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Distribution and abundance of pteropods in the western Barents Sea

by

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Abstract

The abundance and horizontal distribution of three pteropod species, *Limacina helicina*, *Limacina retroversa* and *Clione limacina* were examined in the western entrance of the Barents Sea (Polar Front region) in August 2011. Sixteen samples were collected from 8 sampling sites located along a latitudinal transect. The southern part of the study area (south of 73°N) was dominated by *L. retroversa*, while *L. helicina* was mostly observed north of 73°N. Surface water temperature differences between the coldest and the warmest station were around 8°C. The highest density of *L. retroversa* was found in the south, near the Norwegian coast (nearly 52 000 ind. 1000 m^{-3}), while the highest density of *L. helicina* was observed in the region of the Arctic water masses (nearly 13 000 ind. 1000 m^{-3}). The sampled population of pteropods comprised mainly juvenile stages. Redundancy analysis (RDA) of the relationships between environmental factors (mean and surface salinity, mean temperature, sampling depth, chlorophyll concentration) and the population structure showed that mean temperature was the most important factor in the study area, explaining 70.5% of the pteropod community variation.

Key words: Pteropoda, *Clione limacina*, *Limacina* sp., Barents Sea, species size distribution, West Spitsbergen Current

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Introduction

Pteropods are a crucial group of pelagic fauna in all oceans, playing a key role in the trophic relations in food chains of polar and sub-polar regions. They often create swarms and are an important food source for e.g. baleen whales, but also for several species of commercially important fish and seabirds (Conover & Lalli 1972; Larson & Harbison 1989). The highest biodiversity of these organisms was recorded in tropical regions, however, their highest abundance was observed in cooler waters (e.g. van der Spoel 1967; Lalli & Gilmer 1989; Comeau et al. 2009; Howard et al. 2011). Due to their fragile shells and the associated difficulties in their examination, current knowledge about these organisms is still limited. The studied pteropods belong to two orders: thecosomes that form a shell, and gymnosomes that have no shell at the adult stage. Both orders differ in their food preferences, and thus play different roles in the Arctic marine ecosystem (Lalli & Gilmer 1989). Thecosomes mostly feed on phytoplankton, although small zooplankton is also a substantial component of their diet (Bernard et al. 2009). Thecosomes use a large, spherical external mucous web to collect a wide range of different food types e.g. tintinnids, dinoflagellates and diatoms, which is likely a key adaptation allowing them to live as holoplankton (Gilmer & Harbison 1986; 1991). Adult gymnosomes are predators and feed only on thecosomatous pteropods, but juvenile forms feed on phytoplankton and very small suspensions, which results in their aggregations in more fertile coastal waters (Mileykovsky 1970).

There are no data on the abundance and the trophic role of pteropods in the Barents Sea, but their importance in the food web for the Arctic, North Atlantic and Pacific regions is well documented. *Limacina helicina* was first recognized as a common inhabitant of whaling grounds and as an important food source for baleen whales (Phipps 1974). Because of the commercial importance of many marine fishes, there are more records of euthecosomes being eaten by fish than by other types of predators. In the North Atlantic, fish predators of *Limacina* spp. include herring, mackerel (Lebour 1932) and larvae of cod and redfish (Bainbridge & McKay 1968). Furthermore, Hardy (1924) estimated that *Limacina retroversa* contributed about 2.2% to the annual food supply of North Sea herring. Salmon in the North Pacific Ocean consume *L. helicina* (Ito, 1964).

Pteropods are also important for the functioning of the ocean biochemical cycle. Sediment trap studies have shown that pteropods are the major source of the carbonate flux (> 50%) into the ocean's interior in the polar regions. Those pelagic snails make a contribution to the vertical flux of carbon through the production of fecal pellets, mucous flocs and rapid settling of aragonite shells upon their death (Howard et al. 2011). The thecosomes *Limacina helicina* (Phipps) and *Limacina retroversa* (Fleming), and the gymnosome *Clione limacina* (Phipps) are dominant pteropods in the European part of the Arctic and seasonally occur in large numbers there (Kobayashi 1974; Bauerfeind et al. 2014). These organisms are common components of zooplankton communities in the North Atlantic and Arctic, especially in the region of the Svalbard Archipelago and the Barents Sea (Hop et al. 2002; Karnovsky et al. 2003; Walkusz et al. 2009; Weydmann et al. 2013). *Limacina helicina* was also recorded in the central Arctic, in Svalbard waters and the Barents Sea, especially near shelves, in fjords and close to the coast (Gilmer & Harbison 1991). *Limacina retroversa* is known as a sub-polar species and mainly occurs south of 65°N, although is also observed in the Fram Strait and the Barents Sea (Bathmann et al. 1991). Pteropods' shells are also commonly found in sediment traps (e.g. Bauerfeind et al. 2014).

