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Pelagic coelenterates in the Atlantic sector of the Arctic Ocean – species diversity and distribution as water mass indicators

by

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Abstract

Marginal seas of the Arctic Ocean are well recognized as one of the richest ecosystems in the world's ocean, being at the same time the most vulnerable to climate change. Such vulnerability affects the distribution of water masses, thus influences the pelagic species dispersal and local diversity.

For certain reasons some plankton species can be used as indicators of water mass distribution. Although the use of copepods and chaetognaths in such a manner is well documented, still little is known about the potential of pelagic Coelenterata as possible indicator species; they are still poorly investigated in this part of the Arctic Ocean. Therefore, a survey of these gelatinous animals was conducted in a transect between the Norwegian, Greenland, and Barents Seas in summer 2011. A total of 21 taxa were encountered and the most abundant was *Aglantha digitale*. Species distribution coupled with hydrological analysis of the investigated area enabled us to establish the water mass indicator taxa. Therefore, *A. digitale* was connected with the Atlantic Water Mass, while *Bougainvillia superciliaris* and large numbers of ctenophores were correlated with the Arctic Water Mass.

The results presented herein may provide the basis for developing new tools to analyze changes in the Arctic Ocean.

Key words: gelatinous zooplankton, water mass indicators, Arctic Ocean, Coelenterata

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Introduction

Despite recent increases in the number of studies in the field of Coelenterata, the current state of knowledge about this unique group of animals, especially in polar regions, is rather scarce (Pagès 1997; Panasiuk-Chodnicka et al. 2014; Ronowicz et al. 2015). Studies of zooplankton species composition and their distribution in the Arctic Ocean started approximately a century ago during Nansen's "Fram" expedition (Nansen 1902). Although one might think that one century provides valuable background knowledge, the general approach to taxonomical identification should be considered. Usually, only well known, widely distributed species were identified, while others (e.g. Polychaeta, Siphonophora, Ctenophora, Ostracoda) were disregarded due to the assumption that low abundance reflects low importance (Kosobokova et al. 2011). Only recently it has been found that in susceptible areas of the world's ocean, large and gelatinous zooplankton represent a conspicuous component of the plankton, principally during the productive summer months (Brodeur et al. 2002). Moreover, coelenterates can represent approximately 25% of the zooplankton species richness (Bluhm et al. 2011a; Sirenko et al. 2014).

The trophic position of gelatinous taxa is relatively well studied (Pagès et al. 1996; Purcell et al. 2010). For example, Kosobokova & Hopcroft (2010) have noticed that in spite of having biomass far lower than the pelagic crustaceans, gelatinous zooplankton can represent one of the main predators of the Arctic pelagic food web. However, in understanding the functioning of the Arctic Ocean ecosystem, not just those virtually apex predators are important. Many unique, multispecies communities, common in polar regions, affect the cohesion and equilibrium of gelatinous taxa. For instance, one should recognize sympagic (ice-associated) organisms, like ice-edge algae, which can contribute as much as 50% of the total primary production. The existence of such communities rely on a seasonal retreat of sea ice, which enhances plankton activity (Bluhm et al. 2011a). During this 'ice bloom season', herbivorous zooplankton exhibit survivor-like behavior, engaging in the accumulation of lipid reserves, indispensable for the winter season (Pasternak et al. 2001). Their higher fat content makes them attractive as a food resource for higher taxa. This explains the interest of predatory zooplankton in the continuous availability of such herbivorous species.

For the purpose of the presented study, only knowledge of the plankton in the Arctic is required. For the sake of improving the scientific awareness, however, a short note on the diversity of the Arctic Ocean is given. Species richness is represented by nearly 8000 eukaryotic species. Current estimation of taxonomic inventories revealed "... close to 2000 phytoplankton taxa, over 1000 ice-associated protists, greater than 50 ice-associated metazoans, 350 multicellular zooplankton species, over 4500 benthic protozoans and invertebrates, at least 160 macroalgae, 243 fishes, 64 seabirds, and 16 marine mammals" (Bluhm et al. 2011a). The endemism rate in the organisms listed above is comparatively large, e.g. 15-20% for zooplankton (Kosobokova et al. 2011).

