Elsevier Editorial System(tm) for Progress in Oceanography
Manuscript Draft

Manuscript Number:

Title: Biomass of zooplankton in the eastern Arctic Ocean - a base line study

Article Type: Full Length Article

Keywords: zooplankton; biomass; Arctic Ocean; Arctic Ocean Boundary Current; Calanus

Corresponding Author: Dr. Hans-Juergen Hirche, Ph.D.

Corresponding Author's Institution: Alfred Wegener Institute

First Author: Hans-Juergen Hirche, Ph.D.

Order of Authors: Hans-Juergen Hirche, Ph.D.

Abstract: Abstract

There are only few historical assessments of the zooplankton biomass in the Arctic Ocean, which are difficult to compare due to methodological differences or incomplete sampling of the water column. We present assessments of the zooplankton biomass for 70 locations scattered over the Eurasian and Makarov Basins of the Arctic Ocean and analyze regional variability and factors affecting the biomass distribution. The study is based on material collected during several summer expeditions of RV Polarstern (1993-1998) and processed according to standard methods, i.e. stratified sampling of the entire water column from the bottom to the surface with very similar gear and standardized calculation of biomass. Total zooplankton biomass varied strongly from 1.9 to 23.9 g/m2 dry mass. Regional variability was related to the circulation pattern. A belt of elevated biomass along the Eurasian continental margin was related to the advection of Atlantic pelagic populations within the Arctic Ocean Boundary Current along the Siberian shelves and returning branches along mid-ocean ridges. Biomass was highest in the core of the Atlantic inflow and gradually decreased towards the shelves and basins, but also along the inflow from west to east. Lowest biomass was found in the centers of the basins north of 86°N. In the slope region, three

Calanus species (C. hyperboreus, C. glacialis, C. finmarchicus) and Metridia longa contributed most to the biomass, chaetognaths were also important. In the basins, C. hyperboreus was dominant, copepods made up to 97% of total biomass. Vertical distribution was similar at all stations with biomass maxima in the upper 50 m layer except for stations near Fram Strait and northern Kara Sea, the gateways of Atlantic water to the Arctic Ocean, where maxima where between 25 and 100m. As there was only very little interannual variability of temperature and current velocity in the regions of the Atlantic inflow we speculate that the majority of our samples, which was collected in 1993 and 1995, represent the phase of the 1990s warm event in the Nordic Seas.

Biomass of zooplankton in the eastern Arctic Ocean - a base line study

Ksenia Kosobokova[1] and Hans-Jürgen Hirche[2]

[1]P.P.Shirshov Institute of Oceanology, Russian Academy of Sciences, 36 Nakhimova ave., Moscow 117997, Russia
[2]Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse 1. D-27568 Bremerhaven, Germany

Corresponding author.
e-mail: xkosobokova@ocean.ru

Key words: zooplankton, biomass, Arctic Ocean, Arctic Ocean Boundary Current, Calanus

Abstract

There are only few historical assessments of the zooplankton biomass in the Arctic Ocean, which are difficult to compare due to methodological differences or incomplete sampling of the water column. We present assessments of the zooplankton biomass for 70 locations scattered over the Eurasian and Makarov Basins of the Arctic Ocean and analyze regional variability and factors affecting the biomass distribution. The study is based on material collected during several summer expeditions of RV *Polarstern* (1993-1998) and processed according to standard methods, i.e. stratified sampling of the entire water column from the bottom to the surface with very similar gear and standardized calculation of biomass. Total zooplankton biomass varied strongly from 1.9 to 23.9 g/m^2 dry mass. Regional variability was related to the circulation pattern. A belt of elevated biomass along the Eurasian continental margin was related to the advection of Atlantic pelagic populations within the Arctic Ocean Boundary Current along the Siberian shelves and returning branches along mid-ocean ridges. Biomass was highest in the core of the Atlantic inflow and gradually decreased towards the shelves and basins, but also along the inflow from west to east. Lowest biomass was found in the centers of the basins north of 86°N. In the slope region, three Calanus species (*C. hyperboreus, C. glacialis, C. finmarchicus*) and *Metridia longa* contributed most to the biomass, chaetognaths were also important. In the basins, *C. hyperboreus* was dominant, copepods made up to 97% of total biomass. Vertical distribution was similar at all stations with biomass maxima in the upper 50 m layer except for stations near Fram Strait and northern Kara Sea, the gateways of Atlantic water to the Arctic Ocean, where maxima where between 25 and 100m. As there was only very little interannual variability of temperature and current velocity in the regions of the Atlantic inflow we speculate that the majority of our samples, which was collected in 1993 and 1995, represent the phase of the 1990s warm event in the Nordic Seas.

List of contents:

1. Introduction

The history of zooplankton research in the central Arctic beginning with Nansen's legendary *Fram* expedition (1897-99) can be divided into two phases. During the first, almost 80 years long phase, zooplankton was almost unexceptionally collected from drifting ice islands (Russian "North Pole" drifting stations, American T-3, Alpha, Bravo, Arlis I and II ice islands) or ships frozen in the ice like the Norwegian *Fram* and the Russian ice-breakers *Sedov* and *Sadko*. The drifting routes of these platforms were hardly predictable and strongly dependent on the surface circulation and atmospheric processes. During this phase of sporadic data accumulation basic knowledge on major structural parameters and seasonal dynamic of the zooplankton communities of the Arctic Ocean was obtained (Brodsky and Nikitin, 1955; Virketis, 1957, 1959; Johnson, 1963; Minoda, 1967; Hopkins, 1969a, b; Brodsky and Pavshtiks, 1976; Huges, 1966; Kosobokova, 1978, 1981, 1982, 1986, 1989; Dawson, 1978; Pautzke, 1979). However, the few assessments of zooplankton biomass from this period (Minoda, 1967; Hopkins, 1969a, b; Kosobokova, 1981, 1982), are difficult to compare due to various methodological differences (Hopkins, 1969a, b), or incomplete sampling of the water column (Minoda, 1967).

A new phase started in the beginning of the 1980s with the arrival of modern research ice-breakers, which allowed a better sampling design and interdisciplinary research with physical, chemical, and biogeochemical observations, although ice conditions were still modifying the work at sea. This interdisciplinary research brought a break-through in understanding of relationships between the structure of the pelagic communities with hydrophysical processes and environmental factors. New data on biomass (Hirche and Mumm, 1992; Mumm, 1993; Mumm et al., 1998;

Kosobokova and Hirche, 2000; Auel and Hagen, 2002) showed a strong regional variability of the biomass distribution over the Eurasian basins related to the circulation pattern of Atlantic water (Hirche and Mumm, 1992; Mumm, 1993; Mumm et al., 1998; Kosobokova and Hirche, 2000). A much higher biomass as known before was obviously advected with the Atlantic inflow. The growing number of studies (Wheeler et al., 1996; Mumm et al., 1998; Thibault et al., 1999; Kosobokova and Hirche, 2000; Ashjian et al., 2003) were changing the view of the Arctic Ocean as a monotonous biological desert (Vinogradov and Melnikov, 1980).

An increased interest to study the structure and functioning of the pelagic ecosystem of the Arctic Ocean and to quantify biological processes during the recent years (Kosobokova and Hirche, 2000, 2001; Melnikov and Kolosova, 2001; Auel and Hagen, 2002; Hirche and Kosobokova, 2003; Ashjian et al., 2003, Sherr et al., 2003, Hopcroft et al., 2005; Raskoff et al., 2005; Olli et al., 2007; Lane et al., 2008) was related to observed and predicted changes in global climate, which are expected to have their most pronounced effects at high latitudes. In the Arctic, ongoing climatic change has been reflected in reduction of the ice cover, increase of Atlantic water temperature and Atlantic water circulation pattern (Carmack et al., 1997; Schauer et al., 1997; Rudels et al., 2000a; Carmack et al., 2005; Grebmeier et al., 2006). These changes should have a strong impact on the Arctic ecosystem. Colonization of the Arctic Ocean by Atlantic species (Hirche and Kosobokova, 2007) could cause shifts in the composition and trophodynamics of the pelagic system and affect carbon flux. To detect and quantify possible changes and shifts in the Arctic pelagic ecosystem under climate change, some baseline information is required on various aspects of its diversity and productivity.

The present paper is aimed to synthesize original information on the quantitative distribution of zooplankton in the Arctic Ocean obtained during the mid 1990s. As hitherto there is no possibility to obtain a synoptic coverage for the whole Arctic Ocean, we pooled biomass data from 70 locations sampled during four summer expeditions of RV "Polarstern" scattered over the Nansen, Amundsen and Makarov Basins in order to obtain large regional coverage. The zooplankton sampling in two of these expeditions, in 1993 and 1995, predominantly covered shelves, slopes and basins of the adjacent Nansen and Amundsen Basins, and in the other expeditions in 1996 and 1998 concentrated on the deep Nansen, Amundsen and Makarov Basins. As the data set is consistent, with all sampling performed in the summer using very similar gear, analysis by the same person and standardized calculation of biomass, it was used to review the regional distribution and composition of zooplankton biomass in the Eurasian part of the Arctic Ocean and to analyze the role of hydrography in the biomass distribution. The data set may also serve as a baseline to monitor the influence of global warming and its impact on the arctic pelagic system through ice thinning (Rothrock et al., 1999; Johannessen and Miles, 2001), changing ice coverage (Johannessen, et al., 1995, 1999, 2000, Chapman and Walsh, 1993; Vinnikov et al., 1999) and current regime (Karcher et al. 2003, Carmack et al. 2006).

2. Material and methods

Zooplankton was collected in the Arctic Ocean and adjacent Barents, Kara, Laptev and East-Siberian seas on 70 stations during four RV *Polarstern* ARK cruises (1993-1998). Station locations and sampling dates are presented in Table 1. During ARK IX/4 (September 1993) and ARK XI/1 (July-September 1995) zooplankton was collected along transects from the shelf margin of the Barents, Kara, Laptev and East-Siberian Seas over the continental slope into the adjacent deep Nansen, Amundsen and Makarov Basins, and on one transect across the Lomonosov Ridge at 81°N (Fig. 1). During ARK XII (August 1996) and ARK XIV (August 1998) sampling was carried out in the deep central Amundsen and Makarov Basins (Fig. 1).

During the expeditions ARK IX/4, XI/1, and XII zooplankton was collected vertically with a multinet Type Midi (Hydrobios, Kiel, 0.25 m^2 mouth opening, 150 µm mesh size). During ARK XIV a multinet Type Maxi (0.5 m^2 mouth opening, 150 µm mesh size) was used. During ARK IX/4, five depth strata were sampled from the bottom or 1500 m to the surface. During all other expeditions the entire water column or the upper 3000 m were sampled in two successive vertical hauls (Table 1). Sampling intervals were bottom (3000 m)-2000-1000-750(500)-300-0 m for the deep casts, and 300-200-100-50-25-0 m for the shallow casts. All samples were preserved in 4% borax-buffered formaldehyde.

All mesozooplankton organisms >1 mm from the samples were counted and measured under a stereo microscope. For the smaller organisms (<1 mm), an aliquot (1:8, 1:10) of the sample was counted after fractionation with a stempel-pipette. Most taxonomic groups including Copepoda Calanoida and Cyclopoida, Decapoda, Pteropoda, Chaetognatha, Appendicularia, and Hydromedusae were identified to the species level. Copepodite stages of calanoid copepods were counted separately. Prosome length was used to distinguish adult females (AF) and copepodite stage V (CV) of the two closely related copepods *Calanus finmarchicus* (AF < 3.1 mm, CV < 2.9 mm) and *C. glacialis* (AF > 3.1 mm, CV > 2.9 mm). Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment. Earlier copepodite stages CI-CIV of *Calanus* belonged almost exclusively to *C. glacialis* and *C. hyperboreus*. They were separated by morphology and body size according to Hirche et al. (1994).

Biomass was calculated from published (Richter, 1994) and unpublished taxon-specific length-dry weight relationships, and individual dry weigths (Kosobokova et al., 1998). For rare copepod species and juvenile stages of *Clione limacina* at first wet weights were calculated according to length-weight regressions established by Chislenko (1968). They were then converted to dry weight using a factor of 0.16 established for arctic zooplankton by Kosobokova (unpubl.). For Chaetognatha, Appendicularia, Polychaeta, Ostracoda, Euphausiacea, Decapoda, and Amphipoda length-weight relationships from Richter (1994) were applied. Cnidaria, Ctenophora and Radiolaria were not included in the calculations of the total biomass.

3. Results

3.1. Hydrography

The transects reported here were designed in order to study the circulation regime along the margin of the Arctic Ocean and its mid-ocean ridges. In the Arctic Ocean water of Atlantic origin forms a layer of several hundred meters thickness, between 200 and 1000 m depth. It is supplied by Atlantic water entering mainly via the Fram Strait, the Fram Strait Branch, and the Barents Sea, the Barents Sea Branch (Rudels et al., 1994). This Atlantic inflow is trapped as the Arctic Ocean Boundary Current (Rudels et al., 2000a) running counter-clockwise along the perimeter of the Arctic

Ocean. The core of the Atlantic inflow is characterized by salinities >34.9. Recirculating branches of Atlantic water are deflected where mid-ocean ridges meet the Eurasian Shelf like the Nansen-Gakkel Ridge, the Lomonosov Ridge (Anderson et al., 1989), and the Alpha-Mendeleev Ridge (Rudels et al., 1994). Other relevant water masses are the cold, low-salinity Arctic surface water of ca. 100 to 200 m thickness with negative temperatures and low salinity, and the Arctic bottom water below 1000 m, also with negative temperatures, but with higher salinity. For most transects used here hydrographic data were published previously (Table 2), for a few stations no hydrography data are available at all (ARK XIV), for some data are not yet available (ARK XII). For a number of stations used here hydrographic profiles with special reference to the Atlantic water have been published recently by Rudels et al. (2004). For better illustration of the hydrographic conditions at our sampling positions the depth of the multinet casts was added to the salinity sections. Information on ice cover and ice thickness is presented in Table 1.

3.2. Integrated zooplankton biomass

The distribution of integrated zooplankton biomass in the entire water column was studied along nine south-to-north oriented transects crossing the slope of the Eurasian Basin north of Svalbard and the Kara, Laptev and East-Siberian Seas, on a section across the St. Anna Trough (northern Kara Sea), on two transects across the Lomonosov Ridge at 81˚N and 86˚N, and on a number of stations in the deep central Amundsen and Makarov Basins (Fig. 2). In Figs 3, 4, together with the biomass values the profiles of the net tows are superimposed on the distribution of salinity in order to better relate the biological data to the hydrography. The majority of deep stations (>500 m depths) had ice concentrations from 40 to 100% and ice thickness from 0.3 to 2 m (Table 1). Exceptions were the Transects B and F (ARK XI/1) where the northernmost stations were in ice-free area or next to the ice margin (Rachor, 1997). The majority of the shallower stations on the Laptev and East-Siberian Sea shelves were in open water (Table 1).

