g m^{-2} in the West Spitsbergen Current to less than 2 g m^{-2} in the high-Arctic deep-sea basins. In the central Arctic Ocean, biomass was concentrated in the upper 100 m and was dominated by the large copepods *Calanus hyperboreus* and *C. glacialis*. In contrast, the mesozooplankton in the West Spitsbergen Current was more evenly distributed throughout the upper 500 m, with *C. finmarchicus* as the prevailing species. The distribution of abundant mesopelagic species reflected the hydrographic regime: the calanoid copepod *Gaetanus tenuispinus* and the hyperiid amphipod *Themisto abyssorum* were most abundant in the Atlantic inflow, while *Scaphocalanus magnus* was a typical component of the high-Arctic fauna. The relatively high mesozooplankton biomass and the occurrence of boreal-Atlantic species in the central Arctic Ocean are indicators for the import of organic material from allochthonous sources, especially from the northern North Atlantic. Hence, in spite of its enclosure by land masses, the Arctic Ocean is characterized by an exchange of water masses and organisms with the North Atlantic, and advection processes strongly influence the distribution of plankton species in this high-latitude ecosystem.

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Introduction

The Arctic Ocean has been a field of special interest in plankton research for the last 100 years. Its strongly seasonal light regime and high variability in algal food supply require specific life history adaptations, especially for the dominant herbivorous zooplankton (Clarke and Peck 1991; Conover and Huntley 1991). Diapause and energy storage enable the prevailing *Calanus* species to survive the dark season without food, and lipids may fuel early reproduction independent of algal growth (Smith 1990; Hirche and Kattner 1993). Life-cycles of polar zooplankton are prolonged compared with populations of closely related species at lower latitudes, and often exceed 1 year (Heinrich 1962; Diel 1991; Hirche 1997).

Due to the extreme environmental conditions and the permanent ice cover in the central part of the Arctic Ocean, most studies were restricted to the marginal, seasonally ice-covered seas. Therefore, important general aspects such as stock assessments or large-scale distribution patterns of the Arctic zooplankton could not be addressed satisfactorily (Hopkins 1969a). The challenge of such extensive studies in the central deep basins was first tackled by drift expeditions, beginning with the voyage of the "Fram" (1893–1896). These early investigations in the Eurasian Arctic revealed a strong similarity of the Arctic zooplankton to the Atlantic fauna (Sars 1900). Later expeditions on drifting ice floes elucidated the vertical distribution and seasonal variability in the abundance and biomass of Arctic zoo-

plankton (Minoda 1967; Hopkins 1969a,b; Kosobokova 1982). Highest zooplankton concentrations occurred in the upper 500 m. However, especially the predominating herbivorous *Calanus* species perform extended seasonal migrations from the surface to deeper layers for over-wintering (Grainger 1965, 1989; Rudyakov 1983; Hirche 1991, 1997; Richter 1994).

First synoptic assessments of zooplankton in the ice-covered Arctic were attempted with submarines in the 1930s and 1960s (Farran 1936; Grice 1962). However, they suffered from methodological shortcomings: the high sampling speed resulted in poor quality of the samples, especially for delicate forms (Mohr and Geiger 1962). During the last two decades, modern ice-breakers have opened the way into permanently ice-covered areas and offered the appropriate technology for synoptic large-scale plankton investigations in unprecedented detail. The cruise tracks of the ice-breaker expeditions extended from the continental rise ("Ymer", 1980) into the high-Arctic Nansen Basin ("Polarstern" ARK IV/3, 1987). Finally in 1991, the Swedish ice-breaker "Oden" and R/V "Polarstern" ("International Arctic Ocean Expedition 1991") were the first non-nuclear vessels to cross the North Pole.

The objective of this study is to present a large-scale assessment of zooplankton biomass, differentiating between the surface layer (0–100 m) and deeper waters (0–500 m). Therefore, we combined the results of several expeditions to the Arctic Ocean yielding a wide-ranging transect across the North Pole. The distribution of selected epi- and mesopelagic species is highlighted and discussed in relation to life-cycle strategies and the regional hydrography. A comprehensive data set with respect to biomass, abundance and diversity is essential to allow the early detection of climate-induced changes in the Arctic zooplankton.

Materials and methods

Sampling

Zooplankton was sampled at 58 stations during 5 summer expeditions to the Arctic Ocean (Table 1, Fig. 1). Most of the material was collected during a transpolar cruise with the Swedish ice-breaker "Oden", extending from the Fram Strait into the Canadian Basin. All collections were done by vertical hauls with a Bongo net or a Multinet for stratified sampling (Weikert and John 1981). Since the depth intervals of stratified hauls from different cruises were not always comparable, individual hauls from each station were combined to one standard surface haul (0–100 m) and one standard deep haul (0–500 m). All samples were preserved in a 4% buffered formaldehyde-seawater solution.

Biomass

Bulk biomass (dry mass, DM) was determined from preserved Multinet catches ("Oden" 1991, Table 1). For all other samples biomass was calculated from abundance data applying individual dry mass values derived from species-specific length-mass

relationships after Richter (1994). Samples for dry mass determinations were dried at 60°C for 24 h and subsequently weighed at room temperature on a microbalance (Båmstedt 1974). Losses in body mass due to formaldehyde preservation were taken into account by applying correction factors according to Giguère et al. (1989).