Regardless of its obvious significance for ecosystem homeostasis, the marine organism diversity in the Arctic Ocean has also an economic value. Rich marine biological resources are plentiful in polar regions. In this particular area, the most important fish populations are cod, herring, capelin, and blue whiting, whilst other fished organisms include deep water shrimp (*Pandalus borealis*) and squids (OSPAR 2000). "In recent decades, major facets of the human footprint – resulting primarily from the use of natural resources – are altering marine communities around the globe" (Bluhm et al. 2011b). Although this human impact factor is relevant, the most influential factor is definitely the climate change. Predicted increases in temperatures of the Northern Hemisphere continue, and as Drinkwater (2006) stated – it may change the migration pattern of "warmer water" species from the Atlantic Ocean, causing their earlier arrivals and later departures from the Arctic Ocean. So far it has significantly extended the geographical range of many temperate marine species, and many cold-adapted species have declined (Beaugrand et al. 2002). This northward movement of Atlantic/boreal species is conceivably enhancing the local zooplankton diversity (Błachowiak-Samołyk et al. 2007). If this proceeds, the planktonic detection of global climate change in high latitude areas will become feasible for the first time (ACIA 2005).

The concept of using pelagic animals as water mass indicators, and therefore as global change indicators, has been evolving since the Challenger Expedition (1872-76). Even then Agassiz (1883) used particular pelagic Coelenterates (*Porpita*, *Velella*, and *Physalia*) to identify the course of the Gulf Stream. Those initial studies, although they did once include Coelenterates, were generally focused on Chaetognatha, since they were better recognized and more thoroughly studied (Meek 1928; Russell 1935). In the 1960s and the 1970s, only a few studies of plankton species distribution in relation to water masses were conducted (Colebrook et al. 1961; Russell 1973; Colebrook 1978). With the beginning of the 1980s, attempts to develop constant linkages between plankton and water masses were emerging more frequently, resulting in e.g. the paper by Węsławski et al. (1983) on South Spitsbergen Sea currents and their biological descriptors.

This research provides a unique set of data on the diversity and distribution of planktonic coelenterates in the Atlantic Sector of the Arctic Ocean. We aimed to explain the differences in the species dispersal with hydrological data in order to link the water masses with certain gelatinous taxa, which helped to forecast the possible progression of boreal organisms into the Arctic and further changes in the species inventory.

Materials and methods

Study area

This study was conducted on the transect between mainland Norway and the island of Spitsbergen which comprises the border line of three seas: Greenland, Norwegian, and Barents (Fig. 1). In Figure 1, sampling sites were marked with differentiation of water mass impact.

Further analysis revealed that in this relatively shallow shelf area with an average depth of 230 m,

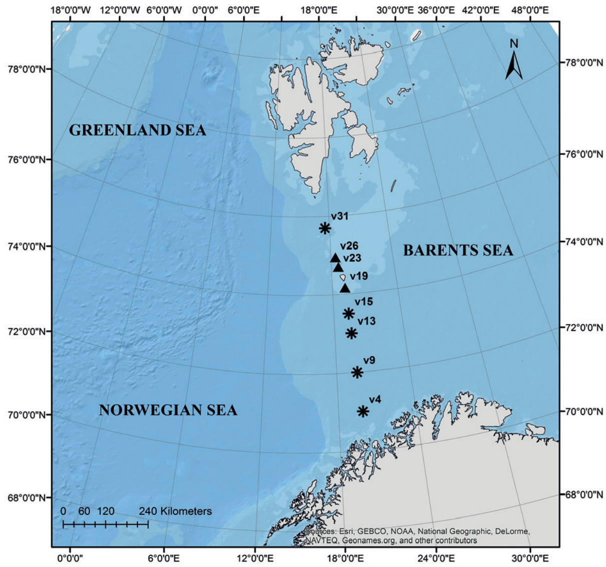

Figure 1

Distribution of sampling sites where triangles mark the Arctic Water Mass influence, and asterisks stand for the Atlantic Water Mass (Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and other contributors)

four main separate water masses exist (Loeng 1991). Their distribution affects the entire environment, explaining why this region is thought to be the most productive in the world's ocean (Arashkevich et al. 2002). Some main features of those water masses were put together (Table 1) to facilitate their further comparison.