The integrated zooplankton biomass from the bottom to the surface outside the shelf break varied more than tenfold, from 1.9 to 23.9 g DW m^{-2}, and typical values were from 5 to 7 g m^{-2} with a mean of 6.9 ± 4.2 g m^{-2} (Fig. 2). The highest values were found on the westernmost Transect W_1 over the slope north-east of Svalbard, and on Transect A, north-west of the Severnaja Zemlja Archipelago, in 1993 and 1995, respectively (Fig. 2). On Transect W_1, the maximum biomass was observed at locations directly influenced by the core of the Atlantic inflow (Fig. 3). The biomass maxima (23.9 g DW m^{-2}) on Transect A, which represent by far the highest values ever registered in the Arctic Ocean, were observed in the area where the Barents Sea Branch of Atlantic water meets the Kara Sea outflow.

Along all transects crossing the Eurasian slope patterns of biomass distribution were rather uniform (Fig. 5). The total zooplankton stock gradually increased from the shelf towards the slope, reached a maximum at the slope stations located between ca. 500 and 2000 m depths, which were most strongly influenced by Atlantic inflow (Figs 3, 4), and then again decreased towards the deep basins where the effect of the Atlantic inflow was less pronounced. In the central basins biomass values ranged from 1.9 to 3.8 g m^{-2} with a mean of 2.5 ± 0.5 g m^{-2}.

Differing bottom depths make it difficult to draw a direct comparison of integrated biomass between different stations, however, together with vertical biomass profiles (see below) integrated values showed two major gradients in the biomass distribution within the study area. (1) A gradual decrease of biomass from the west towards the east within the Atlantic water of the Arctic Ocean Boundary Current was well seen when comparing transects W - G (Fig. 5). This gradient was apparent in both the integrated stock (Fig. 5) as well as in the chaetognath biomass (Fig. 6), although it was more pronounced in the latter. Copepod biomass showed an abrupt drop down between Transects A and B, and almost no gradient along the rest of the area to the east (Fig. 6). (2) A clear biomass decrease from the Siberian continental slope northward, to the centers of the deep Nansen and Amundsen Basins not influenced directly by Atlantic inflow was well pronounced (Figs 2, 3, 5, 6). At locations south of 82ºN, biomass averaged to 6.7 ± 4.1 g m^{-2}, while in the central basins north of 86º N it was only 2.5 ± 0.5 g m^{-2} (Table 3).

Increased biomass values at stations west of the crest of the Lomonosov Ridge (Fig. 5c, Transect H) observed already earlier by Kosobokova and Hirche (2000) with maximum values of 9.5 g m^{-2} demonstrate the strong importance of the Atlantic water also in the vicinity of the mid-ocean ridges.

3.3. Vertical distribution of biomass

Fig. 7 shows three patterns of the vertical distribution of zooplankton biomass concentrations for 38 stations in areas deeper than 500 m. Most profiles (Fig. 7a) demonstrate overall similarity with much of the variability in the upper mixed Arctic surface layer (0-50 m). Three stations were showing extremely high concentrations in the upper 50 m. Two of them (sts 42 and 64) were situated in or near the Laptev Sea polynya, while sta. 51a was near the crest of the Lomonosov Ridge. At all but two stations (sts 91 and 92, Fig. 7b) biomass maxima were observed within the upper 50 m layer, followed by an exponential decrease below 50 m in the halocline and a slower linear decrease below 100 to 200 m in the Atlantic and Arctic bottom water. Within the upper 0-50 m water layer biomass peaked either in the uppermost 0-25 m, or in the subsurface 25-50 m layer (Fig. 7). The stations 91 and 92, which had the highest integrated biomass during this study, showed deviating patterns with maxima located between 25 and 100 m, and an almost even distribution of biomass between 100 m and the bottom, where values five to ten times higher than at other stations were observed (Fig. 7b). Both stations were located on the slope in the western part of the study area most strongly influenced by Atlantic inflow.

The biomass concentration in the upper 0-50 m ranged from 10.1 to 375.8 mg m^{-3}, and was typically 30-70 mg m^{-3} with a mean of 59.3 ± 60.6 mg m^{-3}. Concentrations in the underlying Arctic halocline water (50-200 m) ranged from 2.5 to 77.3 mg m^{-3}, were typically 5-20 mg m^{-3} and averaged 12.7 ± 12.6 mg m^{-3} (Fig. 7). In the Atlantic layer (200-1000 m), biomass varied from 0.15 to 28.2 mg m^{-3}, and was typically 1-6 mg m^{-3} with a mean of 3.8 ± 4.7 mg m^{-3}. Finally, in the deep bottom layer below 1000 m biomass ranged from 0.03 to 2.8 mg m^{-3} with typical values of 0.2-1.0 mg m^{-3} and a mean of 0.6 ± 0.7 mg m^{-3}. In the deep central basins concentrations were among the lowest observed both in the upper and deep layers (Fig. 7c).

3.4. Biomass composition

Zooplankton biomass was overwhelmingly dominated by copepods all over the study area (Fig. 8). At the stations on the slope and in the deep basins south of 82ºN, the relative contribution of copepods ranged from 72.4 to 86.1% averaging to 80.8 ± 4.4%. Chaetognaths ranked second, contributing from 7.3 to 14.4% with a mean of 11.9 ± 3.8%. The share of other groups was low, only ostracods contributed >3% on average and amphipods were abundant at times (Fig. 8). Shares of polychaets, decapods+euphausiids and pteropods did not exceed 0.5%.

In the deep oceanic areas north of 86ºN the relative contribution of copepods was even higher and was on average up to 91.4 ± 42.8% (Fig. 8). Appendicularians were of higher importance than at the more southern stations with a mean of 3.5 ± 3.1%. They ranked second and replaced chaetognaths in importance ranking. Chaetognaths built up only 1.6 to 3.0% with a mean of 2.5 ± 0.8%. Shares of all other taxonomic groups also decreased (Fig. 8).

3.4.1. Composition and distribution of copepods

Among the copepods, the large calanoids *Calanus hyperboreus, C. glacialis, Metridia longa* were the major contributors to the zooplankton biomass (Table 4) and comprised together from 40 to ca.70% of the total. The other important copepod species were *C. finmarchicus,* which contributed 9.5% on average (Table 4) but showed very strong variability from 0.4 to 52%, followed by *Paraeuchaeta spp.,* and *Microcalanus spp.,* which contributed 3.5% on average. *Oithona similis, Spinocalanus spp.,* and *Oncaea* spp. known to be most important in terms of zooplankton numbers (Kosobokova and Hirche, 2000; Auel and Hagen 2003) contributed from 0.6 to 2.4% on average (Table 4). Distinct differences in the contribution of these species were observed between regions south of 82ºN and north of 86ºN. The relative contribution of *Calanus finmarchicus, C. glacialis, M. longa, Paraeuchaeta* spp., and *O. similis* clearly decreased in the deep central basins north of 86º N in comparison to more southern regions (Table 3). Among these species, the decrease of *C. finmarchicus* north of 86ºN was especially pronounced. At the same time, average relative contribution of *C. hyperboreus,* by far the most important component of copepod biomass in the study area, and the deep-dwelling copepods *Microcalanus* spp. and *Spinocalanus* spp., was higher in the central basins.

3.5. Distribution of key species

3.5.1. *Calanus hyperboreus*

A more detailed study of distribution of each of the three dominant arctic species *Calanus hyperboreus, C. glacialis, Metridia longa* and the Atlantic *C. finmarchicus* indicated clear species-specific spatial distributional patterns. The largest arctic copepod, *C. hyperboreus,* was predominantly abundant along the margins of the deep Nansen, Amundsen and Makarov Basins with maximum biomass immediately north of the Eurasian slope (Fig. 9). Typical values there were 2-3 g m^{-2} DW, with similar values all along the margins from the western Nansen to the eastern Amundsen Basin. Up the slope, biomass decreased along all transects, with minimum values found on the artic shelves (Fig. 9). At the northern ends of the transects, in the deep basins, biomass generally decreased; however, an increase of *C. hyperboreus* biomass was observed at transect H across the Lomonosov Ridge at 81ºN, east of the crest of the Ridge in the area of the Atlantic core (Fig. 9). This was a location where the species maximum biomass of 4.0 g m^{-2} DW was registered (Fig.

9). The relative contribution of *C. hyperboreus* showed similar distributional patterns along all transects with the general increase of the share from the outer shelf over the slope into the deep basins (Fig. 10).

3.5.2. *Calanus glacialis*

The second species on the ranking list, *C. glacialis,* exhibited a different distributional pattern. The species formed a belt of high biomass with typical values up to 1.5-2 g m^{-2} over the outer Eurasian shelf margin and along the continental slope. Its biomass was lower both over the shallow shelf (<100 m depth) and in the deep basins (Fig. 11). Very high values from 2.3 to 8.3 g m^{-2} were observed along Transect A, but the maximum species biomass of 9.3 g m^{-2} was found north-west of the East Siberian Sea on Transect G (Fig. 11). This distribution pattern was reflected also in the distribution of the relative contribution of *C. glacialis* to integrated biomass (Fig. 10).

3.5.3. *Metridia longa*

The distribution of *Metridia longa* was similar to that of *C. glacialis,* with high values over the slope and lower ones both on the shallow shelf and in deep central basins (Fig. 12). The typical biomass in the area of high concentrations was 0.5-1.2 g m^{-2} with the maxima of 2.1 and 2.9 g m^{-2} at Transects A and B, respectively.

3.5.4. *Calanus finmarchicus*

Finally, the Atlantic copepod *C. finmarchicus* showed very strong spatial variability. It was most important over the Eurasian slope. Its biomass and relative contribution to the total zooplankton stock showed a pronounced decrease from the west towards the east (Fig. 13). The sharpest decrease was observed over the slope east of Severnaja Zemlja Island (Transect B). In this area, biomass dropped down almost tenfold to 0.7 g m^{-2} in comparison to values of 5-7 g m^{-2} DW upstream on the slopes of the northern Barents Sea (Transect W, W_1) and northern Kara Sea (Transect A) (Fig. 13). Subsequently, the share of *C. finmarchicus* in the integrated biomass decreased from 25-45% to 10-15% (Fig. 10). Both biomass and share of *C. finmarchicus* continued to decrease along the northern Laptev Sea slope. At the border between the Laptev and East Siberian Sea they did not exceed 0.2-0.3 g m^{-2} (Fig. 13) and 6-7% (Fig. 10), respectively. In the western East-Siberian Sea even lower biomass and contribution of *C. finmarchicus* was observed (Figs 10, 13). In the deep basins *C. finmarchicus* biomass also decreased dramatically. It was typically <0.06-0.10 south of 82ºN and <0.01-0.03 g m^{-2} north of 86ºN, showing a pronounced eastward and northward decrease. In contrast to generally low values in the deep basins, an increase of biomass was observed at the transect H across the Lomonosov Ridge at 81ºN, similar to *C. hyperboreus,* east of the crest of the Ridge (Fig. 13).

4. Discussion

Historical assessments of the zooplankton biomass in the Arctic Ocean (Minoda, 1966; Hopkins, 1969a, b; Pautzke, 1979; Kosobokova, 1981, 1982; Conover and Huntley, 1991) are few, and generally difficult to compare due to methodological differences or incomplete sampling of the water column. Recently Ashijan et al. (2003) presented a detailed overview of the methodological pitfalls of the previous biomass studies and suggested that the zooplankton stock may have been underestimated in many of them. Several recent studies (Wheeler et al., 1996;

Mumm et al., 1998; Thibault et al., 1999; Kosobokova and Hirche, 2000; Ashijan et al., 2003) reported the zooplankton standing stocks and production in the Arctic Ocean to be greater than in previous studies, however, most of them were based on observations with restricted spatial coverage.

The large data set presented here confirms strongly that zooplankton stock is significantly higher over a large part of the Arctic Ocean than it was previously believed and reveals consistent patterns of the regional distribution of zooplankton biomass and composition over the area studied. As already suggested earlier, however, based only on limited data grounds (Hirche and Mumm, 1992; Kosobokova and Hirche, 2000), hydrography plays a prominent role shaping the zooplankton distribution. The distribution patterns found during the present study were all related to the spreading of Atlantic water in the Arctic Ocean.

The most prominent pattern shows elevated zooplankton stocks all along the Eurasian slope from the area north of Svalbard to the north-east of the Laptev Sea, where the Lomonosov Ridge hits the continental slope (Figs 2, 5). This area is known to be most strongly affected by the Arctic Ocean Boundary Current which brings Atlantic water from the North Atlantic into the Arctic Ocean via Fram Strait and the Barents Sea (Schauer et al., 1997; Rudels et al., 2000a). The biomass maxima in the core of the Arctic Ocean Boundary Current and elevated concentrations in its vicinity, decreasing towards the shelves and basins (Fig. 3, 4, 5) clearly demonstrate that the Atlantic inflow advects plankton populations from the North Atlantic, and these populations to a large extent remain within the zone affected by the Arctic Ocean Boundary Current. We speculate that on several transects higher biomass values were found had we sampled the core of the Atlantic inflow better. Increased biomass with an increased portion of Atlantic fauna was also observed in recirculating branches of the Atlantic inflow along mid-ocean ridges as the Nansen-Gakkel Ridge (Hirche and Mumm, 1992) and at stations west of the crest of the Lomonosov Ridge at 81ºN (Kosobokova and Hirche, 2000). These observations underline the unique role of the Atlantic inflow in shaping the biomass distribution and composition in the Arctic Ocean.

Another interesting pattern is the consistently decreasing zooplankton stock in a west-east direction along the flow of the Arctic Ocean Boundary Current. This gradient as well as the elevated zooplankton stock along the Eurasian slope are related to the distribution of the dominant zooplankton taxa, the three large *Calanus* species and *Metridia longa* together with a chaetognath, *Eukrohnia hamata*. At least two of the *Calanus* species, *C. glacialis* and *C. finmarchicus,* show the highest overall abundance inside and in the close neighbourhood of the Arctic Ocean Boundary Current. High abundance of *C. glacialis* results from successful reproduction and recruitment over the deep Eurasian shelf and the upper slope in seasonally ice-free areas and in polynyas (Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2003, 2007) and additionally from supply by populations from the northern Barents Sea advected with Atlantic inflow (Hirche and Kosobokova, 2003, 2007). In contrast, the high stock of *C. finmarchicus* (Fig. 13) originates completely in the North Atlantic and southern Barents Sea and represents a strictly allochtonous component of the zooplankton over the Eurasian slope. Many studies have demonstrated that *C. finmarchicus* is not able to maintain sustainable populations and reproduce successfully in the Arctic Ocean (Jaschnov, 1970; Conover, 1988; Hirche and

Mumm, 1992; Kosobokova, et al., 1998; Hirche and Kosobokova, 2007), however, the reasons are still under discussion (Hirche and Kosobokova, 2007). The absence of young copepodids in our study area (Kosobokova, et al., 1998; Hirche and Kosobokova, 2007) supports earlier findings by Hirche and Mumm (1992) and underlines the view of the Arctic Ocean as an expatriation area for *C. finmarchicus.* Its drastic eastward decrease indicates gradual extinction of the population in Arctic waters, while high peaks of *C. finmarchicus* biomass north-east of Svalbard and northwest of Severnaja Zemlja demarcate the gateways where its populations enter the Arctic. A similar eastward decrease was observed in the chaetognath biomass, which is mainly represented by large specimens of the oceanic species *Eukrohnia hamata*. This decrease remains unexplained as, in contrast to *C. finmarchicus*, reproductively active females have been reported for the Arctic Ocean (Timofeev, 1998).