Abundance

Quantitative abundance data (ind. m^{-2}) are based on filtered volumes, calculated either from flow meter data ("Valdivia" 1989, "Polarstern" 1991) or by multiplying mouth opening with vertical hauling distance assuming 100% filtration efficiency ("Polarstern" 1987, "Oden" 1991). The entire sample was analysed for species and stage composition. In the case of very abundant species, the total catch was split to a minimum of 1/32 using a Folsom splitter. Since mesh size deviated between cruises (Table 1) and abundance data are more sensitive to the effects of varying mesh sizes than biomass data, not all species could be considered for regional comparisons. Due to their quantitative representation in the coarsest net (300 µm) and their common occurrence (Mumm 1991), the following seven species were selected for more detailed investigations: the copepodite stages CIV-CVI of the calanoid copepods *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Scaphocalanus magnus* and *Gaetanus tenuispinus* and the hyperiid amphipod *Themisto abyssorum*. This selection includes epipelagic species, e.g. *Calanus* spp., as well as mesopelagic species, e.g. *M. longa*, *S. magnus* and *G. tenuispinus*. Different feeding types from herbivory (*Calanus* spp.) to omnivory (*M. longa*, *G. tenuispinus*) and carnivory (*T. abyssorum*) were considered. The closely related species *C. finmarchicus* and *C. glacialis* were separated according to prosome length (Unstad and Tande 1991; Hirche et al. 1994).

Results

For the presentation of the results, most stations were arranged according to topography and water depth along a transect from the West Spitsbergen Current (WSC) across the North Pole into the Makarov Basin. Supplementary data from neighbouring regions were considered separately.

Biomass

Mean mesozooplankton biomass in the upper 100 m decreased from 2–3 g DM m^{-2} in the West Spitsbergen Current and southern Nansen Basin (south of 83°N) towards the north. In the oceanic regions of the northern Nansen and Makarov Basins and over the Nansen-Gakkel and Lomonosov Ridges, mesozooplankton dry mass averaged around 1 g DM m^{-2} (Table 2). Slightly higher, but more variable, amounts were measured in the Amundsen Basin (2.2 ± 1.5 g DM m^{-2}). Stations on the Yermak and Morris Jessup Plateaus showed similar values. Considerably higher epipelagic biomass of up to 5 g DM m^{-2} – comparable to the Barents and Greenland Seas – occurred at various stations over the continental slope north of Spitsbergen and in the southern Nansen Basin (Fig. 2).

Regional differences in biomass were even more pronounced in the 0 to 500-m layer (Fig. 2). The highest

Table 1 Station data and mesozooplankton biomasss (*RV* research vessels, *P* Polarstern, *V* Valdivia, *O* Oden, *Bo* Bongo, *MN* Multinet)