In recent decades, oceans warming and other changes associated with the climate change are among the challenges faced by fragile aquatic organisms such as pteropods in this rapidly changing environment (Mucci 1983; Comeau 2009). According to the forecasts by the Intergovernmental Panel on Climate Change (IPCC 2001; Johannessen et al. 2004), the temperature in the central Arctic environment will increase by about 3-4°C during the next 50 years, which emphasizes the importance of research in the Arctic and subarctic environment. The increasing sea temperature could potentially lead to a decrease in the abundance of cold-water Arctic species that cannot adapt quickly to this challenge, which will ultimately affect the overall Arctic biodiversity (Grebmeier 2012; Bluhm et al. 2009; Weslawski et al. 2000). Moreover, pteropods are reliant on aragonite – saturated habitats for their shell formation, however, laboratory studies on these organisms from the Southern Ocean suggest that pteropod shell dissolution will occur rapidly as polar waters become undersaturated with aragonite (Fabry et al. 2008; Richardson 2008; Bednarsek et al. 2012a,b; Roberts et al. 2014).

The aim of this study was to provide information about summer species abundance, community composition and first size distributions of observed pteropods, and to examine possible environmental preferences (temperature, salinity, chlorophyll concentration) of these animals in the area of the western Barents Sea and the West Spitsbergen Current.

Materials and methods

Study area

The study area is located between the Archipelago of Svalbard and the northern coast of Norway, in the western part of the Barents Sea. According to Reygondeau et al. (2013), this area can extend in August to the Atlantic Subarctic Biogeochemical Province. The region is strongly influenced by the West Spitsbergen Current and the North Cape Current flowing along the Norwegian coast (Loeng 1991). The West Spitsbergen Current (WSC) is a continuation of the Norwegian Atlantic Current and transports warmer and more saline Atlantic water from the Norwegian Sea into the Arctic Ocean (Piechura et al. 2001; Cottier et al. 2005). The area south of Spitsbergen (74°N) (Hisdal 1998) is under the influence of both the West Spitsbergen Current and the coastal South Cape Current that carries cold, less saline Arctic-type water from the northeast Barents Sea to the West Spitsbergen Shelf. These two distinct external water masses are usually separated on the shelf by the Polar Front (Saloranta & Svendsen 2001). In addition, waters from the Norwegian Sea contribute to the environmental conditions in our study area (Loeng et al. 1997; Walczowski et al. 2012) (Fig. 1).

Sampling methods and data analysis

A total of 16 samples were collected horizontally at eight locations with a HydroBios Bongo net (0.6 m aperture diameter, 500 µm mesh size) and a flowmeter attached to the net. The CTD (Conductivity, Temperature, Depth) device (Sea-Bird Electronics, Inc. SBE 911 plus) was deployed to measure temperature, salinity and depth in the study area at each station. The research was conducted between 70°59.997′N 19°53.924′E and 75°42.002′N 17°32.797′E in August 2011 aboard the R/V Oceania, owned by the Institute of Oceanology Polish Academy of Sciences. The horizontal haul duration was 15 minutes at each station with a speed of 1.5 knots, and the average sampling depth was 122 m (Table 1). The collected samples were preserved in 4% borax – buffered formalin solution. The whole collection volume was analyzed for all samples, with the exception of two stations (V31 and V4), which was split, because the specimen abundance was very high.

Shell diameters of shelled species were determined by measuring the shell diagonally from the end of the outer whorl with an ocular micrometer (Nikon SMZ 800). Ontogenetic stages of *Limacina* species were identified based on the classification of Lalli & Wells (1978): veligers < 0.3 mm, juveniles 0.3-4 mm, males 4-5 mm, females > 5 mm for *Limacina helicina* and veligers < 0.3 mm, juveniles 0.3-1 mm, males 1.0-1.2 mm, females > 1.3 mm for *Limacina retroversa*. Gymnosomes were measured from the base of the anterior tentacles to the posterior end of the trunk according to Conover & Lalli (1972). Only juvenile gymnosomes without shells were present in the samples. In addition, ciliary bands were taken into account to define the ontogenetic stage. Adult specimens of *Clione limacina* are separated from the larvae based on the body length (1-15 mm – larvae with ciliary bands and > 15 mm without ciliary bands – adult specimens; Lalli & Gilmer 1989).