Another striking regional pattern is the much lower zooplankton biomass in the central deep basins in comparison to the high biomass belt along the Eurasian continental slope (Fig. 2). The values in the central basins ranged from 2 to a maximum of 3.8 g m^{-2}, which is 2 to 3 times lower than over the slope. This difference between regions under Atlantic influence and basins has been noticed by Hirche and Mumm (1992) as a drastic drop of zooplankton biomass and abundance at a frontal zone at ca. 83ºN in the Nansen Basin, in the area where hydrophysical characteristics of water masses changed abruptly from those representative of their Fram Strait and Barents Sea sources to those more typical for the central Arctic Ocean. Hydrophysical observations in the Arctic Ocean since 1987 confirm that the central deep basins experience much less input by the Atlantic inflow (Schauer et al., 1997; Rudels et al., 2000aa,b), as the Arctic Ocean Boundary Current remains confined to the slope break and recirculates north along the western slopes of the underwater ridges (Anderson et al., 1989; Aagard, 1989; Rudels et al., 1994, 2000a,b; Schauer et al., 1997). Both the dramatic decrease of the zooplankton stock and absence of juveniles in the plankton populations beyond this front are in accordance with a strong decrease of exchange with Atlantic populations and a clear indication for long expatriation of species present there. The majority of other data from the central basins also show rather stable and generally low biomass (Mumm et al., 1998; Auel and Hagen, 2002). Our values compare well with those obtained by other authors using similar methods. Calculation of average biomass integrated over the upper 500 m using our original and published values for the central basins resulted in a value of 2.5 ± 0.5, Mumm et al. (1998) found 1.88 ± 0.6. We speculate that this value for the upper part of the water column and the biomass range of 2-4 g DW m^{-2} for the entire water column demarcate the level of sustainable authochtonous zooplankton production independent from advection. Thibault et al. (1999) using another method to determine biomass arrived at somewhat higher values.

There are large differences between the basin and margin communities. While the share of copepods is already high in the shelf and slope areas, it reaches its maximum in the basins and seems there higher than in any other region of the world ocean. Of the four most important species considering all stations, *C. hyperboreus* doubled its portion in the basins, and *C. glacialis* remained more or less constant, while*, M. longa* decreased significantly, and *C. finmarchicus* almost completely disappeared (Figs. 10, 13). It is unclear whether C. *hyperboreus* maintains a local population as its reproductive success there seems to be low (Kosobokova et al., 1998; Olli et al, 2007). Alternatively, this large species may have just the largest survival potential. At times, however, the almost pure “copepod” communities are skewed by accidental catches of chaetognaths and large amphipods or euphausiids. Such long living and quite patchy organisms, once caught, may cause a more than twofold increase of biomass (Wheeler et al., 1996; Thibault et al., 1999).

The vertical distribution patterns presented here are typical of the summer season only, as the vertical distribution of the zooplankton stock is subject to seasonal vertical migration of most herbivorous species in the North Atlantic and Arctic Oceans (Vinogradov, 1970; Kosobokova, 1980; Geynrikh et al., 1983; Richter 1994; Ashjian et al, 2003). Biomass profiles based on data collected during seasonal observations by the Russian drifting stations NP-22 and NP-23 show that seasonal downward migration in the central Canada Basin started in September (Kosobokova, 1982). By this time, the copepod biomass maximum shifted from the surface layer to the depths between 200 and 300 m, where it remained until next May/June. Thereafter, copepod populations concentrated in the upper 50 m. A large portion of this translocated biomass was made up by two Calanus species, *C.hyperboreus* and *C. glacialis*.

At the majority of locations studied here, up to 55% of the zooplankton biomass was concentrated in the upper 50 m and the deep layers were strongly impoverished (Fig. 7). Only on Transect W_1 close to Fram Strait and north of the Kara Sea a set of deviating patterns was observed with either a shift of the maximum concentrations to deeper layers, or with a much slower decrease with depth than in most of the other profiles (Fig. 7). These profiles may reflect the adjustment of the populations to the transition from the Atlantic to the Arctic Ocean, as in Fram Strait the Fram Strait

Branch of Atlantic water enters the Arctic Ocean, while in the northern Kara Sea the Barents Sea Branch joins the Atlantic inflow (Rudels et al. 2000a, Rudels et al. 2004). The role of vertical distribution in advection of Atlantic populations and their distribution in the Arctic Ocean has already been discussed by Hirche and Mumm (1992). Two modes of advection have to be considered depending on the season. From spring to summer a large portion of the Calanus species is dwelling in surface waters, while from late summer to early spring, the populations overwinter in deep waters (Kosobokova, 1982; Geynrikh et al., 1983; Hirche, 1991; Richter 1994; Ashjian et al, 2003). Advection of these populations depends largely on vertical profiles of current directions and velocities. However, so far no synoptic investigations of the behaviour of zooplankton populations in regions of submergence of Atlantic water in different seasons are available. This subject certainly deserves future studies, which should combine high resolution vertical distribution of zooplankton and current profiles along transects in regions of submergence.

For this study we compiled samples obtained between 1993 and 1998 which may bias regional differences and gradients due to interannual variability. Indeed, information on interannual variability in the temperature and intensity of the Atlantic inflow, but also the Pacific inflow (Shimada et al., 2004, 2006) is increasing in the Arctic Ocean (e.g. Grotefend et al., 1998; Karcher et al., 2003). However, as the majority of our samples were collected in 1993 and 1995, the time interval is relatively short. In 1996 four stations in the St. Anna Trough were added, and in 1998 sampling was carried out only on 3 stations in the deep central Amundsen and Makarov Basins. In the six deep basin stations presented here standard deviation was very low (2.5 ± 0.5 g DW m^{-2}) suggesting a stable community and little effect of interannual changes despite the five years interval covered by the samples. In contrast, on stations south of 82°N biomass variability was much higher (6.9 ± 4.1 g DW m^{-2}). In this region we found large along-transect variability related to the mesoscale hydrographic variability, which makes interannual comparison extremely difficult. As this region is strongly affected by advection, changes in the intensity of advection should find their clearest expression there. In a numerical model Karcher et al. (2003) simulated these parameters for 350m depth in the Arctic Ocean Boundary Current at the Siberian Shelf north of Franz Josef Land and northeast of Severnaja Zemlja (their Fig. 5). The model shows that our sampling period falls into a phase of elevated velocities and temperatures, with relatively similar values for both parameters between 1993 and 1995. Hence we do not expect large interannual variability in the advective intensity during the sampling period. However, the samples may represent the phase of the 1990s warm event in the Nordic Seas.

In order to monitor zooplankton in the future for an assessment of the effect of climate change the two communities of the central basins and of the Arctic Ocean Boundary Current have to be considered separately. While for the basins only few samples are required, we suggest to sample along similar transects as during this study for the shelf and slope community with sufficient spatial resolution to get the core of the Atantic inflow and its northern frontal zone.

Acknowledgements

We appreciate the help of H.Hanssen, B. Strohscher, T. Scherzinger and S.Timofeev with sample collection. U. Schauer and B. Rudels provided hydrography data, We are greatly thankful to A. Wisotzki for producing the hydrographic sections. This work was supported by BMBF Grant 03F11GUS, RFBR grant 06-05-65187 and visiting scientist grants from the Alfred Wegener Institute for Polar and Marine Research to K. Kosobokova.

References

Aagaard, K., 1989. A synthesis of the Arctic Ocean circulation. Rapports et Proces Verbaux des Reunions. Conseil Permanent International pour l'Exploration de la Mer 188, 11-22.

Anderson, L.G., Jones, E.P., Koltermann, K.P., Schlosser, P., Swift, J.H., Wallace, D.W.R., 1989. The first oceanographic section across the Nansen Basin in the Arctic Ocean. Deep-Sea Research 36, 475-482.

Auel, H, Hagen, W., 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Marine Biology 140, 1013-1021.

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.

Brodsky, K.A., Nikitin, M.N., 1955. Observational data of the scientific research drifting station of 1950-1951. Hydrobiological work (in Russian). Morskoy Transport 1, 404-410.

Brodsky, K.A., Pavshtiks, E A., 1976. Plankton of the central part of the Arctic Basin (in Russian). Polar Geography 1, 143-161.

Carmack, E.C., Aagaard, K., Swift, J.H., MacDonald, R.W., McLaughlin, F.A., Jones, E.P., Perkin, R.G., Smith, J.N., Elis, K.M., Killius, L.R., 1997. Changes in temperature and tracer distributions within the Arctic Ocean, results from the 1994

Arctic Ocean section. Deep-Sea Research Part II. Topical Studies in Oceanography 44, 1487-1502.

Carmack, E., Barber, D.G., Christensen, J.R., Macdonald, R.W., Rudels, B., Sakshaug, E., 2005. Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. Progress in Oceanography 71, 145-181.

Carmack, E., McLaughlin, F., Zimmermann, S., Proshutinsky.A., 2006. Pacific ocean inflow: influence on catastrophic reduction of sea ice cover in the Arctic Ocean. Geophysical Research Letters 33(L08605). doi: 10.1029/2005GL025624.

Chapman, W.L., Walsh, J.E., 1993. Recent variations of sea ice and air temperature in high latitudes. Bulletin of the American Meteorological Society 74, 33–47

Chislenko, L.L., 1968. Nomogramms for determining the weight of aquatic organisms according to the size and shape of their body, marine mesobenthos and plankton (in Russian). Nauka, Leningrad

Conover, R.J., 1988. Comparative life histories in the genera Calanus and Neocalanus in high latitudes of the northern hemisphere. Hydrobiologia 167/168, 127 - 142.

Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. Journal of Marine Systems 2, 1-41.

Dawson, J.K., 1978. Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. Limnology and Oceanography 23, 950-957.

Geynrikh, A.K., Kosobokova, K.N., Rudyakov, Y.A., 1983. Seasonal variations in the vertical distribution of some prolific copepods of the Arctic basin. Canadian Translation Fisheries and Aquatic Sciences 4925, 1-22.

Grebmeier, J.M., Overland, J. , Moore, S.E., Farley, E.V., Carmack, , E., Cooper, L.W., Frey, K., Helle, J.H., McLaughlin, F.A., McNutt. S.L., 2006. A major ecosystem shift in the Northern Bering Sea. Science 311, 1461-1464. doi: 10.1126/science.1121365.

Grotefendt, K., Logemann, K., Quadfasel, D., Ronski, S., 1998. Is the Arctic Ocean warming? Journal of Geophysical Research 103. C12, 27679-27687.

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., Mumm, N., 1992. Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. Deep-Sea Research 39 Supplement 2, S485-S505.

Hirche, H.J., Kosobokova, K.N., 2003. Early reproduction and development of dominant calanoid copepods in the ice zone of the Barents Sea – need for a change of paradigms? Marine Biology 143, 769-781.

Hirche, H.J., Kosobokova, K.N., 2007. Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean - expatriation and potential colonization. Deep-Sea Research Part II. 54, 2729-2747

Hopcroft, R.R., Clarke, C., Nelson, R.J., Raskoff, K.A., 2005. Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. Polar Biology 28, 197-206.

Hopkins, T.L., 1969a. Zooplankton standing crop in the Arctic Basin. Limnology and Oceanography 14, 80-95.

Hopkins, T.L., 1969b. Zooplankton biomass related to hydrography along the drift track of Arlis II in the Arctic Basin and the East Greenland Current. Journal of Fisheries Research Board of Canada 26, 305-310.

Huges, K.H., 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, W.A., 1970. Distribution of Calanus species in the Seas of the Northern Hemisphere. Internationale Revue der gesamten Hydrobiologie 55, 197-212.

Johannessen, O.M., Miles, M., Bjørgo, E., 1995. The Arctic´s shrinking sea ice. Nature 376, 126-127.

Johannessen, O.M., Shalina, E.V., Miles, M.W., 1999. Satellite evidence for an Arctic sea ice cover in transformation Science 286, 1937 - 1939.

Johannessen, O.M., Miles, M. W., 2000. Arctic sea ice and climate change - will the ice disappear in this century? Science Progress 83, 209-222.

Johnson, M.W., 1963. Zooplankton collections from the high polar basins with special reference to the Copepoda. Limnology and Oceanography 8, 89-102.

Karcher, M.J., Gerdes R., Kauker, F., Köberle, C., 2003. Arctic warming: Evolution and spreading of the 1990s warm event in the Nordic seas and the Arctic Ocean. Journal of Geophysical Research 108, C2, 16-1-16-15.

Kosobokova, K. N., 1978. Diurnal vertical distribution of *Calanus hyperboreus* Krøyer and Calanus glacialis Jaschnov in the Central Polar basin. Oceanology 18, 476-480

Kosobokova, K.N., 1981. Zooplankton of the Arctic Ocean (in Russian). PhD Thesis, Institute of Oceanology, Akademy of Sciences, Moscow, 1-150.

Kosobokova, K.N., 1982. Composition and distribution of the biomass of zooplankton in the central Arctic Basin. Oceanology 22, 744-750.

Kosobokova, K.N., 1980. Seasonal changes of the vertical distribution and age composition of *Microcalanus pygmaeus, Oithona similis, Oncaea borealis* and *O. notopus* populations in the central Arctic basin (in Russian). In: Vinogradov, M.E. (Ed.), Biologiya Tsentral´nogo Arkicheskogo basseyna (Biology of the central Arctic Basin). Nauka, Moscow pp. 167-182.

Kosobokova, K.N., 1989. Vertical distribution of plankton animals in the eastern part of the central Arctic Basin (in Russian). Explorations of the Fauna of the Seas, Marine Plankton, Leningrad 41 (49), 24-31.

Kosobokova K.N., 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., Hirche H.-J., 2001. Reproduction of *Calanus glacialis* in the Laptev Sea, Arctic Ocean. Polar Biology 24, 33-43.

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.

Lane, P.V.Z., Llinás L., Smith S.L., Pilz, D., 2008. Zooplankton distribution in the western Arctic during summer 2002: Hydrographic habitats and implications for food chain dynamics. Journal of Marine Systems 70, 97-133.