| Region	Stn. no.	RV	Date [d.m.y.]	Lat. N	Long.	Depth (m)	Net	Mesh (μm)	Dry mass (g m^{-2}) 0–100 m	0–500 m
Greenland Sea	89–091	P	16.06.93	74°45′	1°02′E	3770	MN	150	6.04	11.38
	89–177	V	19.08.93	74°45′	1°04′E	3780	MN	150	1.25	5.62
Barents Sea	91–064	P	30.06.95	76°35′	19°56′E	216	Bo	300	0.94	–
	91–052	P	28.06.95	77°28′	19°02′E	183	Bo	300	0.88	–
	91–040	P	23.06.95	76°36′	34°50′E	195	Bo	300	0.61	–
	91–138	P	26.07.95	77°27′	33°02′E	155	Bo	300	1.78	–
	91–136	P	26.07.95	77°59′	32°54′E	139	Bo	300	2.29	–
	91–134	P	25.07.95	78°39′	32°09′E	288	Bo	300	10.11	–
	91–129	P	24.07.95	79°30′	30°29′E	99	Bo	300	3.21	–
	91–124	P	23.07.95	80°20′	29°08′E	356	Bo	300	1.36	–
Yermak Plateau	87–412	P	17.08.91	82°02′	15°11′E	2043	MN	300	2.43	4.13
	91–056	O	01.10.95	82°17′	14°58′E	2220	MN, Bo	200,300	0.66	1.46
	91–055	O	01.10.95	82°36′	13°38′E	970	MN, Bo	200,300	0.87	2.64
	91–054	O	30.09.95	82°43′	12°56′E	2170	MN, Bo	200,300	0.60	–
	91–053	O	30.09.95	82°48′	14°17′E	2297	Bo	300	0.52	–
Morris Jessup Plateau	91–044	O	20.09.95	85°04′	14°12′W	2230	MN	200	0.38	1.28
	91–043	O	19.09.95	85°05′	15°09′W	1015	Bo	300	1.38	–
	91–040	O	17.09.95	85°18′	14°09′W	1075	MN, Bo	200,300	0.91	1.80
	91–041	O	18.09.95	85°25′	11°59′W	1400	MN	200	0.75	1.57
	91–039	O	16.09.95	85°28′	12°06′W	2355	Bo	300	0.86	–
West Spitsbergen Current	91–079	P	04.07.95	79°01′	6°42′E	1242	Bo	300	1.51	–
	91–085	P	07.07.95	80°15′	8°50′E	593	Bo	300	1.98	–
	91–100	P	12.07.95	81°22′	17°28′E	875	Bo	300	3.07	–
	91–004	O	19.08.95	81°20′	19°50′E	750	MN	200	4.64	10.86
	91–060	O	04.10.95	81°20′	18°52′E	575	MN	200	0.40	7.29
	91–113	P	20.07.95	81°30′	30°54′E	748	Bo	300	1.45	–
	87–276	P	08.07.91	81°31′	31°27′E	571	MN	300	1.39	6.90
Southern Nansen Basin	87–280	P	09.07.91	81°35′	31°33′E	1028	MN	300	2.47	4.98
	91–108	P	17.07.95	81°40′	29°48′E	2542	Bo	300	3.31	–
	87–296	P	13.07.91	81°49′	31°35′E	3014	MN	300	3.00	4.82
	87–310	P	14.07.91	82°10′	31°53′E	3056	MN	300	4.28	5.44
	87–393	P	15.08.91	82°51′	17°16′E	3411	MN	300	1.61	2.31
	87–340	P	18.07.91	82°59′	31°59′E	3784	MN	300	4.16	5.40
Northern Nansen Basin	87–382	P	14.08.91	83°25′	20°02′E	4064	MN	300	1.35	1.70
	91–005	O	21.08.95	83°34′	27°49′E	4050	MN, Bo	200,300	0.43	1.63
	87–358	P	21.07.91	84°02′	30°37′E	4044	MN	300	1.07	1.76
	91–009	O	25.08.95	85°04′	42°29′E	4008	Bo	300	1.98	–
	87–362	P	27.07.91	85°05′	29°18′E	4037	MN	300	0.82	1.16
	91–011	O	27.08.95	86°07′	52°44′E	3970	Bo	300	1.79	–
Nansen-Gakkel Ridge	87–376	P	11.08.91	85°22′	21°54′E	2874	MN	300	0.67	0.89
	91–013	O	29.08.95	86°44′	57°04′E	3400	MN	200	0.96	1.30
	91–014	O	29.08.95	87°00′	59°58′E	4323	Bo	300	1.44	–
Amundsen Basin	87–370	P	01.08.91	85°55′	22°46′E	4536	MN	300	1.64	2.09
	91–036	O	14.09.95	86°00′	0°01′E	4260	Bo	300	2.20	–
	91–033	O	12.09.95	86°45′	10°03′E	4385	MN	200	–	1.39
	91–032	O	11.09.95	87°29′	11°06′E	4392	Bo	300	2.54	–
	91–031	O	10.09.95	88°16′	9°26′E	4400	MN	200	0.80	1.33
	91–016	O	30.08.95	87°36′	69°43′E	4422	Bo	300	1.67	–
	91–017	O	31.08.95	88°00′	85°17′E	4420	MN	200	–	2.15
	91–018	O	01.09.95	88°11′	98°47′E	4400	Bo	300	5.59	–
	91–029	O	08.09.95	90°00′		4266	MN, Bo	200,300	1.58	2.33
Lomonosov Ridge	91–020	O	02.09.95	88°15′	127°06′E	2390	MN	200	1.29	1.90
	91–021	O	03.09.95	88°14′	130°47′E	1490	MN	200	0.95	1.69
	91–023	O	03.09.95	87°59′	145°23′E	1470	MN, Bo	200,300	0.74	1.04
	91–028	O	06.09.95	88°31′	157°46′E	1782	MN	200	1.11	1.70
Makarov Basin	91–025	O	04.09.95	88°01′	151°32′E	3390	MN	200	0.56	0.93
	91–027	O	06.09.95	88°10′	169°34′E	3992	MN, Bo	200,300	0.97	1.36
	91–026	O	05.09.95	88°01′	163°27′E	4000	MN	200	–	1.83
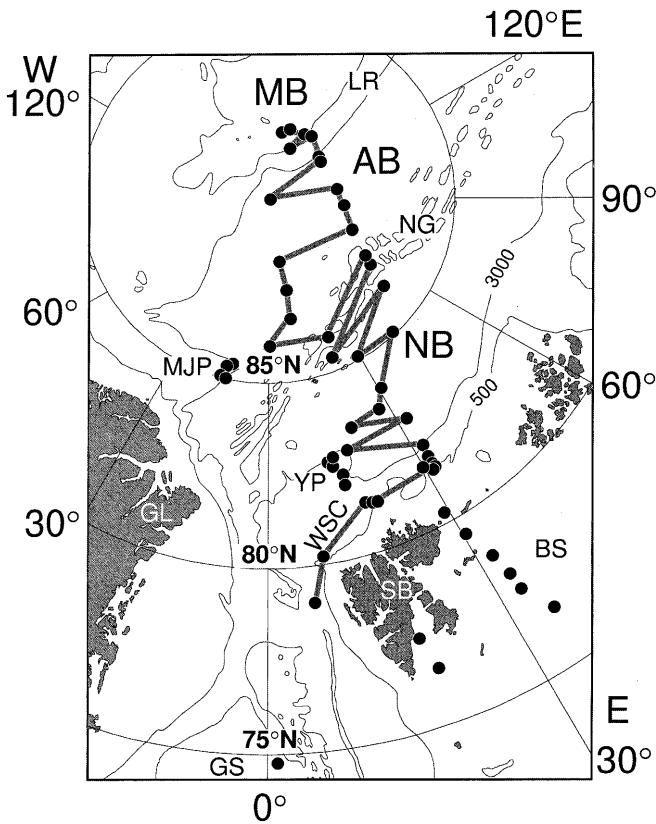
Fig. 1 Station map: the *dark line* connects stations of different expeditions to a transpolar transect (*AB* Amundsen Basin, *BS* Barents Sea, *GL* Greenland, *GS* Greenland Sea, *LR* Lomonosov Ridge, *MB* Makarov Basin, *MJP* Morris Jessup Plateau, *NB* Nansen Basin, *NG* Nansen-Gakkel Ridge, *SB* Spitsbergen, *WSC* West Spitsbergen Current, *YP* Yermak Plateau; generated after Diepenbroek et al. 1997)