The relationship between the abundance of pteropods' ontogenetic stages and the following environmental variables was examined: sampling and station depth, temperature (mean over the sampling depth), and salinity (mean), as well as chlorophyll concentrations in August and the mean from April-August. Chlorophyll data were obtained using MODIS Satellite from the NASA Ocean Color Web with the spatial resolution of 4 × 4 km. Constrained ordination techniques were applied using CANOCO 5 (ter Braak & Šmilauer 2012). To this purpose, we

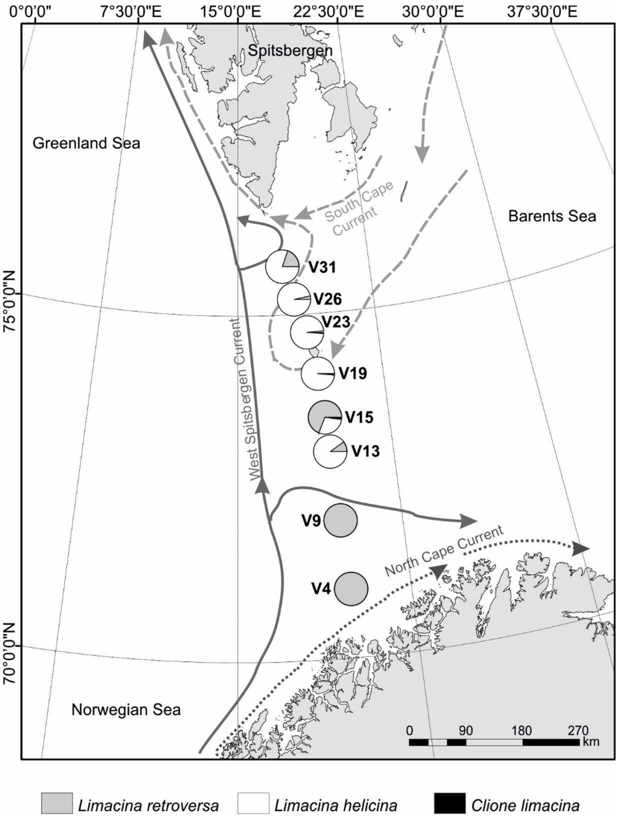

Figure 1

Map of species composition in the study area

Table 1

Sampling details with the specification of sampling stations

Station	Longitude	Latitude	Sampling date	Time	Max haul depth (m)	Filtered water volume (m^3)	Net obliquity (°)	Water mass
V31	75°42.002'N	17°32.797'E	10.08.2011	6:04:00	153	2128	50	Atlantic
V26	74°57.001'N	18°25.047'E	10.08.2011	12:50:00	49	2115	45	Arctic
V23	74°41.972'N	18°39.208'E	10.08.2011	15:30:00	57	1621	45	Arctic
V19	74°09.897'N	19°09.453'E	10.08.2011	20:00:00	49	2381	45	Arctic
V15	73°29.932'N	19°19.694'E	11.08.2011	1:00:00	212	4099	45	Atlantic
V13	73°00.056'N	19°27.466'E	11.08.2011	6:10:00	212	4778	45	Atlantic
V9	71°59.990'N	19°41.012'E	11.08.2011	15:00:00	141	3754	45	Atlantic
V4	70°59.997'N	19°53.924'E	11.08.2011	20:00:00	106	4246	45	Atlantic

*Net obliquity = line obliquity of the towing net

used redundancy analysis (RDA) following the square root transformation of the abundance data. The environmental variables were ranked according to their quantitative importance by interactive forward selection, based on the Monte Carlo permutation test (ter Braak & Prentice 1988). Permutation test parameters were set as a hierarchical design, with stations defined as spilt plots to avoid pseudoreplications of environmental data, which had been collected once at a given station.

Results

Hydrological conditions

A clear pycnocline was present at almost all stations, being most pronounced at stations V4 and V9, located closest to the Norwegian coast, where temperature of surface water reached positive values (from +8°C to +11°C). Stations V23 and V31 were the only part of the study area where the typical thermocline was not observed. The thermocline usually occurred at a depth of ~ 60 m, indicating significant vertical differences in temperature and thereby in densities of water masses (Fig. 2). Based on the surface water temperature, we noticed the presence of water masses of different origin in the study area: stations V19 and V23 were cold (Arctic water masses), while stations V4, V9, V13, V15 were relatively warm and under the influence of Atlantic water masses (Table 1) (Sakshaug et al. 1994; Walczowski et al. 2012).

Chlorophyll concentration data were also obtained for the period from April to August and the mean value for these months was also calculated (Table 3).

Species abundance and composition

The total number of sampled specimens was 143 178 ind. 1000 m^{-3}. *Limacina helicina* was most abundant in the water mixing zone (station V26), with 13 764 ind. 1000 m^{-3}. The southern parts of the study area were dominated by *L. retroversa* individuals, while *L. helicina* was the most frequently occurring species in the northern parts of this region (Fig. 1). *L. retroversa* specimens dominated in the region around station V4 (26% of all measured individuals) close to the Norwegian coast, with counts of 55 293 ind. 1000 m^{-3}. The gymnosome *Clione limacina* was also recorded in the largest concentration around station V4, with 356 ind. 1000 m^{-3} (33% of all measured individuals). The smallest concentration of Pteropoda species was observed in the northernmost station V31, with only

Table 2

Ranges of *Limacina helicina*, *Limacina retroversa* and *Clione limacina* densities (ind. 1000 m^{-3}) at sampling stations