Melnikov, I.A., Kolosova, E.G., 2001. The Canada Basin zooplankton in recent environmental changes in the Arctic. In Semiletov, I.P. (Ed.), Proceedings of the Arctic Regional Center 3. Pacific Institute of Oceanology, Vladivostok, 165-176.

Minoda, T., 1967. Seasonal distribution of Copepoda in the Arctic Ocean from June to December, 1964. Records of Oceanographic Works in Japan 9, 61-168.

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.

Olli, K., Wassmann P., Reigstad, M., Ratkova, T., Arashkevich, E., Pasternak, A., Matrai, P.A., Knulst, J., Tranvik, L., Klais, R., Jacobbsen, A., 2007. The fate of production in the central Arctic Ocean – top-down regulation by zooplankton expatriates? Progress in Oceanography 72, 84-113.

Pautzke, C.G., 1979. Phytoplankton primary production below the Arctic Ocean pack ice, an ecosystems analysis. Ph. D. Thesis, University of Washington, 181 pp.

Rachor, E., 1997. Scientific cruise Report of the Arctic Expedition ARK-XI/1 of RV "Polarstern" in 1995 (German-Russian project LADI: Laptev Sea – Arctic Deep Basin interactions). Reports on Polar and Marine Research 226, 1-336.

Raskoff, K.A., Purcell, J.E., Hopcroft, R.R., 2005. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Polar Biology, 28, 207-217.

Richter, C., 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Thesis. University of Kiel, 1-101.

Rudels, B., Jones, P., Anderson, L., Kattner, G., 1994. On the intermediate depth waters of the Arctic Ocean. In: Johanessen, R.D., Muench, R.D., Overland, J.E. (Eds.) The Polar Oceans and Their Role in Shaping the Global Environment. Geophysical Monograph, 85, Washington DC, pp. 33-46.

Rudels, B., Muench, R.D., Gunn, J., Schauer, U., Friedrich, H.J., 2000b. Evolution of the Arctic boundary current north of the Siberian Shelves. Journal of Marine Systems 25, 77-99.

Rudels, B., Meyer, R., Fahrbach, E., Ivanov, V. V., Østerhus, S., Quadfasel, D., Schauer, U., Tverburg, K., Woodgate, R.A., 2000b. Water mass distribution in Fram Strait and over the Yermak Plateau in summer 1997.

Rudyakov, Y. A., 1983 . Vertical distribution of *Calanus hyperboreus* (Copepoda) in the Central Arctic Basin. Oceanology 23, 249-254.

Schauer, U., Muench, R.D., Rudels, B., Timokhov, L., 1997. Impact of eastern shelf waters on the Nansen Basin intermediate layers. Journal of Geophysical Research 102 (C2), 3371-3382.

Sherr, E.B., Sherr, B.F., Wheeler, P.A., Thompson, K. 2003. Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. Deep-Sea Research I, 50:557-571.

Shimada, K., McLaughlin, F., Carmack, E., Proshutinsky, A., Nishino, S., Itoh, M., 2004. Penetration of the 1990's warm temperature anomaly of Atlantic water in the Canada Basin. Geophysical Research Letters. 31(20), 1-4.

Thibault, D., Head, E.J.H., Wheeler, P.A., 1999. Mesozooplankton in the Arctic Ocean in summer. Deep Sea Research I 46, 1391-1415.

Timofeev, S.F., 1998: Reproduction of the chaetognath *Eukrohnia hamata* (Mobius, 1875) in the Arctic Ocean. Reports on Polar and Marine Research 287, 70 93.

Vinogradov, M.Y., 1970. Vertical distribution of oceanic zooplankton. Israel Program for Scientific Translatioms, Jerusalem, 339 pp.

Vinogradov, M.E., Melnikov, I.A., 1980. Studies of the pelagic ecosystems of the central Arctic basin. In: Vinogradov, M.E. (Ed.), Biologiya Tsentral´nogo Arkicheskogo basseyna (Biology of the central Arctic Basin). Nauka, Moscow pp. 5-14.

Vinnikov, K.Y., Robock, A., Stouffer, R.J., Walsh, J.E., Parkinson, C.L., Cavalieri, D.J., Mitchell, J. F. B., Garrett, D., Zakharov, V.F., 1999. Global Warming and Northern Hemisphere Sea Ice Extent. Science 286, 1934 - 1937.

Virketis, M.A., 1957. Some data on the zooplankton from the central part of the Arctic Basin (in Russian). Materials of scientific observations of the drift stations "North Pole 3" and "North Pole 4" 1954/55 1, Moscow, 238-311.

Virketis, M.A., 1959. Materials on the zooplankton of the central part of the Arctic Ocean (in Russian). Results of scientific observations on the drift stations "North Pole 4" and North Pole 5", 1955-1956, Moscow, 132-206.

Wheeler, P.A., Gosselin, M., Sherr, E., Thibault, D., Kirchman, D.L., Benner, R., Whitledge, T.E., 1996. Active cycling of organic carbon in the central Arctic Ocean. Nature 380, 697-699

Table 1. Cruises, station locations, bottom depth, sampling depths, and ice conditions

Station No.	Transect	Date	Latitude, ºN	Longitude, ºE	Depth, m	Maximum sampled depth, m	Ice thickness (cm)	Ice concentration, %
ARK IX/4								
6	W	12.08.93	81°12'	30°36'	179	160	No data	90
7		13.08.93	81°40'	30°16'	494	500	No data	90-100
14		13.08.93	81°27'	34°35'	2719	1500	No data	90-100
16	W_1	15.08.93	82°12'	30°53'	2465	1500	No data	100
19		18.08.93	82°45'	40°15'	2994	1500	No data	90-100
24		20.08.93	82°09'	42°02'	1004	1000	No data	90-100
27		21.08.93	82°01'	43°34'	280	260	No data	90-100
31	F	01.09.93	76°30´	133°20´	38	20	0	0
32		02.09.93	78°43´	132°21´	2975	1500	0	0
35		04.09.93	78°23´	133°04´	2062	1500	0	0
38		05.09.93	78°10´	133°25´	982	980	0	0-10
39		05.09.93	78°06´	133°31´	514	450	0	0
40		05.09.93	78°04´	133°33´	243	200	0	0
41		06.09.93	77°54´	133°34´	72	50	130	0-10
43		06.09.93	77°24´	133°35´	53	30	130	30-50
44	E	07.09.93	77°02´	126°24´	93	70	130	60
47		08.09.93	77°11´	126°14´	990	990	80-160	90
48		09.09.93	77°08´	126°23´	544	500	130	70-80
49		09.09.93	77°06´	126°19´	200	200	130	90
50		10.09.93	77°44´	125°46´	1990	1500	150	90
53		12.09.93	79°15´	122°53´	3244	1500	170	90-100
54	D	13.09.93	79°11´	119°54´	3071	1500	170-190	70-80
56		14.09.93	78°40´	118°34´	2618	1500	140	90-100
58		15.09.93	78°00´	118°44´	1930	1500	190-220	80-90
60		16.09.93	77°34´	118°26´	1181	1000	220	90
62		17.09.93	77°24´	118°11´	554	500	200	80-90
64		18.09.93	77°16´	118°32´	230	299	No data	80
65		18.09.93	77°11´	118°44´	106	80	No data	80-90
67	C	20.09.93	78°16´	109°15´	51	30	150	70
68		20.09.93	78°28´	110°49´	101	100	150	90-100
69		21.09.93	78°42´	112°32´	518	500	250-300	100
70		21.09.93	78°45´	112°42´	1141	1140	300	100
71		22.09.93	78°35´	111°22´	235	200	No data	100
ARK XI/1								
4	G	24.07.95	78°00,5´	144°53,6´	54	45	0	0
7		26.07.95	79°27,3´	148°06,6´	223	200	70-120	50
8		28.07.95	79°08,9´	146°21,1´	100	100	70-120	50
9		29.07.95	78°39,3´	144°07,4´	78	65	30-70	50
65		30.08.95	79°30,0´	148°14,2´	245	200	70-120	40
64		30.08.95	70°52,9´	149°49,1´	536	500	30-120	40
62		29.08.95	80°04,8´	149°50,7´	1072	1000	70-120	40-50
60		28.08.95	80°17,3´	150°17,5´	1642	1500	70-120	50
27	B	08.08.95	81°14,3´	106°45,4´	3133	3000	0	0

25		07.08.95	81°06,2´	105°23,7´	2642	2500	0	0
31		11.08.95	80°46,4´	103°23,1´	1484	1435	30-70	60-70
32		11.08.95	80°39,0´	103°03,0´	621	500	30-70	60
33		12.08.95	80°25,5´	101°59,9´	266	245	30-70	70
42		16.08.95	78°42,2´	134°41,7´	2149	2000	70-120	40-70
45		18.08.95	80°00,0´	134°55,9´	3426	3200	30-200	50
47	H	20.08.95	80°55,1´	132°00,0´	3907	3500	30-120	50
49		22.08.95	81°03,4´	136°32,4´	2708	2600	30-120	50
51a		23.08.95	81°07,3´	138°47,3´	1830	1750	70-120	50
52		24.08.95	81°10,5´	140°06,3´	1292	1200	70-120	50
55		25.08.95	81°10,6´	143°24,2´	1693	1600	70-120	50
57		27.08.95	81°12,5´	150°14,8´	2643	2500	70-120	50
75		04.09.95	80°55,6´	122°39,8´	3566	3566	70-120	50
91	A	10.09.95	82°04,2´	91°02,4´	1079	1000	No data	30-40
92		10.09.95	82°02,2´	90°56,1´	525	5252	No data	30-40
93		10.09.95	81°57,9´	91°01,2´	240	240	No data	30-40
94		10.09.95	81°49,0´	90°46,6´	95	90	No data	30-40
ARK XII								
5	SAT	24.07.96	81°28,05´	66°56,6´	552	530		90-100
7		25.07.96	81°13´	70°03´	591	300		90-100
10		26.07.96	81°22,6´	72°55,5´	580	550		100
24		30.07.96	81°42´	82°08´	323	300		90-100
48	K	05.08.96	84°46,7´	105°46,9´	3863	3000		90
55		09.08.96	86°09,6´	125°48,8´	4384	3500		70
72		14.08.96	85°49,7´	161°40,9´	3923	3500		30-40
76		17.08.96	82°31,5´	143°33,6´	1958	1900		90-100
ARK XIV								
34	L	15.07.98	85°22,3´	155°24,1´	2092	2030		90-100
38		16.07.98	85°08,0´	172°24,5´	1518	1450		90-100
47		18.07.98	85°45,0´	177°03,5´	2452	2350		90-100

Table 2. References for hydrography during our transects

ARK IX/4 (1993)

Transect	Reference
W	Schauer et al. (1997, their Transect I).Hirche and Kosobokova, 2007
W1	Schauer et al. (1997, their Transect II).
C	general description in Kosobokova et al., 1998
D	Schauer et al. (1997, their Transect III)
E	Schauer et al. (1997, their Transect IV); Hirche and Kosobokova, 2007
F	Schauer et al. (1997, their Transect V); Hirche and Kosobokova, 2007

ARK XI/1 (1995) (Rudels et al. 2000) Transects A,

A	Rudels et al. (2000, their Transect A).
B	Rudels et al. (2000, their Transect B); Hirche and Kosobokova, 2007
G	Rudels et al. (2000, their Transect B)*.
H	Rudels et al. (2000a, part of their Transect C), partly also in Kosobokova and Hirche (2000)

*Only northern part shown, as due to ice conditions the two parts were sampled 5 weeks apart.

Table 3. Relative contribution of dominant copepod species to the integrated zooplankton biomass (%)

	All stations		South of 82ºN		North of 86ºN	
	Mean	SD	Mean	SD	Mean	SD
C. finmarchicus	9.5	12.09	11.2	12.47	0.5	0,27
C. glacialis	18.9	11.39	19.6	12.01	14.8	6,50
C. hyperboreus	25.4	14.20	21.5	11.54	46.5	5,82
Metridia longa	10.8	5.53	12.1	5.13	4.4	2,05
Oithona similis	2.4	1.22	2.7	1.16	1.1	0,50
Microcalanus spp.	3,5	2.16	3.1	1.78	5.5	3.03
Oncaea spp.	0.6	0.26	0.5	0.27	0.7	0,24
Spinocalanus spp.	1,8	2.30	1.1	1.71	5.5	1.19
Paraeuchaeta	3.5	1.77	3.8	1.79	2.2	0,90
Other Copepoda	5,9	3.73	4.9	2.95	11.3	2.85

Table 4. Comparison of integrated zooplankton biomass at all stations <500m, all stations >500m south of 82°N (continental margin), and all stations north of 86°N (deep basins)

Region	Number of stations	Biomass, g m^{-2} (mean ± SD)
Stations <500m	43	6.2 ± 4.13
South of 82ºN	37	6.9 ± 4.14
North of 86ºN	6	2.5 ± 0.49

Figure captions

Fig. 1. Station locations and transects (letters) in the Arctic Ocean. Circles – ARK IX/4 and ARK XI/1, diamonds – ARK XII, squares – ARK XIV

Fig. 2. Distribution of integrated zooplankton biomass in the Arctic Ocean. For station locations see Fig. 1

Fig. 3. Integrated zooplankton biomass (vertical bars) along 5 sections in the Arctic Ocean during ARK IX/4, 1993, with salinity sections and sampling depth. For station location see Fig. 1. (After Schauer et al., 1997)

Fig. 4. Integrated zooplankton biomass (vertical bars) along 4 sections in the Arctic Ocean during ARK XI/1, 1995, with salinity sections and sampling depth. For station location see Fig. 1. (After Rudels et al., 2000a)

Fig. 5. Integrated zooplankton biomass (bars) along 10 transects during 2 cruises ARK IX/4, 1993 (a), and ARK XI/1, 1995 (b, c). Open bars = shelf, hatched bars = slope, solid bars = basin. Lines with diamonds represent bottom depth. For station location see Fig. 1.

Fig. 6. Integrated biomass (bars) of copepods and chaetognaths along 9 transects combing 2 cruises (ARK IX/4, 1993 - solid bars; ARK XI/1, 1995 - hatched bars). Lines with diamonds represent bottom depth. Missing bars on chaetognath stations indicate no data availability. For station location see Fig. 1.

Fig. 7. Three patterns of vertical distribution of zooplankton biomass concentration. Stations in vicinity of the Arctic Ocean Boundary Current (a), near gateways to Arctic Ocean (b), and in the central basins (c). Note different scale in (c)

Fig. 8. Relative composition of zooplankton biomass in the Arctic Ocean along transects during ARK IX/4, 1993 (Transects W, W_1, D), ARK XI/1, 1995 (A, B, G, H), ARK XII, 1996 (K) and ARK XIV, 1998 (L). For station location see Fig. 1.

Fig. 9. Distribution of *Calanus hyperboreus* biomass in the Arctic Ocean during 3 cruises.