values of 8.4 ± 2.2 g DM m^{-2} were determined in the WSC. Mean biomass decreased sharply towards the high-Arctic deep-sea basins: 4.6 ± 1.3 g DM m^{-2} were detected over the continental slope and in the southern Nansen Basin, while mesozooplankton biomass over the northern Nansen, Amundsen and Makarov Basins was as low as 1–2 g DM m^{-2} for the upper 500 m (Table 2). This decrease in mesozooplankton biomass towards the central Arctic deep-sea basins was accompanied by shifts in the vertical distribution. In the area influenced by the WSC only a quarter of the biomass in the upper 500 m was located in the top 100 m (Table 2). In contrast, over the deep-sea basins a much larger fraction (57–75%) was concentrated in the upper 100 m.

Dominant species

In the central Arctic Ocean mesozooplankton biomass was dominated by the large copepods *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus* and *Metridia longa*. Along the transect these four calanoid species composed two-thirds to three-quarters of the total biomass (Fig. 3). In contrast, other taxa, mainly chaetognaths, ostracods and euphausiids, were more important in the Greenland Sea. *C. hyperboreus*, *C. finmarchicus* and *M. longa* contributed only 45% to the total dry mass in the central Greenland Sea, and *C. glacialis* did not occur at all in this region. Significant changes were also observed among the Arctic basins. The biomass share of *C. finmarchicus* decreased from 35% in the southern Nansen Basin to 2% in the Amundsen and Makarov Basins. Conversely, *C. hyperboreus* and *C. glacialis* became more important towards the north (Fig. 3), representing 46% and 22%, respectively, of total mesozooplankton biomass in the Amundsen and Makarov Basins.

Calanus hyperboreus was mainly restricted to the upper 100 m, averaging 380 ind. m^{-2} over the entire transect. Much higher numbers, exceeding 800 ind. m^{-2}, were found at stations in the southern Nansen Basin (sts. 87–310, 87–340) and in the Amundsen Basin (sts. 91–018, 91–029; Fig. 4a). In contrast, *C. hyperboreus* was less common (116 ind. m^{-2}) in the Atlantic WSC. The smaller *C. finmarchicus* and *C. glacialis* were also concentrated in the surface layer. *C. finmarchicus* reached a maximum abundance of >8,500 ind. m^{-2} at st. 91–100 in the WSC. With an average population of 3,250 ind. m^{-2} and 35% of the biomass along the southern part of the transect, *C. finmarchicus* was by far the dominant mesozooplankton species in the WSC and

Table 2 Average mesozooplankton biomass for different Arctic regions. Asterisk (*) indicates no percentage due to different positions for surface and deep hauls