The characteristics of water masses presented here were used for the description of hydrological conditions in the study area. Later, they were combined with Coelenterates species distribution to compile a list of water mass indicators.

For the sake of facilitating further reasoning, a map of currents' pattern, mesoscale gyres and polar front formation (Fig. 2), has been prepared according to Hop et al. (2006).

Table 1

Water masses in the Barents Sea with temperature, salinity, and other information (modified after Loeng 1991, Wiborg 1955)

Name	Acronym	Temperature (ºC)	Salinity (PSU)	Other descriptors
Coastal Water	CW	>2.0	<37.7	only one stratified throughout year
North Atlantic Water	AtW	>3.0	>35.0	characterized by *Calanus hyperboreus*
Arctic Water	ArW	<0.0	34.3-34.8	characterized by *Calanus finmarchicus*
Polar Front Water	PFW	-0.5-2.0	34.8-35.0	mixture of AtW and ArW

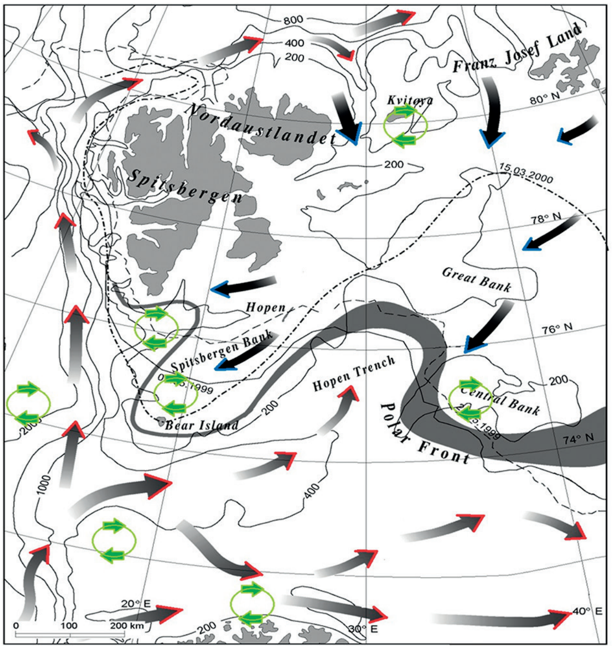

Figure 2

Hydrological map of the sampling area with identified water masses (darker arrow – ArW, brighter arrow – AtW), mesoscale gyres (circular arrows), and polar fronts (identified by name) (modified after Mitcheslon-Jacob 1993; Hop et al. 2006)

In Figure 2, depths are marked in addition to the previously listed hydrological features. Such data confirms the existence of a transitional channel southward from Bear Island. This steep pass is streamlining the transition of AtW into the Central Barents Basin. Moreover, information on mesoscale gyres and polar front formation in this figure is also relevant, because of their possible enhancing effect on the biodiversity and production (Owen 1981).

Sampling methods

Samples for this study were taken during a cruise in the summer of 2011 aboard S/Y Oceania (property of the Institute of Oceanology of the Polish Academy of Sciences). Collection was conducted using a Bongo (500 μm) net with a mounted flowmeter. Each sampling was associated with carrying a CTD probe for water mass detection. Detailed description of sampling, including precise depth strata, trawling velocity etc. is in the supplementary material (Online Resource 1). Samples were immediately preserved in 4% borax-buffered formalin/seawater solution for later processing. Laboratory analysis was conducted under a stereomicroscope where all coelenterates were identified and counted. In the case of Siphonophora, only nectophore numbers are presented, as there is no existing formula to estimate the number of colonies based on swimming zooids (Hosia & Bamstedt 2008). Later calculations of frequency and the number of individuals per cubic meter were performed with formulas presented by Harris et al. (2000).

Statistical analysis

The Kruskal-Wallis test was applied to all the results to test their interdependence, using Statistica v.10. Other analyses were conducted using PRIMER v.5 software (Clarke & Gorley 2001), including Principal Component Analysis (PCA), Multidimensional Scaling (MDS), and Similarity Percentages (SIMPER) (Clarke 1993; Clarke & Gorley 2001; Hopcroft et al. 2010). In order to include all taxa, even those occurring in a minority (at least 3%), the Bray-Curtis similarity matrix between sites with square root transformation was calculated (Hopcroft et al. 2010). Also Spearman's correlation coefficient was calculated to determine correlations between Coelenterata diversity/distribution and physical characteristics of the water (Węsławski et al. 1983).