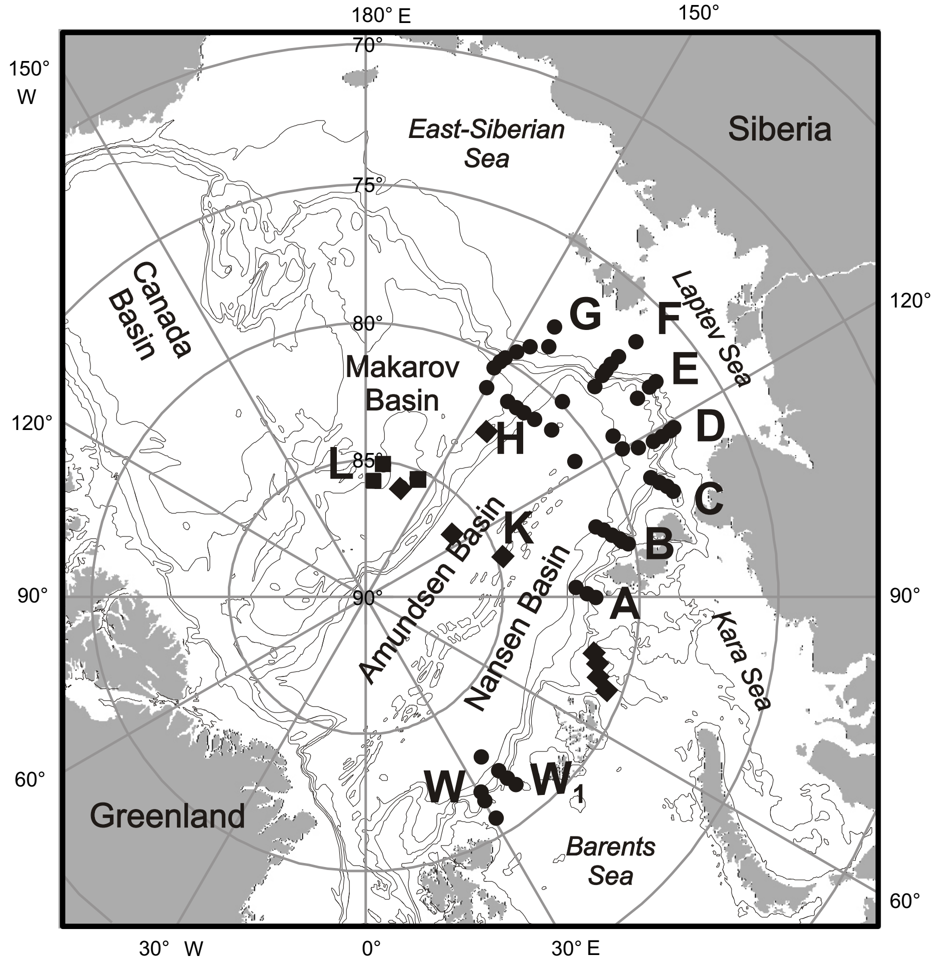
Fig. 10. Relative composition of the biomass of the Calanus group (*Calanus hyperboreus, C. glacialis*, *C. finmarchicus*) on 11 transects in the Arctic Ocean.

Fig. 11. Distribution of *Calanus glacialis* biomass in the Arctic Ocean during 3 cruises.

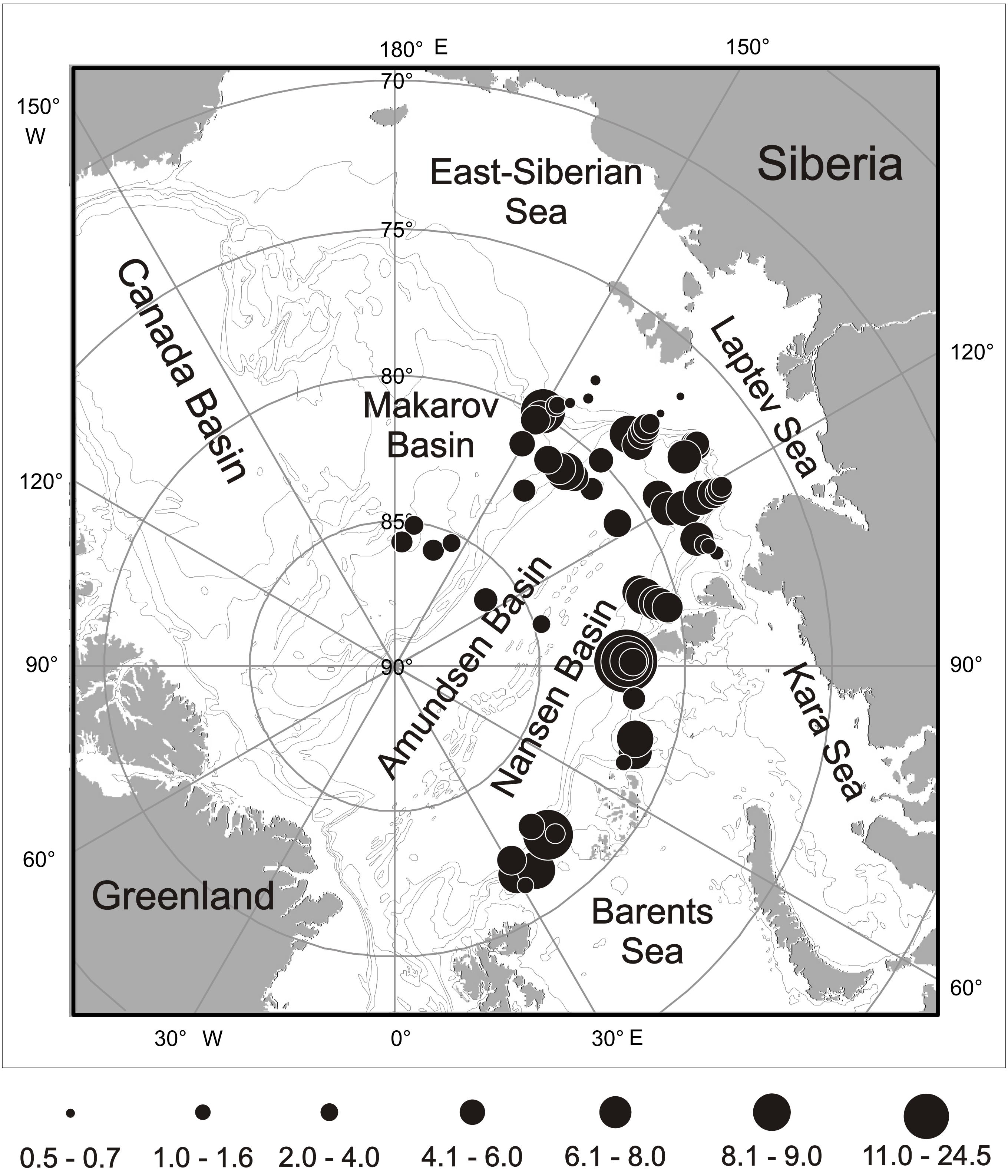
Fig. 12. Distribution of *Metridia longa* biomass in the Arctic Ocean during 3 cruises.

Fig. 13. Distribution of *Calanus finmarchicus* biomass in the Arctic Ocean during 3 cruises.

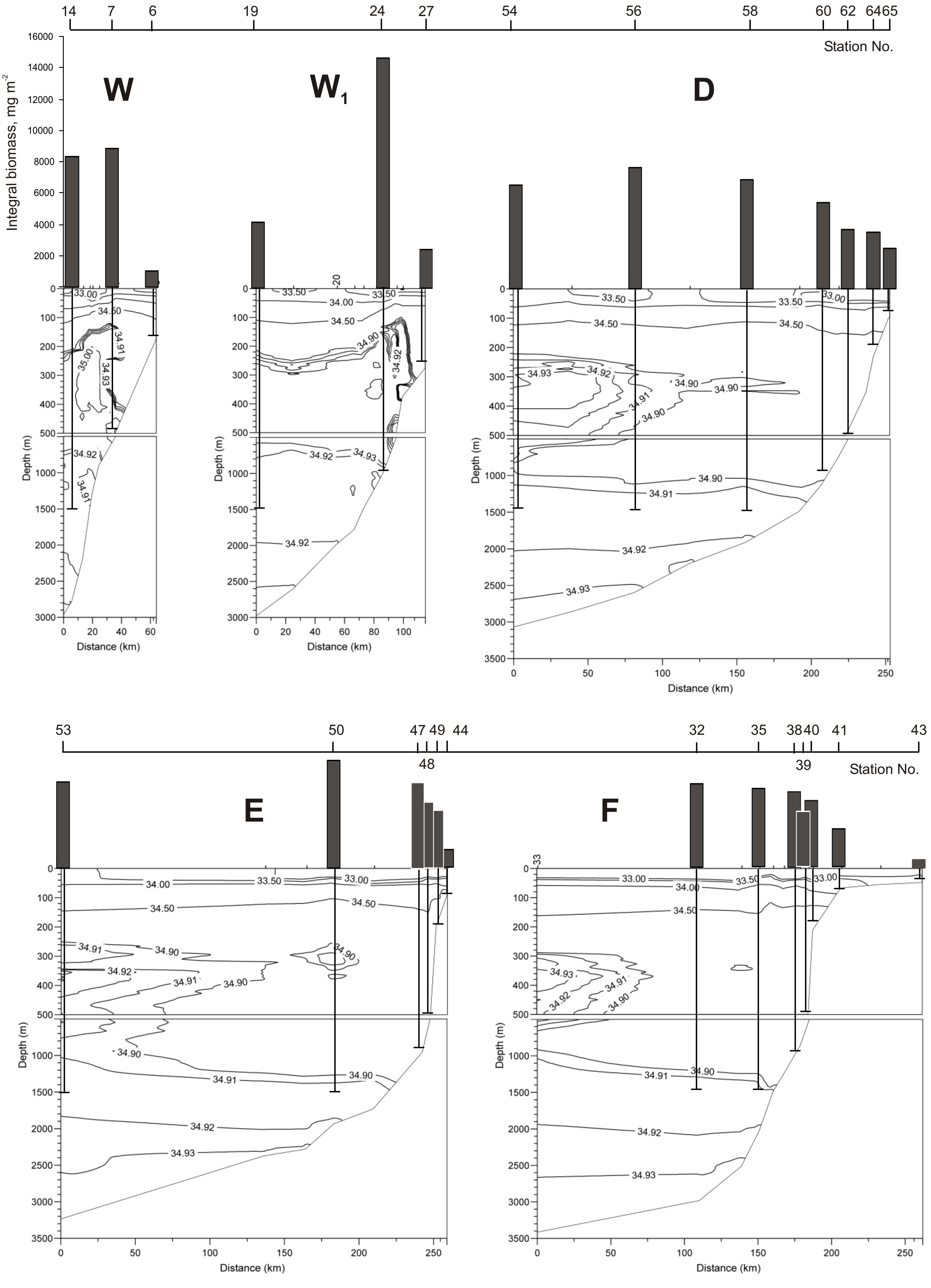
Figure


180° E
150°
70°
150°
W
East-Siberian
Sea
Siberia
75°
Canada
Basin
G
F
Laptev Sea
120°
80°
Makarov
Basin
E
120°
H
D
85°
L
C
K
B
Amundsen Basin
Nansen Basin
90°
90°
90°
A
Kara Sea
60°
W
W1
Greenland
Barents
Sea
60°
30° W
0°
30° E

Figure

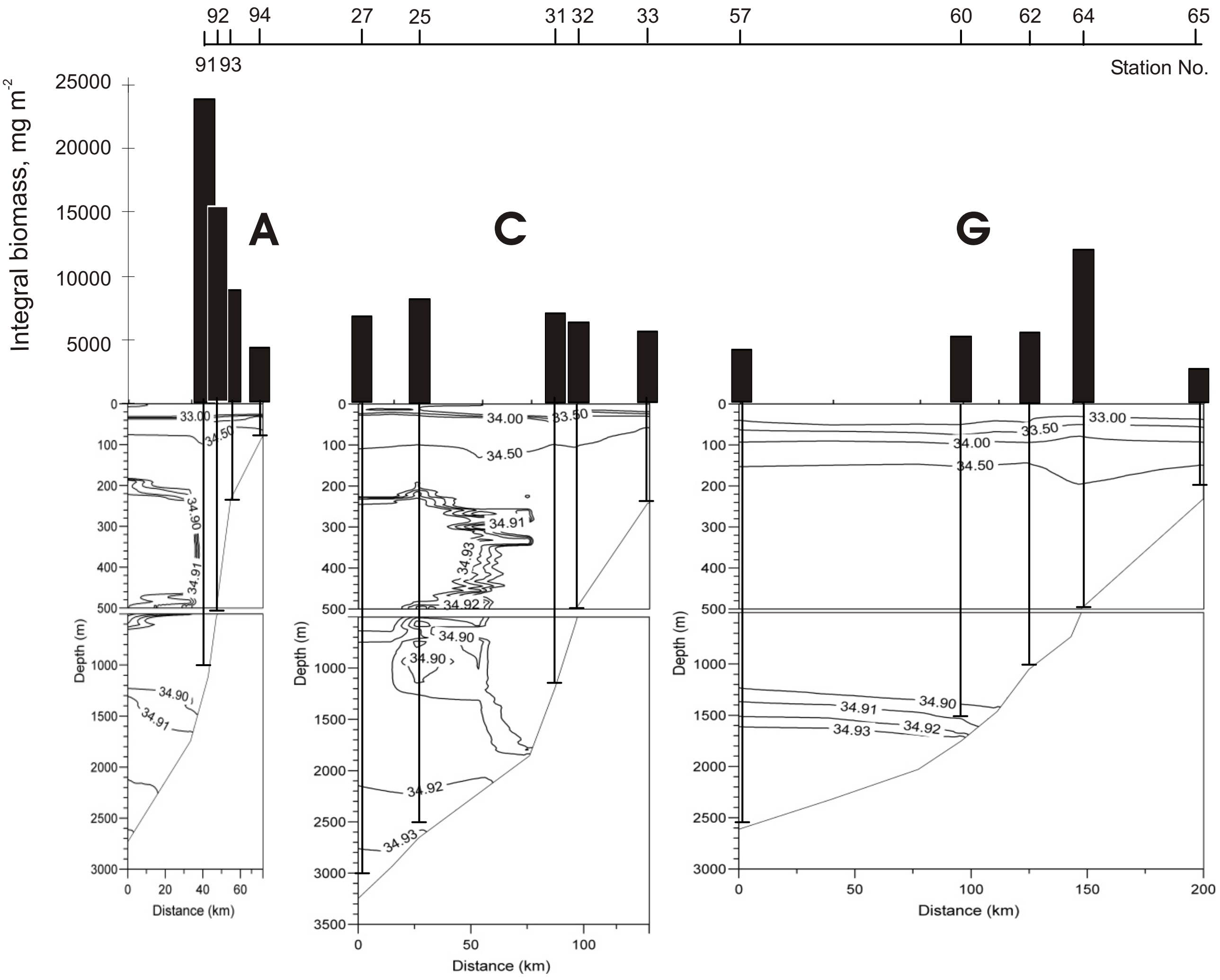

180° E
150°
70°
150° W
East-Siberian Sea
Siberia
75°
Canada Basin
Laptev Sea
120°
80°
Makarov Basin
120°
85°
Amundsen Basin
Nansen Basin
90°
90°
90°
Kara Sea
60°
Greenland
Barents Sea
60°
30° W
0°
30° E
0.5 - 0.7
1.0 - 1.6
2.0 - 4.0
4.1 - 6.0
6.1 - 8.0
8.1 - 9.0
11.0 - 24.5