| Region	Mean dry mass (g DM m^{-2} ± SD)		DM$_{0-100}$/DM$_{0-500}$ (%)
	0–100 m	0–500 m	
West Spitsbergen Current	2.1 ± 1.4	8.4 ± 2.2	25
Southern Nansen Basin (<83°N)	3.1 ± 1.0	4.6 ± 1.3	67
Northern Nansen Basin (>83°N)	1.2 ± 0.6	1.6 ± 0.3	75
Nansen-Gakkel Ridge	0.8 ± 0.2	1.1 ± 0.3	73
Amundsen Basin	2.2 ± 1.5	1.9 ± 0.5	*
Lomonosov Ridge	1.0 ± 0.2	1.6 ± 0.4	63
Makarov Basin	0.8 ± 0.3	1.4 ± 0.5	57
Barents Sea (<500 m)	2.6 ± 3.1	–	–
Greenland Sea	3.6 ± 3.4	8.5 ± 4.1	42
Yermak Plateau	1.0 ± 0.8	2.7 ± 1.3	37
Morris Jessup Plateau	0.9 ± 0.4	1.6 ± 0.3	56
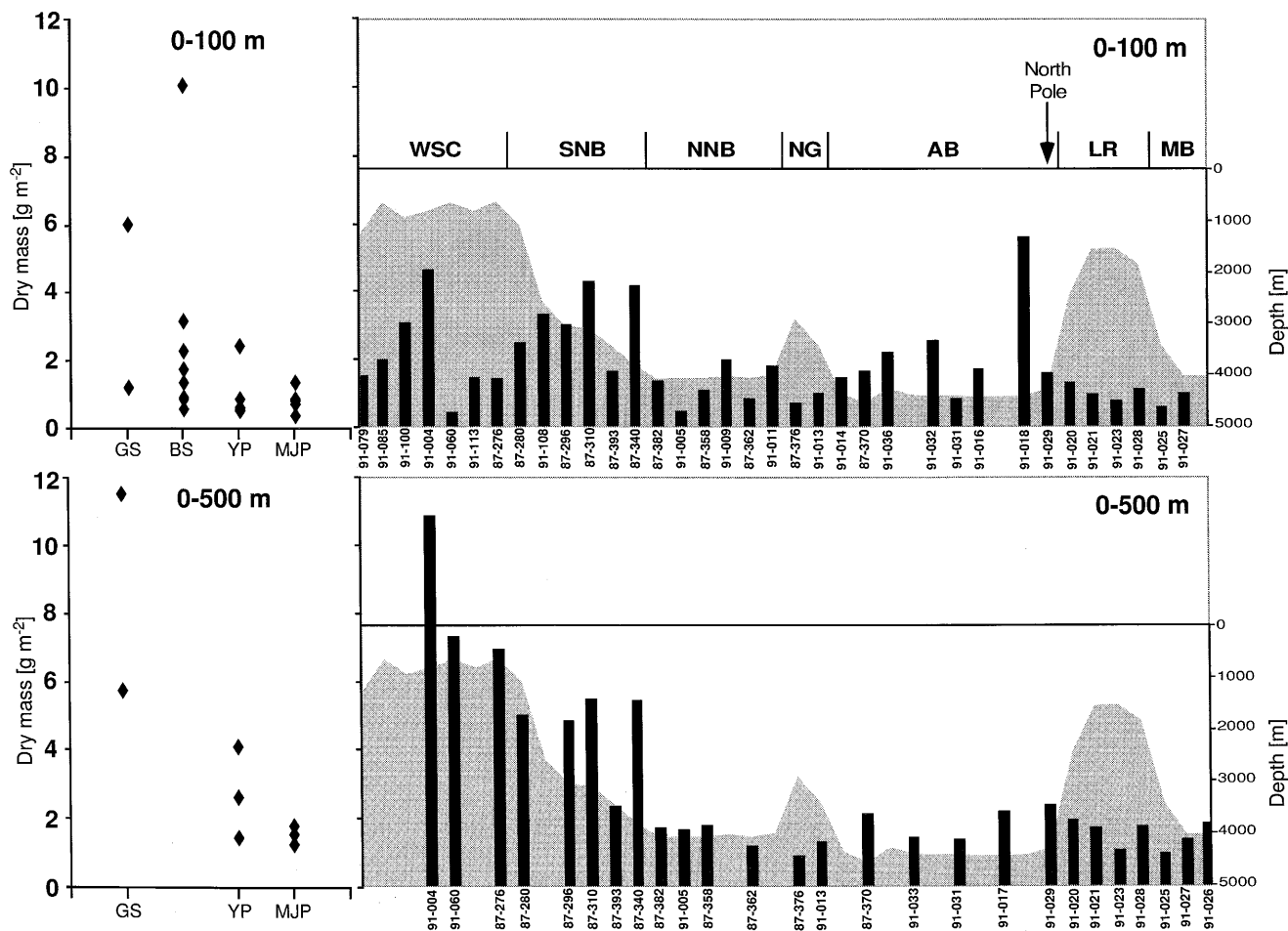
Fig. 2 Mesozooplankton dry mass along an Arctic transect and in adjacent regions in 0- to 100-m and 0- to 500-m depth. Bottom profile indicated by *shaded background* (*AB* Amundsen Basin, *BS* Barents Sea, *GS* Greenland Sea, *LR* Lomonosov Ridge, *MB* Makarov Basin, *MJP* Morris Jessup Plateau, *NG* Nansen-Gakkel Ridge, *NNB* northern Nansen Basin, *SNB* southern Nansen Basin, *WSC* West Spitsbergen Current, *YP* Yermak Plateau)

south of the central Nansen Basin (Figs. 3, 4b). Further north, *C. finmarchicus* was much less abundant (<200 ind. m^{-2}) and was replaced by the Arctic *C. glacialis*, which usually occurred with about 300 ind. m^{-2} throughout the northern Nansen, Amundsen and Makarov Basins (Fig. 4b).

In waters below 100 m *Metridia longa* was another very important calanoid, with regard to both abundance and biomass (Figs. 3, 5). Its abundance in the upper 500 m ranged generally around 1,200 ind. m^{-2} at the oceanic stations in the central Arctic Ocean. However, more than 8,000 ind. m^{-2} occurred near the shelf break north of Spitsbergen (sts. 87–276, 87–280). Two typical mesopelagic representatives were the calanoid copepods *Scaphocalanus magnus* and *Gaetanus tenuispinus*, which were concentrated between 100 and 500 m with up to 240 ind. m^{-2} (Fig. 6). *S. magnus* occurred regularly throughout the central Arctic Ocean, including the Nansen, Amundsen and Makarov Basins, with abun-

dances from 100 to >200 ind. m^{-2}. Over the continental rise in the southern Nansen Basin its abundance decreased to less than 30 ind. m^{-2}. Conversely, *G. tenuispinus* was most abundant over the shelf break with more than 200 ind. m^{-2}. In the central Arctic Ocean the species was present, but never exceeded 20 ind. m^{-2}. The hyperiid amphipod *Themisto abyssorum* showed the same distribution pattern as *G. tenuispinus*. Maximum abundances of >200 ind. m^{-2} were found over the continental slope north of Spitsbergen. Densities decreased towards the central Arctic deep-sea basins (<40 ind. m^{-2}, Fig. 7).