Station	*Limacina helicina*	*Limacina retroversa*	*Clione limacina*
	ind. 1000 m^{-3}		
V31	177	44	-
V26	12584	446	-
V23	1317	26	15
V19	1632	2	22
V15	56	134	4
V13	1213	136	1
V9	-	1640	4
V4	44	51826	267

Table 3

Chlorophyll concentration (mg m^{-3}) in the study area

Station	Chlorophyll (mg m^{-3})					
	April	May	June	July	August	Mean
V31	7.183	8.297	0.842	1.688	0.696	3.741
V26	1.205	0.941	2.324	0.532	0.977	1.196
V23	0.480	0.885	2.004	0.392	0.765	0.905
V19	1.126	1.990	1.862	NoData	0.684	1.416
V15	1.365	3.570	2.068	0.488	0.539	1.606
V13	2.270	9.077	8.564	NoData	0.643	5.138
V9	0.783	0.951	0.962	0.269	0.467	0.687
V4	0.477	0.934	1.242	0.880	0.528	0.812

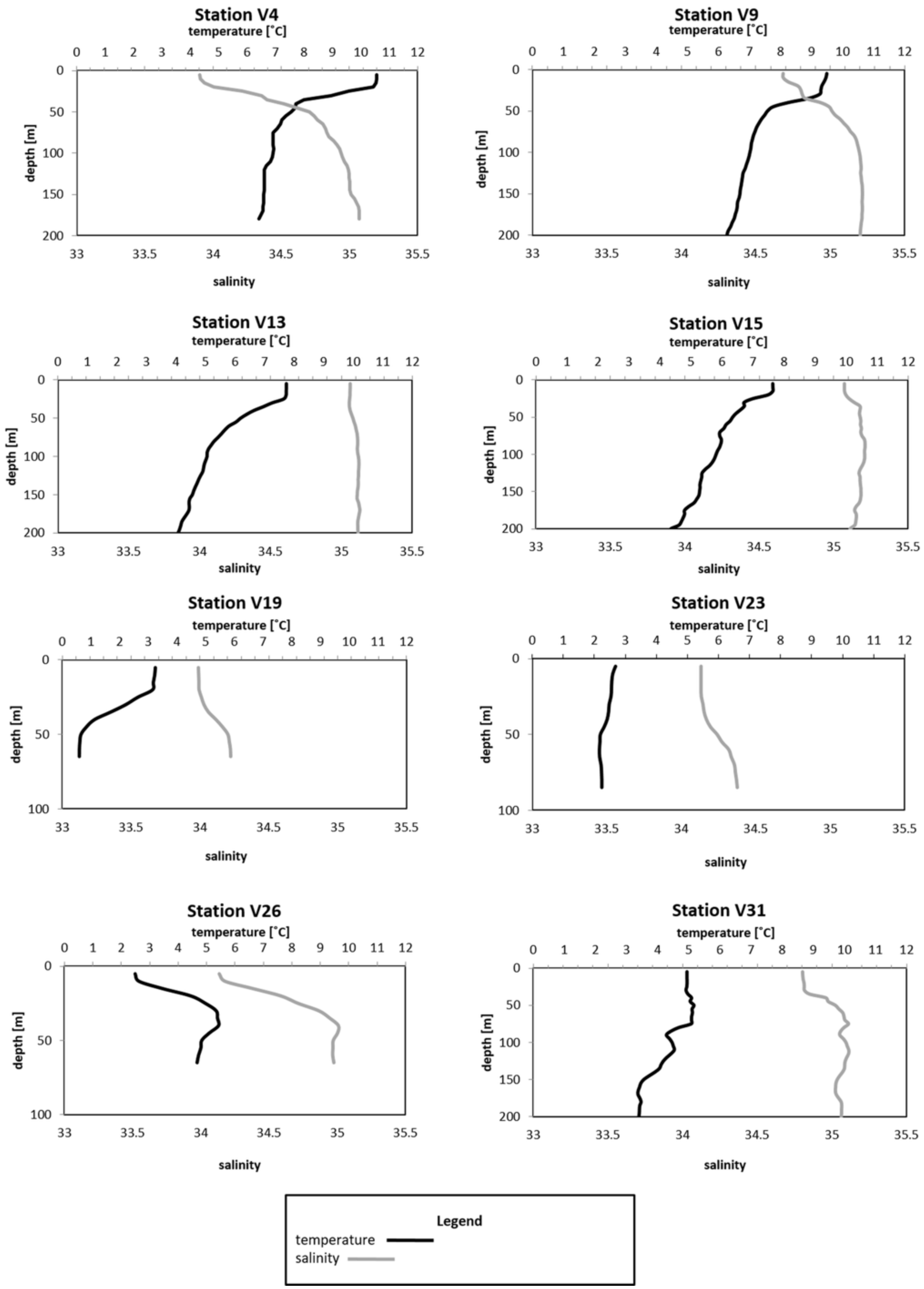

Figure 2

Variability in temperature and salinity of surface water at the sampling stations along the studied transect (the value of 200 m was used for the deeper stations and 100 m was used for the shallower stations)