Figure

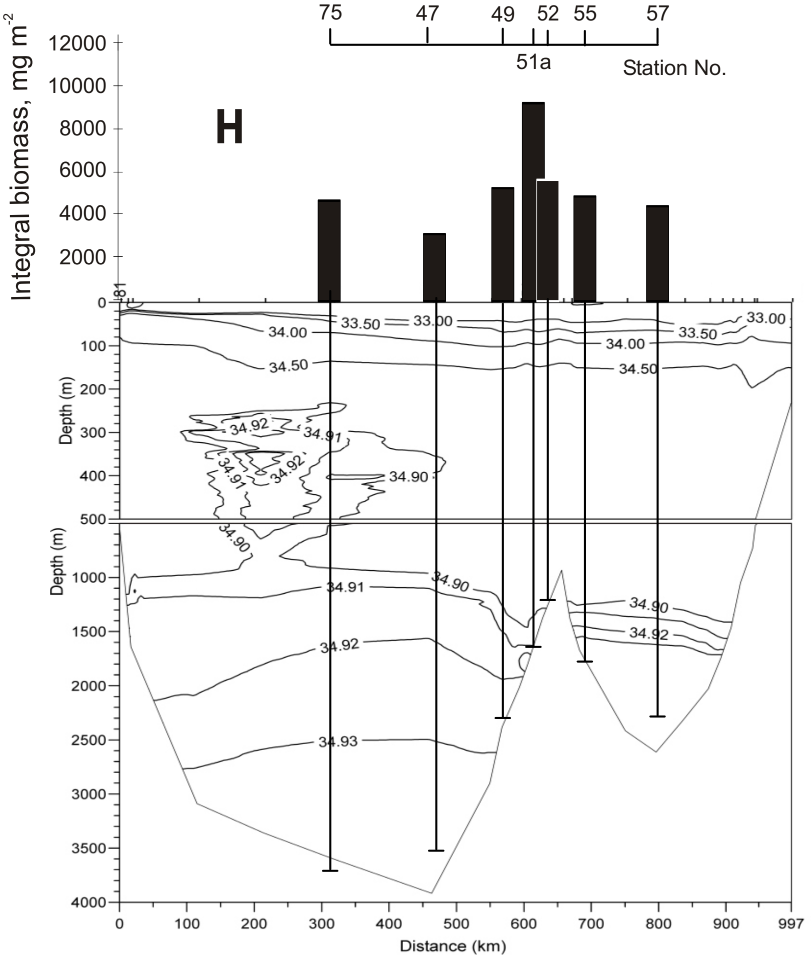


14 7 6 19 24 27 54 56 58 60 62 64 65
Station No.
Integral biomass, mg m-2
16000
14000
12000
10000
8000
6000
4000
2000
0
W
W1
D
Depth (m)
Distance (km)
33.00
33.50
34.00
34.50
34.90
34.91
34.92
34.93
35.00
20
53 50 47 48 49 44 32 35 38 39 40 41 43
E
F
33

Figure

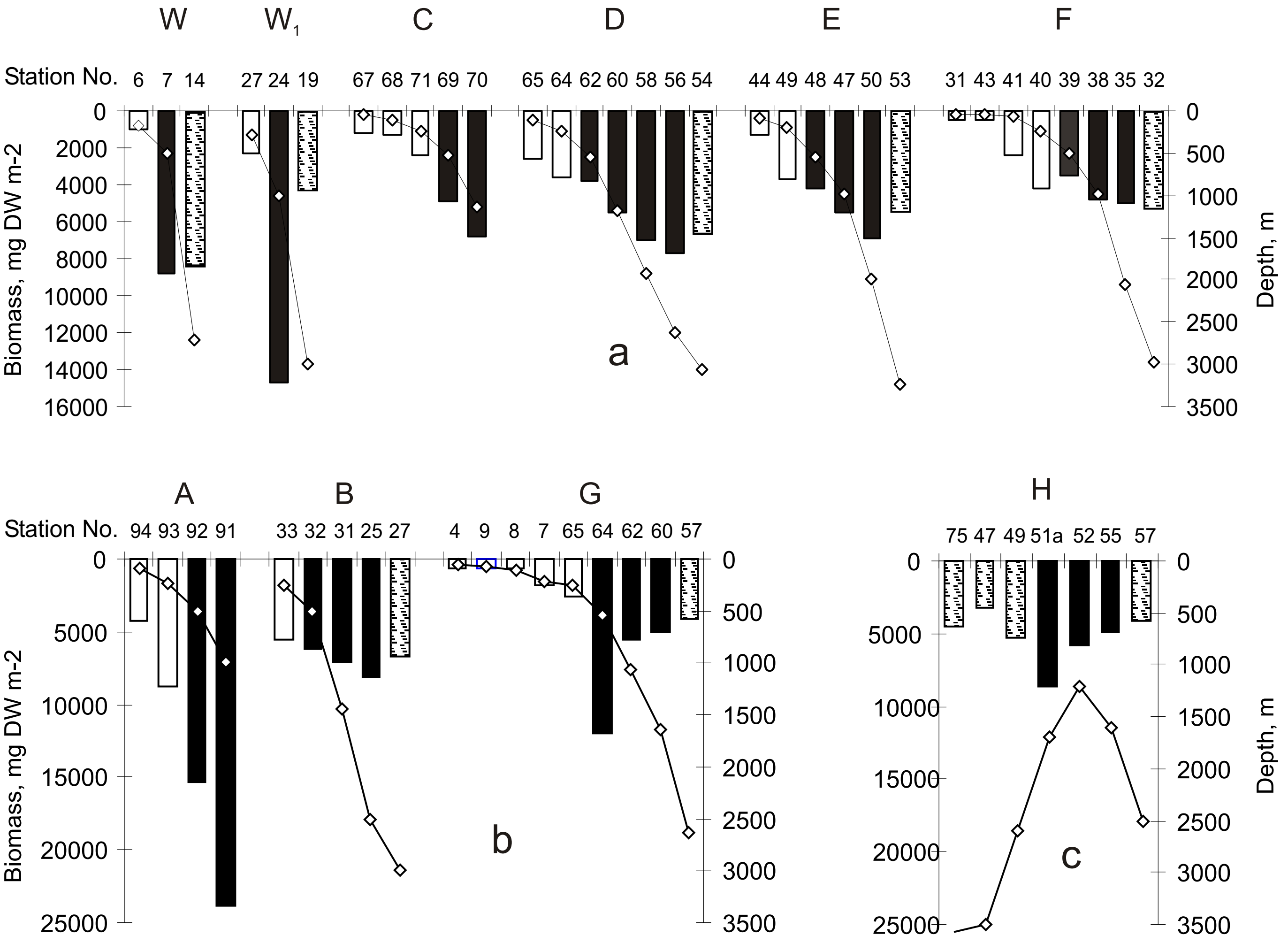


Station No.
91
92
93
94
27
25
31
32
33
57
60
62
64
65
Integral biomass, mg m-2
25000
20000
15000
10000
5000
0
A
C
G
33.00
34.50
34.90
34.91
34.00
33.50
34.93
34.92
34.90
34.91
Depth (m)
100
200
300
400
500
1000
1500
2000
2500
3000
3500
Distance (km)
0
20
40
60
50
100
150
200

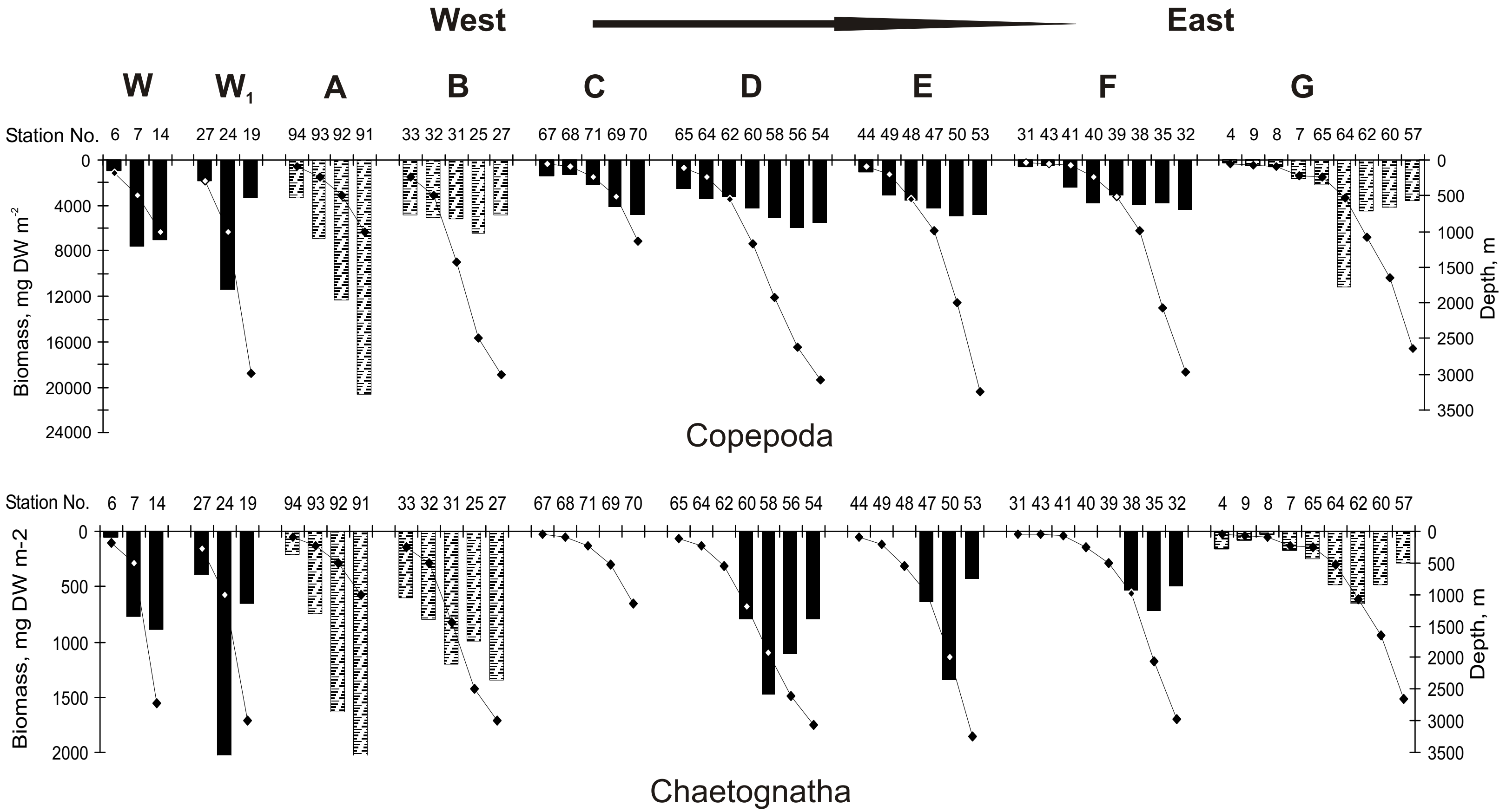


75
47
49
52
55
57
51a
Station No.
Integral biomass, mg m-2
12000
10000
8000
6000
4000
2000
0
H
81
33.50
33.00
34.00
34.50
33.00
33.50
34.00
34.50
34.92
34.91
34.91
34.92
34.90
34.90
34.91
34.90
34.90
34.92
34.92
34.93
Depth (m)
100
200
300
400
500
1000
1500
2000
2500
3000
3500
4000
0
100
200
300
400
500
600
700
800
900
997
Distance (km)

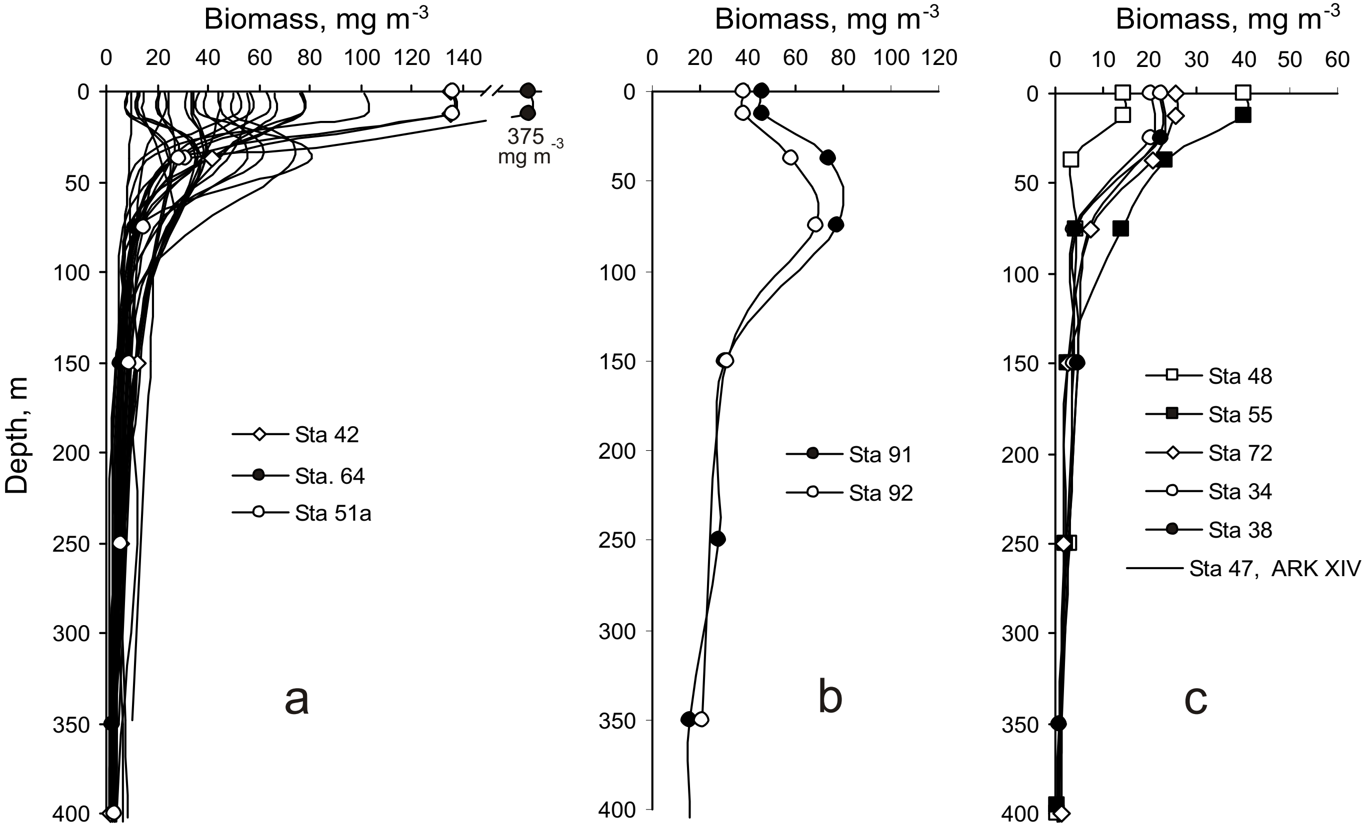
Figure


W
W$_1$
C
D
E
F
Station No.
6 7 14
27 24 19
67 68 71 69 70
65 64 62 60 58 56 54
44 49 48 47 50 53
31 43 41 40 39 38 35 32
Biomass, mg DW m-2
0
2000
4000
6000
8000
10000
12000
14000
16000
Depth, m
0
500
1000
1500
2000
2500
3000
3500
a
A
B
G
Station No.
94 93 92 91
33 32 31 25 27
4 9 8 7 65 64 62 60 57
Biomass, mg DW m-2
0
5000
10000
15000
20000
25000
0
500
1000
1500
2000
2500
3000
3500
b
H
75 47 49 51a 52 55 57
0
5000
10000
15000
20000
25000
0
500
1000
1500
2000
2500
3000
3500
Depth, m
c