Discussion

First estimates of mesozooplankton biomass in the Arctic Ocean were based on net hauls conducted from drift-ice stations. Exceptionally low values were observed during the "Arlis II" expedition in 1964/1965: zooplankton biomass in the upper 500 m of the central Arctic basin was a meagre 0.29 g DM m^{-2} and increased to only 4.52 g DM m^{-2} in the East Greenland Current (Hopkins 1969b). Our summer data from this and previous studies (Mumm 1991; Hirche and Mumm 1992) confirm the decrease in biomass towards the cen-
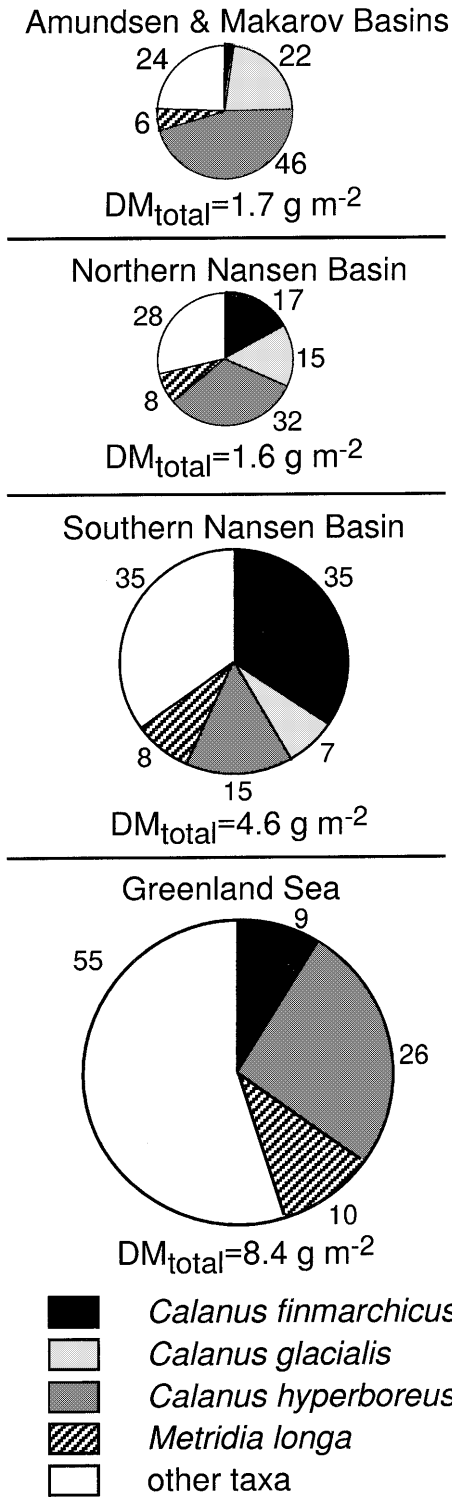
Fig. 3 Biomass share (% of total mesozooplankton dry mass) of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa* and other taxa in 0- to 500-m depth of different Arctic regions (DM_{total} mean total dry mass)
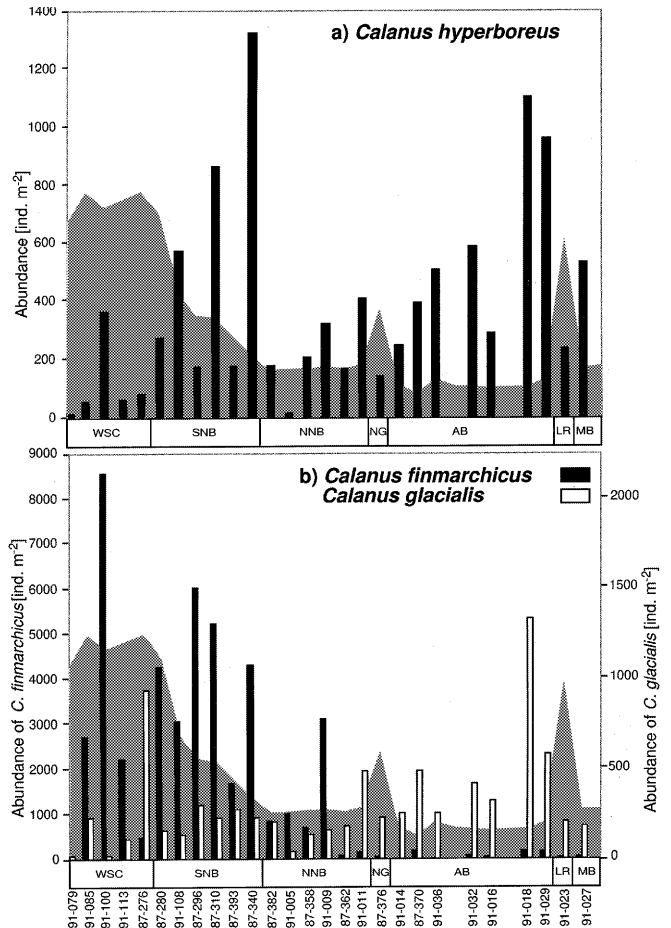