Results

Hydrological conditions

Three separate water masses were detected in the study area: the Arctic Water Mass (ArW), the Atlantic Water Mass (AtW), and Coastal Waters (CW) (Fig. 3, 4). ArW was encountered at sites V19, V23, and V26, as identified by its relatively low temperatures and more pronounced salinity stratification than in AtW. CW, on the contrary, was stratified throughout all depths, both in temperature and in salinity. The presence of eddies should be noted here, since their influence was detected at sampling sites V4 and V31. Formation of the Polar Front Water – an isopycnal mixture of ArW and AtW – should also be recognized as an important element influencing the Barents Sea ecosystem. In this study, such information cannot be directly inferred as frequency of CTD recordings

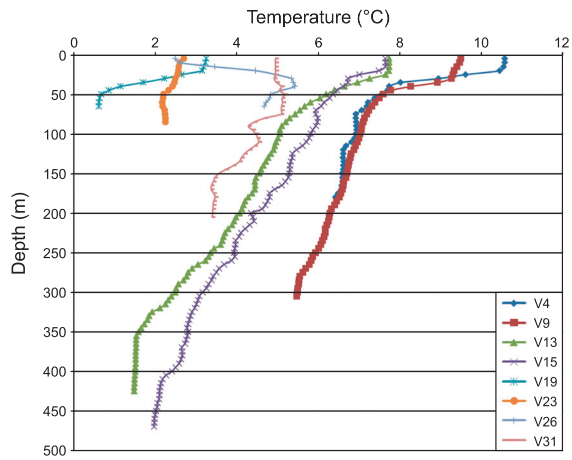

Figure 3

Temperature in relation to the depth at each site

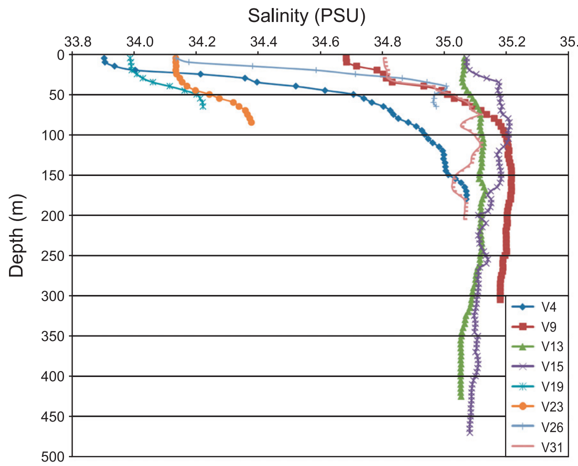

Figure 4

Salinity in relation to the depth at each site

was too limited for such an accuracy in describing the water mass composition.

Species composition and abundance

In the study area, a total of 21 taxa were encountered. In Table 2, their maximum abundance and frequencies were listed. The largest number of individuals per cubic meter was recorded for *Aglantha digitale*. Other frequently encountered medusa were *Euphysa flammea* and *Bougainvillia superciliaris*, with the distribution of the latter highly correlated with water masses (see further considerations). Amongst ctenophores, the largest number of individuals was determined for *Beroe cucumis*, although due to relatively small sizes (below 1 cm) and not particularly good preservation techniques, most comb jellies were unidentifiable.

Spearman's correlation coefficient revealed the influence of hydrological parameters on the biodiversity of Coelenterata and the number of individuals per cubic meter (Table 3).

Although the correlation has been confirmed, one should recognize differences in the strength of the presented relations. From the perspective of statistical significance, the relationships between the number of species and individuals per cubic meter, and salinity can be disregarded.