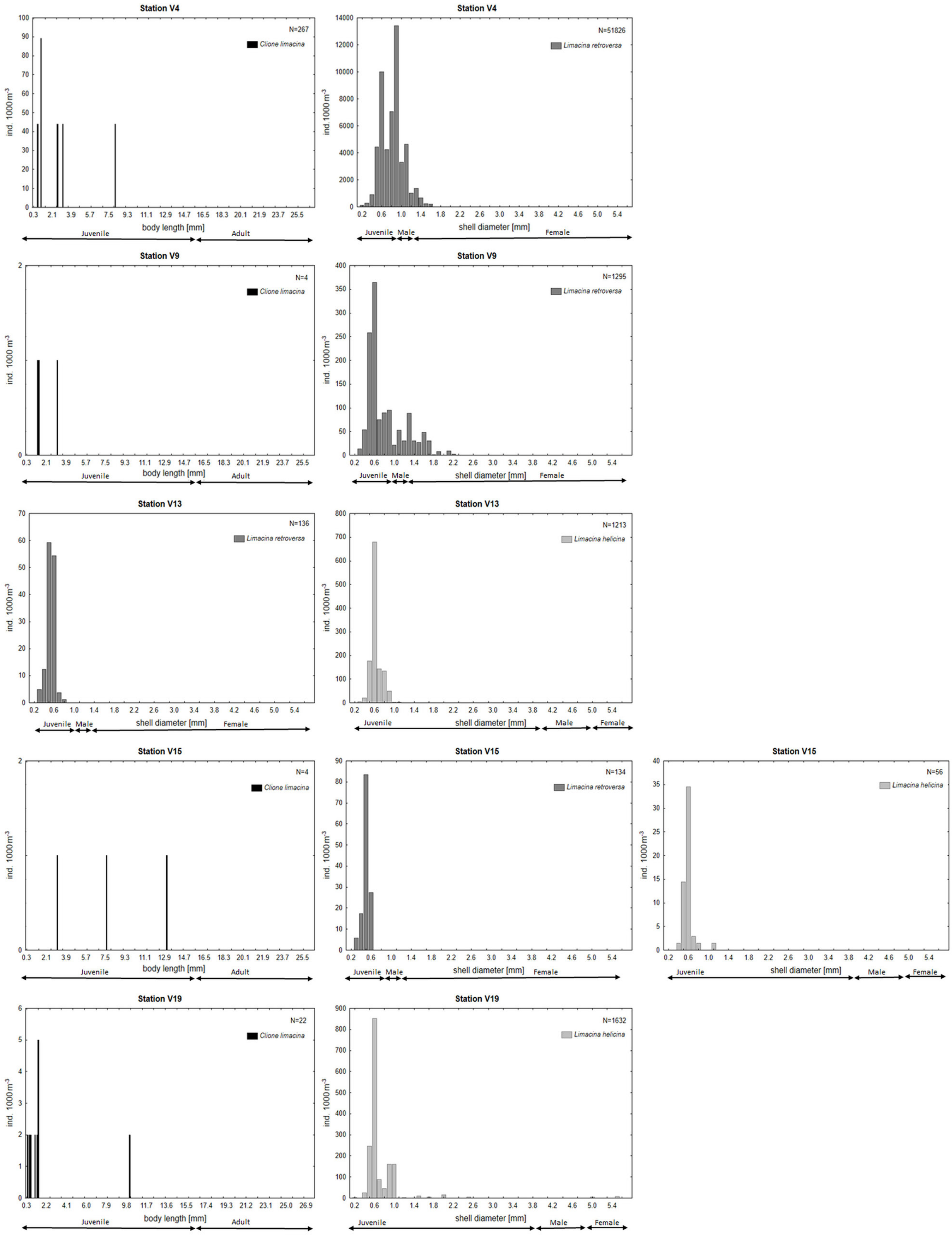

Figure 3 (continued on next page)