Fig. 4 Abundance of *Calanus hyperboreus* CIV–CVI (**a**) and *C. finmarchicus* and *C. glacialis* CIV–CVI (**b**) in 0- to 100-m depth. Note different scales in Fig. 4b
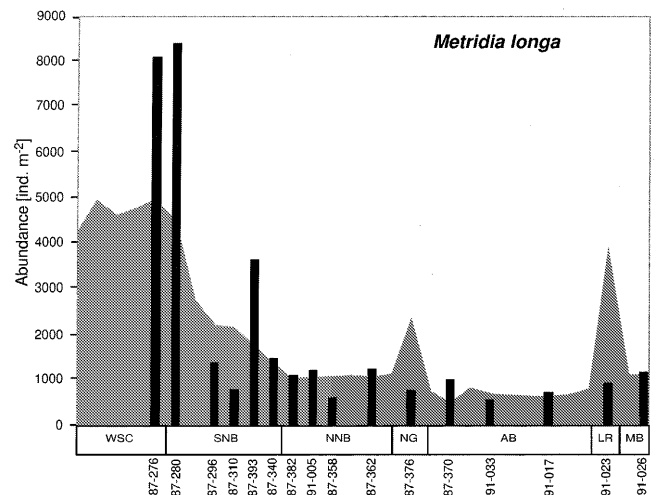

Fig. 5 Abundance of *Metridia longa* CIV–CVI in 0- to 500-m depth

tral Arctic basin, although these data are 2–6 times higher than those observed during "Arlis II". Hopkins's low figures may be partly explained by the winter situation, since his samples were collected between October and April. However, seasonal vertical migrations in the central Arctic Ocean are usually limited to the upper 500 m (Kosobokova 1982) and are not as extensive as in subpolar and boreal seas, e.g. in the Greenland Sea
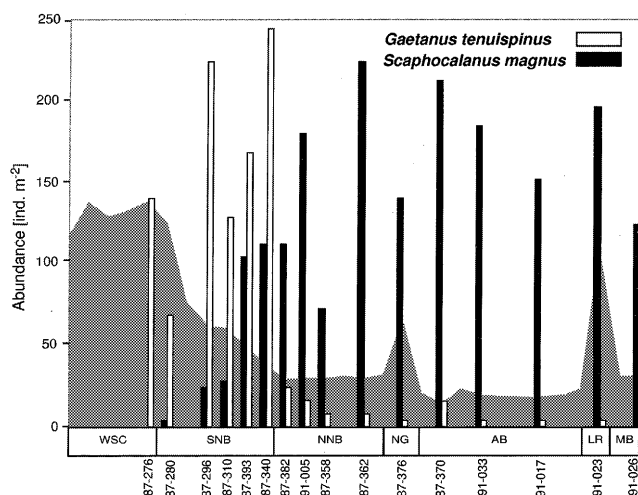
Fig. 6 Abundance of *Scaphocalanus magnus* and *Gaetanus tenuispinus* CIV–CVI in 0- to 500-m depth
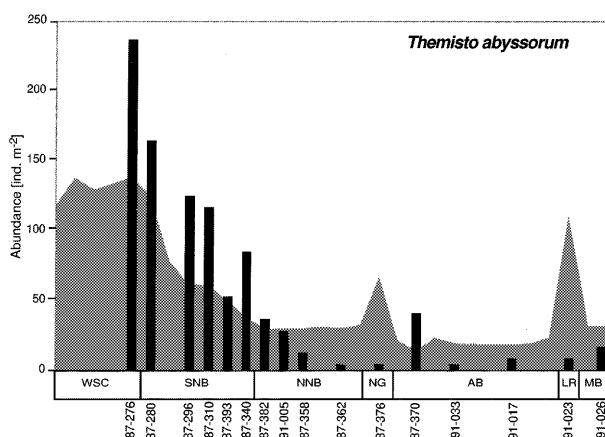

Fig. 7 Abundance of *Themisto abyssorum* in 0- to 500-m depth

(Richter 1994). Therefore, mesozooplankton biomass in the Arctic Ocean integrated over the upper 500 m should be fairly constant throughout the year. Hence, seasonal vertical migration does not satisfactorily explain the low biomass during "Arlis II".

Higher biomass values of 1.5–3 g DM m^{-2} in the upper 100 m of the central Arctic basin were reported by Kosobokova (1982) and Kosobokova et al. (1998). On a recent transect across the Canadian Basin, high amounts of about 4 g DM m^{-2} were measured in the upper 100 m of the northern Makarov Basin (Wheeler et al. 1996). These studies indicate mesozooplankton stocks comparable to our data or even higher, supporting the assumption that the Arctic Ocean is more productive than previously believed.

Zooplankton is not distributed evenly throughout the Arctic Ocean. Studies in the Nansen Basin revealed a sharp decline in zooplankton biomass north of 83°N (Mumm 1991; Hirche and Mumm 1992), similar to Hopkins's findings (1969b). The data presented here substantiate these findings on a larger data base and

show that latitudinal changes are not restricted to total biomass, but are also connected to differences in the species composition. *Calanus hyperboreus* and *C. glacialis* dominate the biomass in the high-Arctic Amundsen and Makarov Basins. Conversely, most of the higher biomass in the West Spitsbergen Current and southern Nansen Basin is composed of *C. finmarchicus*. In the Greenland Sea more than half of the mesozooplankton biomass is represented by other taxa, mainly euphausiids, chaetognaths and ostracods (Richter 1994).