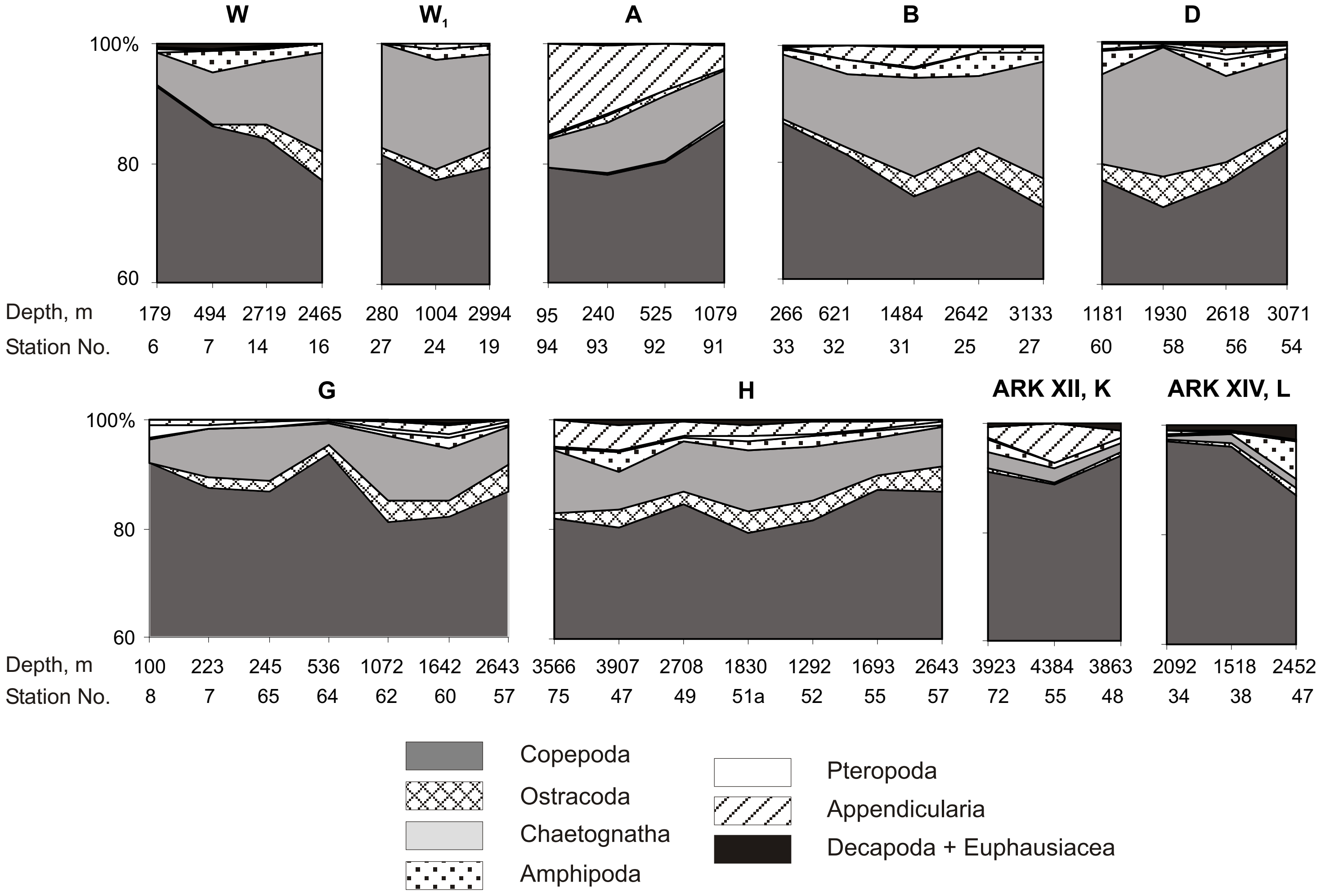
Figure


West
East
W
W1
A
B
C
D
E
F
G
Station No.
6 7 14 27 24 19 94 93 92 91 33 32 31 25 27 67 68 71 69 70 65 64 62 60 58 56 54 44 49 48 47 50 53 31 43 41 40 39 38 35 32 4 9 8 7 65 64 62 60 57
Biomass, mg DW m-2
0
4000
8000
12000
16000
20000
24000
Depth, m
0
500
1000
1500
2000
2500
3000
3500
Copepoda
Station No.
6 7 14 27 24 19 94 93 92 91 33 32 31 25 27 67 68 71 69 70 65 64 62 60 58 56 54 44 49 48 47 50 53 31 43 41 40 39 38 35 32 4 9 8 7 65 64 62 60 57
Biomass, mg DW m-2
0
500
1000
1500
2000
Depth, m
0
500
1000
1500
2000
2500
3000
3500
Chaetognatha

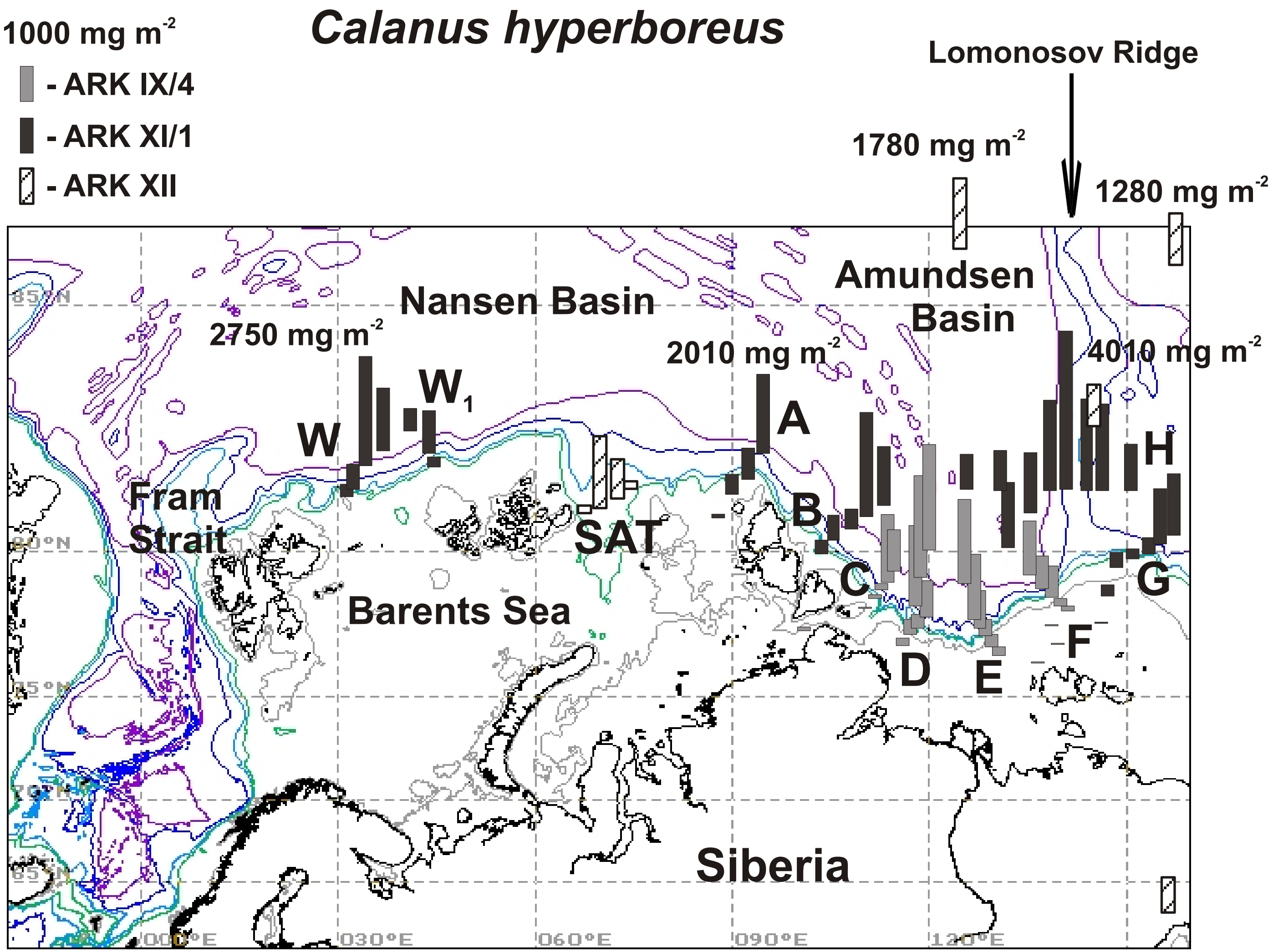
Figure


Biomass, mg m-3
0
20
40
60
80
100
120
140
375 mg m-3
Depth, m
0
50
100
150
200
250
300
350
400
Sta 42
Sta. 64
Sta 51a
a
Biomass, mg m-3
0
20
40
60
80
100
120
Sta 91
Sta 92
b
Biomass, mg m-3
0
10
20
30
40
50
60
Sta 48
Sta 55
Sta 72
Sta 34
Sta 38
Sta 47, ARK XIV
c

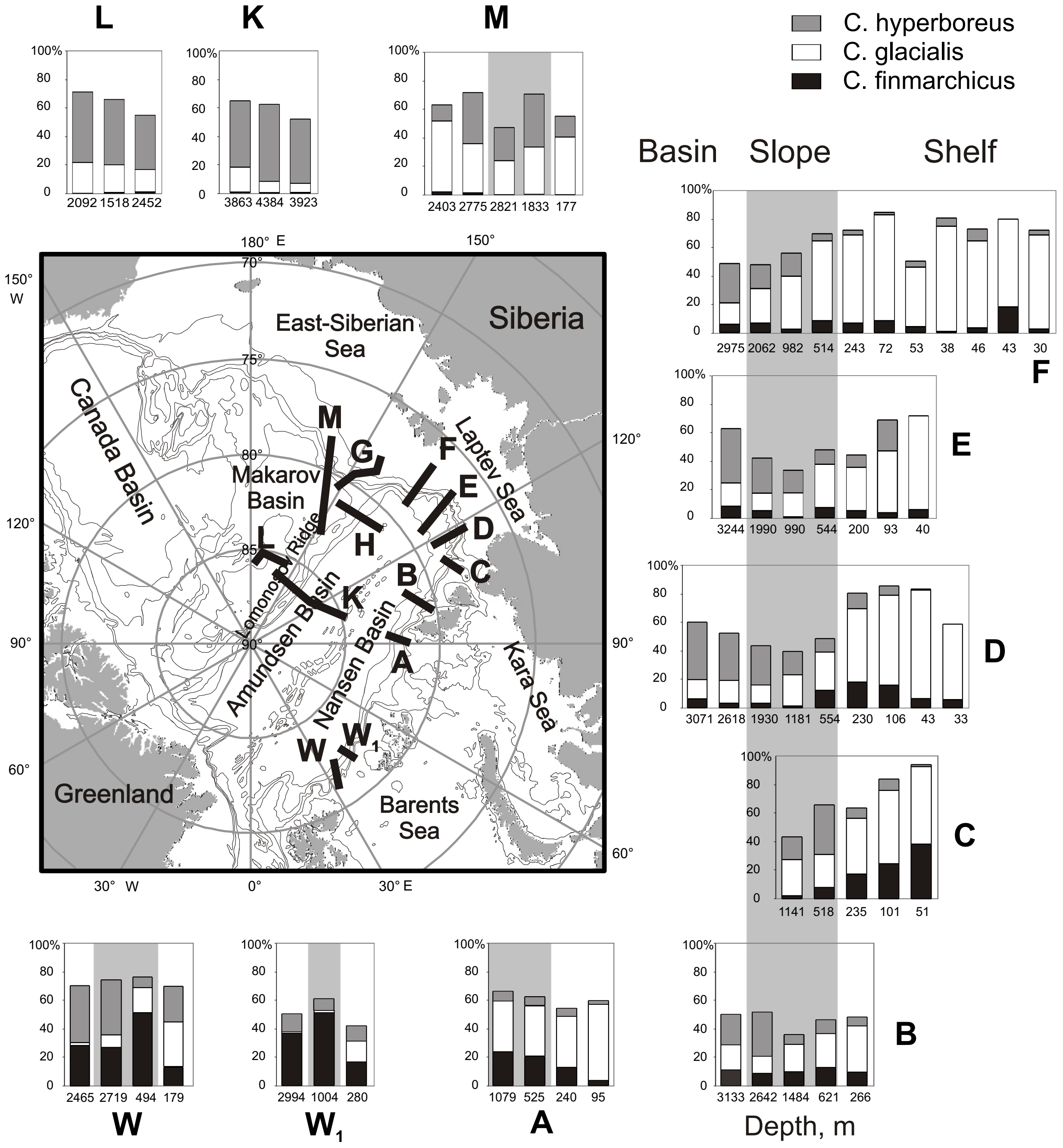
Figure


W
W1
A
B
D
100%
80
60
Depth, m
179 494 2719 2465
280 1004 2994
95 240 525 1079
266 621 1484 2642 3133
1181 1930 2618 3071
Station No.
6 7 14 16
27 24 19
94 93 92 91
33 32 31 25 27
60 58 56 54
G
H
ARK XII, K
ARK XIV, L
100%
80
60
Depth, m
100 223 245 536 1072 1642 2643
3566 3907 2708 1830 1292 1693 2643
3923 4384 3863
2092 1518 2452
Station No.
8 7 65 64 62 60 57
75 47 49 51a 52 55 57
72 55 48
34 38 47
Copepoda
Ostracoda
Chaetognatha
Amphipoda
Pteropoda
Appendicularia
Decapoda + Euphausiacea