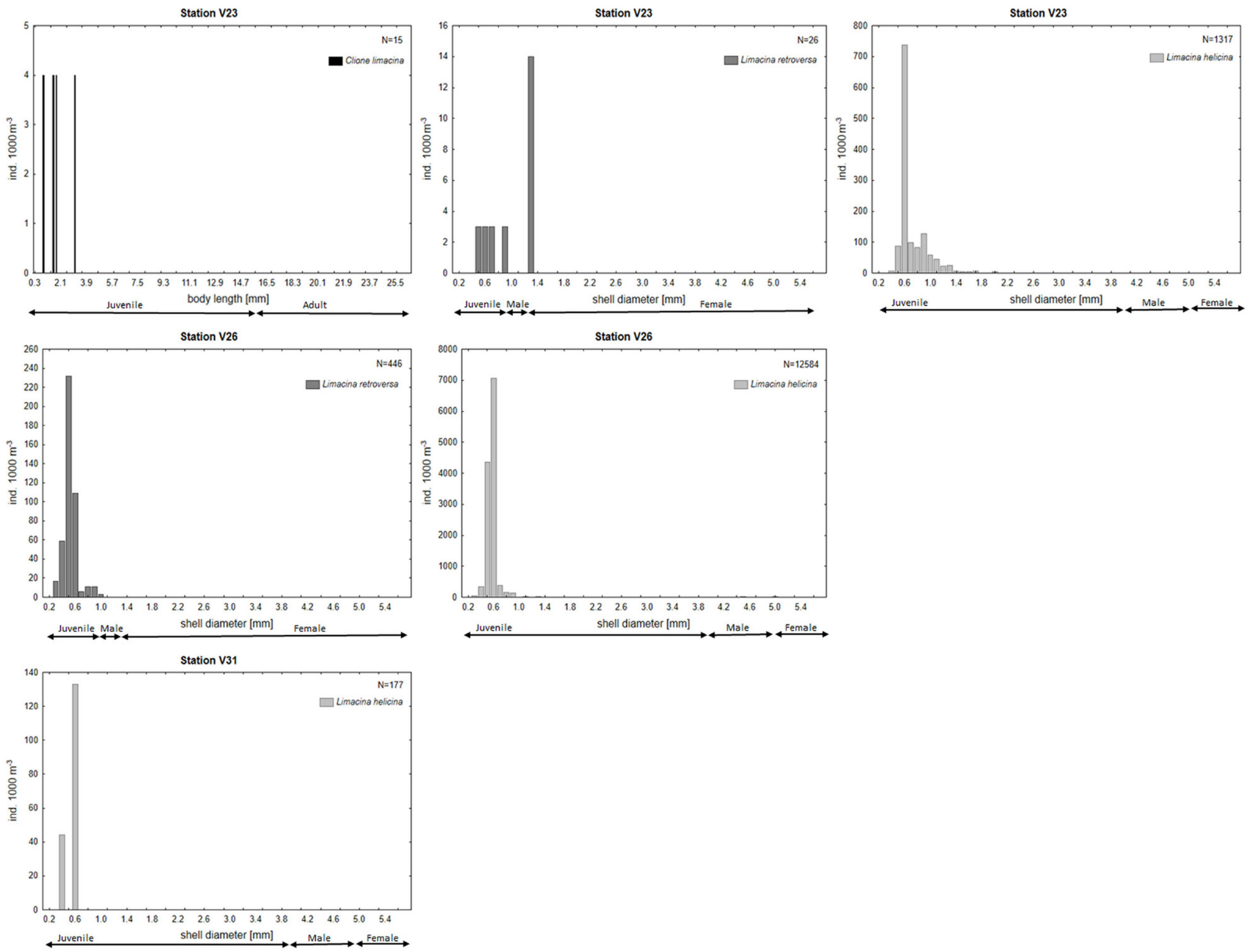

Figure 3 (continued)

Size distributions for pteropods in the study area in August 2011 (some species were omitted due to the absence in the station area or due to the low abundance of specimens)

89 ind. 1000 m^{-3} of both *L. retroversa* and *L. helicina* (Table 2, Fig. 1). Changes in the species composition were observed along the North-South gradient and the number of *L. helicina* specimens increased gradually (Fig. 1), while *L. retroversa* individuals were less numerous. *L. helicina* dominated at the remaining stations in the northern, cooler part of the basin (Fig. 1). The size distribution of pteropod taxa varied along the transect. The size distribution for *L. retroversa* and *C. limacina* at the northernmost station V4 had two peaks, with the main peak at 0.9 mm size and almost all specimens classified as juvenile forms (Fig. 3). Specimens of *L. retroversa* from station V9 were mainly identified as juvenile forms, most abundant at 0.6 mm size but males and females also occurred. Further north (station V13 northward), adults of either species were not found with the exception of stations V19 and V26, where a few adult specimens of *L. helicina* and *C. limacina* were observed (Fig. 3).

The RDA analysis demonstrated a significant relationship between variation in the abundance of pteropods and the environment – 84.3% (pseudo-F = 36.9, p = 0.0078). According to the interactive forward selection, only two of the tested environmental variables were significant: mean temperature (pseudo-F = 33.4, p = 0.0048), which explained 70.5% of the species variability, and chlorophyll concentrations in August (pseudo-F = 11.4, p = 0.0209), explaining 13.8%. The abundance of *Limacina retroversa* corresponded to the increasing mean temperature eigenvector, while *L. helicina* abundance peaks in higher chlorophyll concentrations (Fig. 4). The abundance of *C. limacina* was not correlated with any of the above eigenvectors.