Such regional differences in species composition are characteristic of the epipelagic community, as shown by the variations in the *Calanus* species, but they also extend to the mesopelagic fauna. For instance, the deeper-dwelling amphipod *Themisto abyssorum* and the copepod *Gaetanus tenuispinus* were also more abundant in the southern parts of the investigation area. Their concentration in 100- to 500-m depth over the continental rise north of Spitsbergen indicates an import by the inflowing Atlantic water masses. Other data support the classification of *T. abyssorum* as a subarctic-boreal or Atlantic species (Koszteyn et al. 1995 and references therein). *G. tenuispinus* is also widespread in the northern Atlantic Ocean, including the Norwegian and Greenland Seas (Markhaseva 1996), and is probably exported into the Arctic Ocean. Thus, the distribution of these species reflects the circulation of the Atlantic water, which enters the Arctic Ocean north of Spitsbergen and extends to the east as a cyclonic boundary current along the Eurasian continental rise (Aagaard 1989; Rudels et al. 1994). In contrast to the boreal-Atlantic species mentioned above, the truly Arctic *Calanus glacialis* and *Scaphocalanus magnus* are more abundant in the Amundsen and Makarov Basins.

Hopkins (1969a) assessed the total mesozooplankton dry mass in the central Arctic Ocean at 1–2 million tons. Based on primary production rates measured by Apollonio (1959) and English (1961), he suggested that phytoplankton production alone could not meet the metabolic demands of the mainly herbivorous zooplankton population. The results presented here reveal even larger mesozooplankton stocks in the central Arctic Ocean and raise the question of how their nutritional demands are satisfied.

Two explanations are possible: either more primary production is available as food for the zooplankton, or the nutritional demands of zooplankton are lower than assumed. Probably a combination of both notions holds true. During the last decade we learned that ice algae greatly contribute to total primary production (Legendre et al. 1992) and may present up to two-thirds of total primary production in ice-covered areas (Wheeler et al. 1996). In early spring ice algae constitute a reliable food source for zooplankton in the underlying water column. Haline stratification due to melt water and river discharge stabilizes the sunlit surface layer and triggers an early start to the pelagic production, especially in marginal ice zones and over the vast Siberian shelf regions.

The production period in the Arctic Ocean may therefore extend to 120 days per year (Wheeler et al. 1996), which is more than twice as long as the 6–8 weeks assumed by Hopkins (1969a). Consequently, total annual primary production in the central Arctic Ocean probably reaches 10 g C m^{-2} (Subba Rao and Platt 1984; Wheeler et al. 1996), at least 1 order of magnitude higher than the estimates by Apollonio (1959) and English (1961).

Additional organic material is imported into the Arctic Ocean by the enormous freshwater runoff from the Siberian rivers (3,300 km^3 yr^{-1}, Aagaard and Carmack 1989). Even more important is the advection of organisms and detritus by the Atlantic inflow. This is a well-known phenomenon and also evident in this study. The West Spitsbergen Current imports species of Atlantic origin into the Arctic basin. Like a conveyor belt the inflow extends as a cyclonic boundary current along the Eurasian continental rise and connects more productive shelf regions with the central Arctic deep-sea basins. Organic matter, both organisms and detritus, produced in the nutrient-rich and seasonally ice-free shelf areas, is transported east and finally, as the current returns along the Lomonosov Ridge (Rudels et al. 1994), into the central Amundsen Basin. Thus, it contributes to the food supply of the zooplankton community living under the permanent ice cover. Hence, apart from the moderate autochthonous production in the central Arctic Ocean, there is a strong import from allochthonous sources into this region. All these processes enhance the available food supply for the Arctic zooplankton.

Moreover, the energetic demands of Arctic zooplankton organisms may have been overestimated. Between late summer and early spring the dominant *Calanus* species overwinter at depth in a dormant state with a severely reduced metabolism (Hirche 1996, 1997). The life-cycles of Arctic species are often prolonged compared to populations of closely related species at lower latitudes (Heinrich 1962; Diel 1991). Due to low predation rates high zooplankton biomass may be accumulated although production and food uptake are low. Thus, low P/B ratios may explain the comparatively high standing stocks in spite of limited food resources.

The herbivorous nature and surface affinity of the dominant Arctic forms *Calanus hyperboreus* and *C. glacialis* indicate a close coupling of primary and secondary production processes controlled by the limited availability of food. The faunistic paucity below about 100 m during summer shows that organic material is effectively retained in the surface layer, with limited export to the deep-sea basins (Wassmann et al. 1991). In the West Spitsbergen Current, by contrast, the biomass-rich subsurface community points at a more abundant and patchy occurrence of food at the surface with higher losses of organic matter from the epipelagic layer and substantial recycling of this material in deeper waters. These recent results explain how the Arctic Ocean can sustain larger zooplankton stocks than previously believed.

The Atlantic inflow via the Fram Strait and Barents Sea is one of the most important features structuring the Arctic Ocean and determining the distribution of zooplankton biomass, as well as extending the distribution ranges of certain plankton species. Hence, in spite of its enclosure by land masses the Arctic Ocean is obviously not an isolated system. It is characterized by an exchange of water masses and organisms, particularly with the Atlantic Ocean. Future studies focusing on the energy and carbon flux within the Arctic Ocean should therefore include advection processes in their budgets.

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