Figure

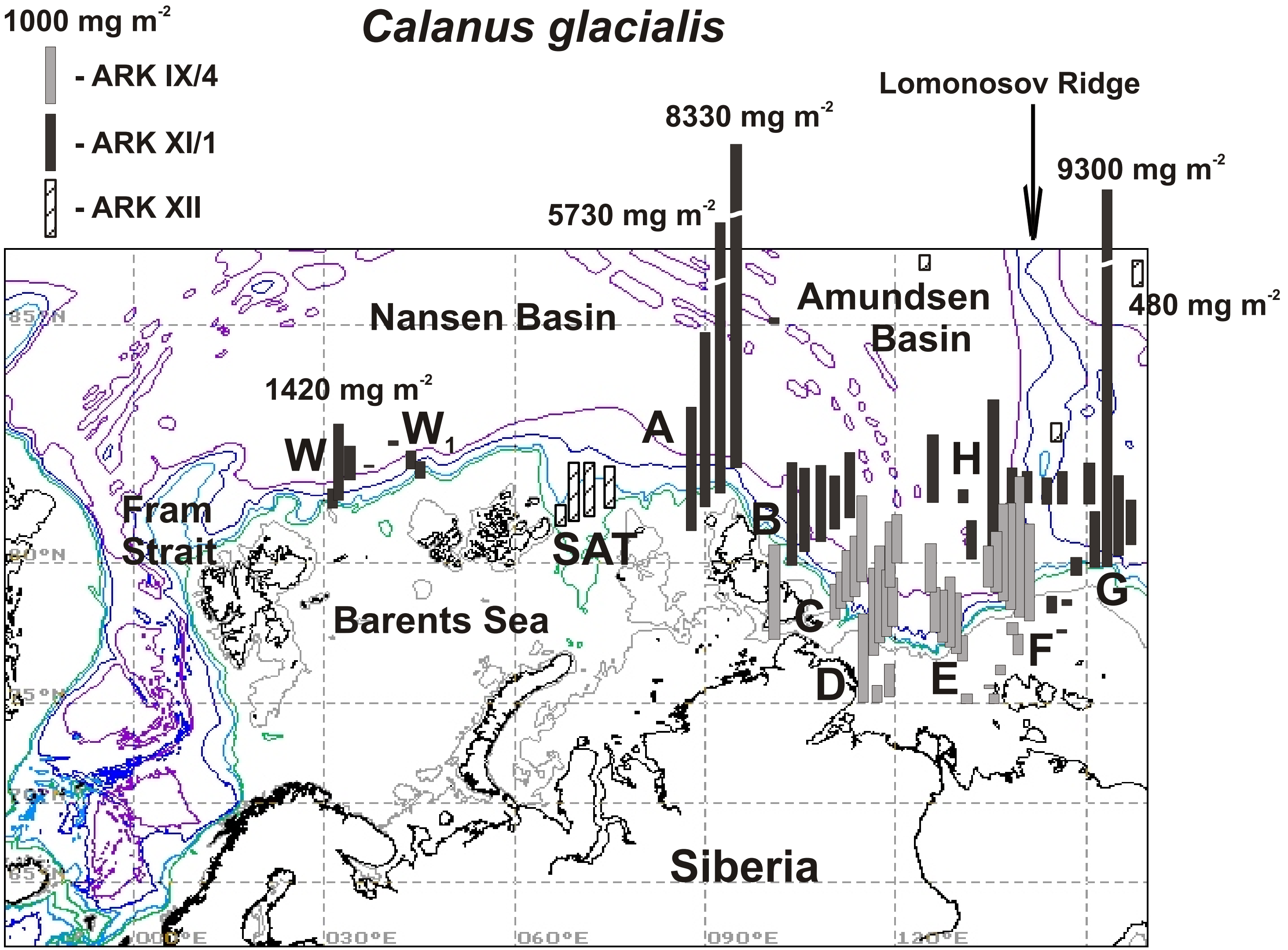

Calanus hyperboreus
1000 mg m-2
- ARK IX/4
- ARK XI/1
- ARK XII
Lomonosov Ridge
1780 mg m-2
1280 mg m-2
Amundsen Basin
Nansen Basin
2750 mg m-2
2010 mg m-2
4010 mg m-2
W
W1
A
B
C
D
E
F
G
H
SAT
Fram Strait
Barents Sea
Siberia
85°N
80°N
75°N
70°N
65°N
000°E
030°E
060°E
090°E
120°E

Figure

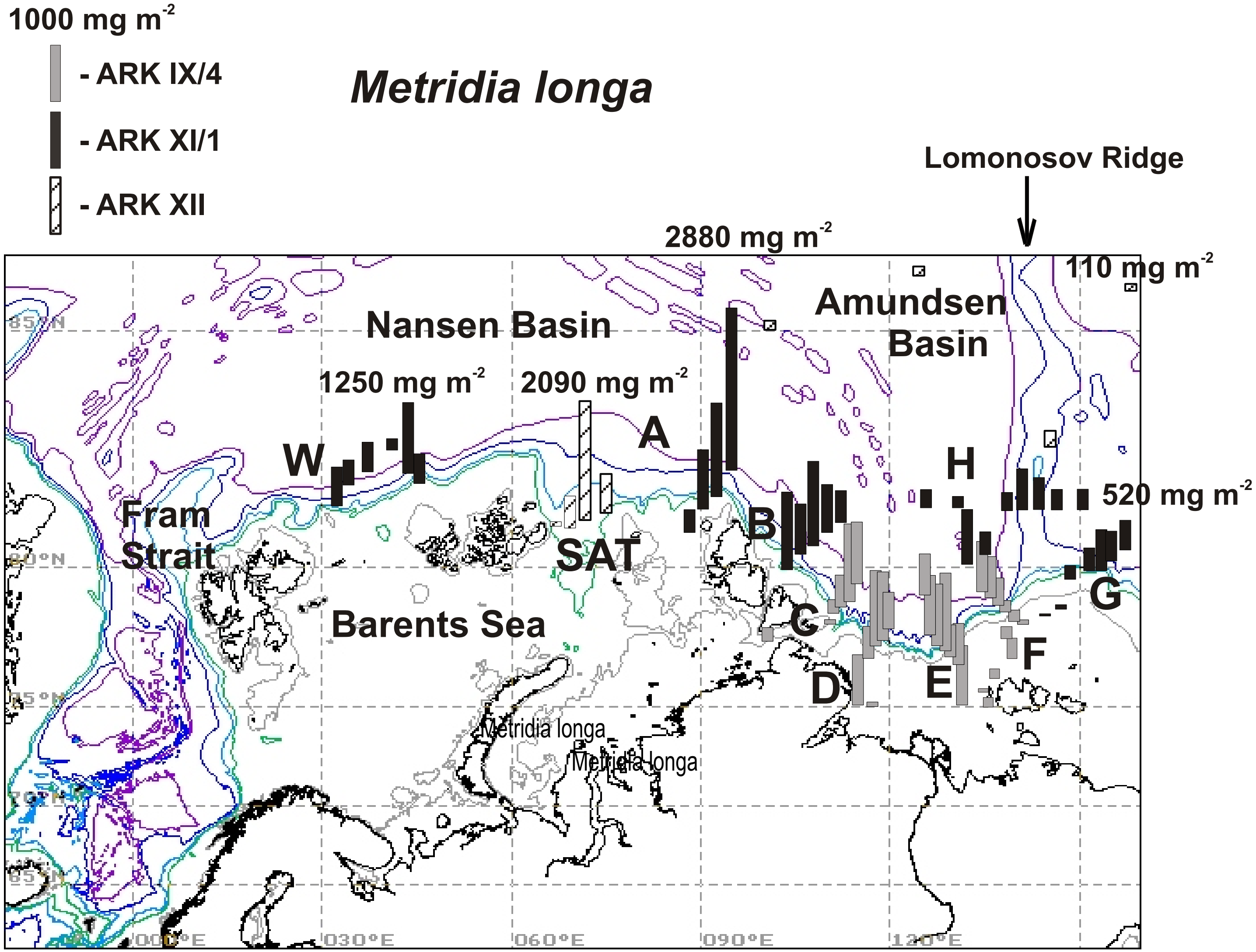


C. hyperboreus
C. glacialis
C. finmarchicus
Basin
Slope
Shelf
L
2092 1518 2452
K
3863 4384 3923
M
2403 2775 2821 1833 177
F
2975 2062 982 514 243 72 53 38 46 43 30
E
3244 1990 990 544 200 93 40
D
3071 2618 1930 1181 554 230 106 43 33
C
1141 518 235 101 51
B
3133 2642 1484 621 266
A
1079 525 240 95
W1
2994 1004 280
W
2465 2719 494 179
Depth, m
100%
80
60
40
20
0
180° E
150°
120°
90°
60°
150° W
120°
90°
60°
30° W
0°
30° E
70°
75°
80°
85°
90°
East-Siberian Sea
Siberia
Canada Basin
Makarov Basin
Lomonosov Ridge
Amundsen Basin
Nansen Basin
Laptev Sea
Kara Sea
Barents Sea
Greenland
M
G
F
E
D
C
B
H
L
K
A
W
W1

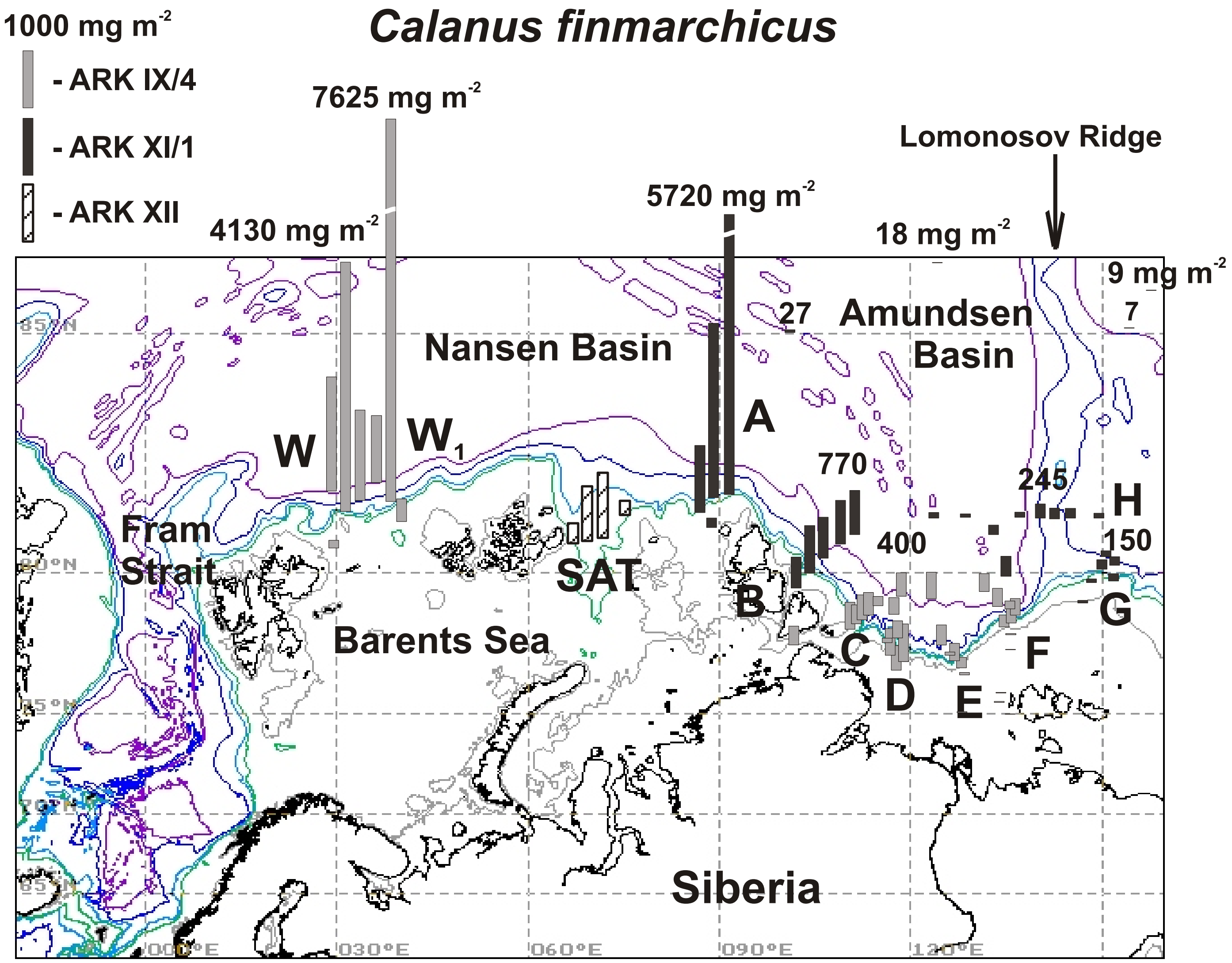
Figure


Calanus glacialis
1000 mg m^{-2}
- ARK IX/4
- ARK XI/1
- ARK XII
8330 mg m^{-2}
5730 mg m^{-2}
Lomonosov Ridge
9300 mg m^{-2}
480 mg m^{-2}
1420 mg m^{-2}
Nansen Basin
Amundsen Basin
W
W$_1$
A
B
C
D
E
F
G
H
SAT
Fram Strait
Barents Sea
Siberia
85°N
80°N
75°N
70°N
65°N
000°E
030°E
060°E
090°E
120°E

Figure


1000 mg m-2
- ARK IX/4
- ARK XI/1
- ARK XII
Metridia longa
Lomonosov Ridge
2880 mg m-2
110 mg m-2
Amundsen Basin
Nansen Basin
1250 mg m-2
2090 mg m-2
A
W
H
520 mg m-2
Fram Strait
B
SAT
C
G
Barents Sea
F
D
E
Metridia longa
Metridia longa
85°N
80°N
75°N
70°N
65°N
000°E
030°E
060°E
090°E
120°E

Figure


Calanus finmarchicus
1000 mg m-2
- ARK IX/4
- ARK XI/1
- ARK XII
7625 mg m-2
4130 mg m-2
5720 mg m-2
18 mg m-2
Lomonosov Ridge
9 mg m-2
7
27
Amundsen Basin
Nansen Basin
A
W
W1
770
245
H
400
150
Fram Strait
SAT
B
G
C
F
Barents Sea
D
E
Siberia
85°N
80°N
75°N
70°N
65°N
000°E
030°E
060°E
090°E
120°E