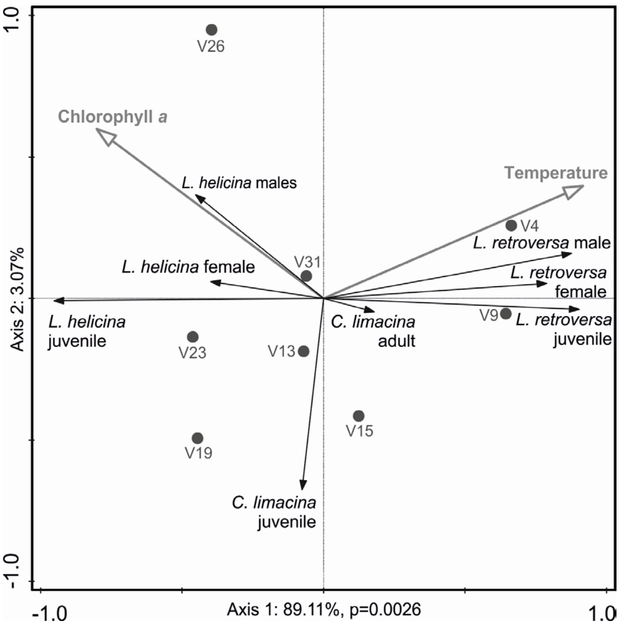

Figure 4

Redundancy analysis (RDA) ordination plot showing the relationship between the abundance of Pteropoda ontogenetic stages and the significant environmental variables, with the proportion of total variability explained by the first two canonical axes. Note that males and females are identified based on respective sizes.

Discussion

Sampling took place at the end of the Arctic summer when the primary production in this region is usually still quite high and starts to decrease. The most abundant stages of the recorded species were juveniles, while the older individuals occurred very rarely at the surveyed stations. *Limacina retroversa* was represented also by males and females in the most southern part of the study area (Fig. 3). This may lead to the conclusion that it was a very intensive breeding season for these organisms, thus confirming the earlier results. According to Lalli and Gilmer (1989), late summer and early autumn is the most intensive period of breeding. The abundance of pteropods in the study area is correlated with certain water masses and their properties. The species of thecosomes and gymnosomes observed in the western Barents Sea are typical for this region (van der Spoel 1967; 1976; Bauerfeind et al. 2014; Busch et al. 2015), and our results confirm the existence of relatively distinct distribution ranges of different species. These differences in the species composition and abundance of pteropods were related mainly to mean temperatures in the study area (Fig. 4). The optimal temperature for *L. helicina* ranges from -0.4°C to +4.0°C, while *L. retroversa* tolerates temperatures from the wider range, from +2.0°C to +16°C (van der Spoel 1967) and has been reported to be strongly correlated with the increasing temperatures in the West Spitsbergen Current, based on the redundancy analysis (Weydmann et al. 2014). Our findings agree with the optimal temperature ranges reported by Van der Spoel (1967; 1976). In the area of the Polar Front, we observed the disappearance of taxa associated with warmer waters, which were gradually replaced by cold-water species. The species *L. retroversa* was more abundant in the southern parts, while the density of *L. helicina* was very high in the northern, colder part of the study area. The disappearance of *L. retroversa* accompanied by an increased number of *L. helicina* was particularly observed in a transitional zone between different water masses near the stations (V13 and V15) (Fig. 1). This trend was closely associated with the temperature requirements of the analyzed species.

One of the stations (V31) in the north was significantly different from the others because it was located within the range of the eastern branch of the West Spitsbergen Current (Walczowski et al. 2013), which resulted in a high proportion of *L. retroversa* individuals in the vicinity of the station (Fig. 3; Table 2). Gymnosomes were represented by a single species – *C. limacina*, which is described as a widely distributed Arctic and Atlantic Arctic-boreal, circumpolar species (Mileykovsky 1970). It spawns in all types of water masses where it commonly occurs and its most intensive spawning is correlated with the spring/summer period and peak abundance of phytoplankton species that serve as food for veliger and polytrochous larvae. After this period, the intensity of spawning declines sharply in local populations, but is continued with lower intensity during the autumn/winter season. The species is basically continuously breeding (Mileykovsky 1970). This taxon was observed only in the southern parts of the transect, below the Polar Front Zone. The individuals of *C. limacina* are highly specialized predators, so their presence should be strongly dependent on the occurrence of their main prey – thecosome pteropods (Lalli & Gilmer 1989). Interestingly, no correlation was found in this study between *C. limacina* and any of the *Limacina* species (Fig. 4) and between any of the abiotic factors.

Previous studies have shown that *Limacina helicina* spawned during July and August in the vicinity of the Svalbard Archipelago, while subarctic-boreal *L. retroversa* spawned in more southern regions such as e.g. Lofoten Basin in September and was advected by the Norwegian Atlantic Current and the West Spitsbergen Current into the North Atlantic (Bathmann et al. 1991; Gannefors et al. 2005). The body size of juvenile *L. helicina* individuals doubled in winter – from October to May and in late summer, their growth rates decreased (Kobayashi 1974). The author also recorded juvenile pteropods in August, confirming the results presented in this paper (Fig. 3). The youngest specimens of *L. helicina* collected (0.2 to 0.4 mm) were found concentrated in the upper 50 m. The larger sizes dispersed during the summer months and tended to concentrate in the top 150 m during the rest of the year (Kobayashi 1974). This author reported that in the central Arctic Ocean, *L. helicina* has 1.5-2-year life cycle. This estimation was supported by the observations of spawning time: the major spawning period started in May when the population reached the average size of 0.8 mm, and veligers grew to 0.8 mm by May of the following year and the maximum size of ~ 3 mm was reached in November. After this, large specimens disappeared in March of the following year. The life cycle of this organism may be longer if *L. helicina* in the subarctic waters reaches the size of 8 mm (Kobayashi 1974). On the other hand, other authors presumed that the life cycle of *L. helicina* is shorter than observed by Kobayashi. In Kongsfjorden, Svalbard, *L. helicina* developed a reproductive strategy with peak spawning in late summer and autumn. The lipid-rich veligers develop and overwinter as a juvenile form in autumn (Gannefors et al. 2005). They suggest a one-year life cycle for this organism in the coastal region around Svalbard based on the high presence of lipids in veligers and its depletion in females, but also disappearance of larger specimens in late September.

As evidenced by the previous studies, the life cycle of *Limacina retroversa* is slightly different. In the Gulf of Maine, the highest spawning activity was recorded in May (Hsiao 1939), however, the reproduction continued also in autumn. Studies of the South Atlantic population of *L. retroversa* also indicated that major spawning pulses occurred in spring and late summer (Dadon & Cidre 1992). Based on its apparent life span of about 6 months, it is assumed that most likely there is more than one generation per year in the Gulf of Maine and in the Southern Atlantic region (Thabet et al. 2015).

During our research conducted at the end of August, individuals of *Limacina helicina* were mostly juvenile at all surveyed stations and correlated with increasing chlorophyll concentrations, while *L. retroversa* was represented by all stages and juveniles were most abundant, which seems to confirm the previous studies. Based on the previous analysis as well as our data, it is highly likely that the life span of pteropods is also region dependent.

Limacina helicina is a stenothermic species with temperature limits that are 2-4 times narrower compared to its sibling species *L. retroversa* from a lower latitude and warmer water (Cheung et al. 2009). The increasing temperature resulted in the reduction in the low-latitude range of this polar species (Fabry et al. 2008). This situation may lead to a high local extinction of the species and, at the same time, an increase in the abundance of organisms from warmer water regions (Cheung et al. 2009), for example *L. retroversa.* Bauerfeind et al. (2014) reported that the number of this species significantly increased in the Fram Strait during the study carried out between 2000 and 2009, and the dominance of *L. helicina* (adapted to cold waters) was replaced by the dominance of subarctic-boreal *L. retroversa* after 2005/6, i.e. when the strong influx of Atlantic waters into the Arctic took place. Moreover, Busch et al. (2015) confirmed that polar *L. helicina* from the Fram Strait was outnumbered by *L. retroversa* in the whole study area during the 4-year study, and the authors observed a trend toward the dominance of this subarctic species. This may imply ecological disturbances that potentially disrupt the ecosystem functioning (Doney et al. 2012).

The results presented in this study confirm the ability of pteropods to form large clusters especially in the coastal, surface waters and in water mixing zones (Table 1). In the polar regions, Pteropoda have previously been recorded in high densities. For example, in Kongsfjorden, i.e. one of the fjords on the western coast of Spitsbergen, and in the area of the West Spitsbergen Current, *Limacina helicina* occurred in large concentrations, while *L. retroversa* and *C. limacina* were clearly less abundant (Węsławski et al. 2000; Weydmann et al. 2014). Pteropods are also very numerous in the Subantarctic region where the highest abundance of *L. helicina antarctica* was recorded in the Scotia Sea and on the South Georgia shelf (Bednarsek et al. 2012b). In the Southwest Atlantic, the gymnosome pteropod *Spongiobranchaea australis* was the most frequent along the continental slope, while *Clione limacina antarctica* has its maximum density along the shelf (45°31'S-61°31'W) in association with swarms of *L. helicina* (Dadon et al. 1998).

In conclusion, we found that water temperature was the most significant abiotic factor, defined by the prevailing water masses that largely determine the distribution of pteropods. It is also a well-known fact that the species' reproduction cycle is closely related to seasonal changes in food availability and to species biology and ecology, hence the importance of chlorophyll concentration for the variability of pteropods. The duration of this research was too short to conclude possible changes in the distribution patterns of pteropod species. However, this paper is a good introduction to further consideration about the effect of abiotic factors on the ecology of these planktonic organisms. Our research gives also the first insight into the detailed size distribution and abundance of pteropods in the specific region of the western Barents Sea, created by the Atlantic and Arctic waters.

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