Table 2

List of taxa recorded in the investigated area

Taxa	Max abundance (ind. m^{-3})	Freq. (ind. sample^{-1})
Beroe cucumis	1.09	0.11
Ctenophora undet.	27.28	3.70
Aeginopsis laurenti	0.83	0.06
Aglantha digitale	771.52	95.67
Bougainvillia superciliaris	11.48	1.40
Catablema vesicarium	3.34	0.21
Euphysa flammea	11.6	1.37
Euphysa aurata	1.66	0.17
Halitholus cirratus	3.59	0.31
Halopsis ocellata	0.17	0.01
Hybocodon prolifer	1.65	0.09
Leuckartiara octona	0.83	0.05
Mitrocomella polydiademata	0.72	0.04
Pentachogon haeckeli	0.34	0.02
Proboscidactyla flavicirrata	0.17	0.01
Ptychogena hyperborea	1.35	0.08
Rathkea octopunctata	3.59	0.47
Tiaropsis multicirrata	1.66	0.17
Hydromedusae undet.	4.23	1.15
Physophora hydrostatica (nect.)	2.69	0.17
Siphonophora (nect.) undet.	40.92	3.45

Table 3

Spearman's correlation coefficient between hydrological parameters and biodiversity or the number of specimens

Parameters		Spearman's correlation coefficient
Number of species	temperature	-0.667
Number of individuals per cubic meter	temperature	-0.613
Number of species	salinity	-0.315
Number of individuals per cubic meter	salinity	0.321

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Water mass indicators

The collected data were transformed for the requirements of PRIMER v.5, and the subsequent processing was performed in this form. The first analysis consisted in clustering of similar sampling sites – distinguishing between both subnets in the Bongo net – based on biological differences/similarities (Fig. 5). Figure 5 displays sites which undoubtedly should be considered separately, like V9 and V31. While sites V26 and V4, both characterized by a strong similarity in biological parameters, are very different in hydrological terms, they still need a coupled interpretation (Fig. 5).

In order to identify some ecological/biodiversity indices for each sample, they were analyzed collectively using Principal Component Analysis (PCA) to better understand the relationships between the species diversity, the environment, and sampling sites (Fig. 6). In the presented graph plotted on the two-dimensional coordinate system, four main groups may be found (marked by circles). First from the left there are samples affected by ArW, while the lowest circle comprises those influenced by AtW. V31 and V26 in this graph are grouped together due to significant impact of environmental conditions in such analysis, contrary to cluster analysis (Fig. 5) where biological parameters had stronger influence. The only left group is the single-sample group of V9, which confirms its definite isolation and potential CW influence.

After receiving such results, analysis of similarity percentages (SIMPER) was performed. The previously obtained Bray-Curtis matrix with square root transformation was chosen with a breakdown at 90% for further calculations. The contribution of each species or higher taxa to the similarity of AtW and ArW was evaluated. For clarity, only results with further implications are presented (Table 4).

As shown in Table 4, some of the marked species with previously noted high abundance might be interpreted as typical of each water mass. It is also conspicuous that *Aglantha digitale* is of the highest significance in both cases. Although *A. digitale* dominated in both areas, we assume that the high abundance of this species may result from its correlation with the Atlantic Water Mass. Contribution of *Euphysa flammea* to Arctic species is negligible as similar abundance values were also

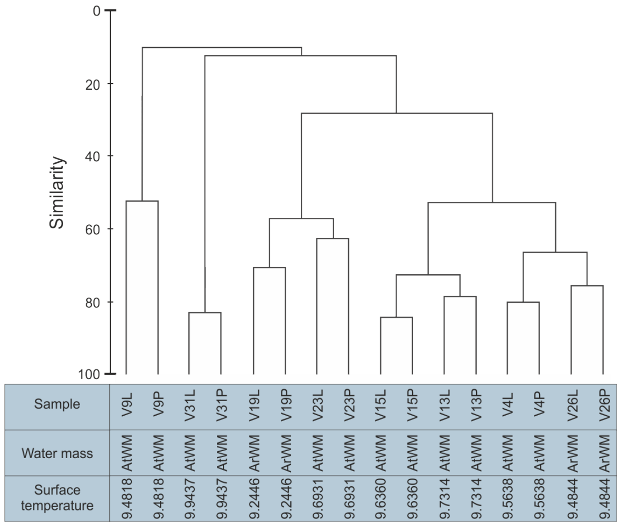

Figure 5

Cluster analysis for sites with water masses and surface temperatures taken into account

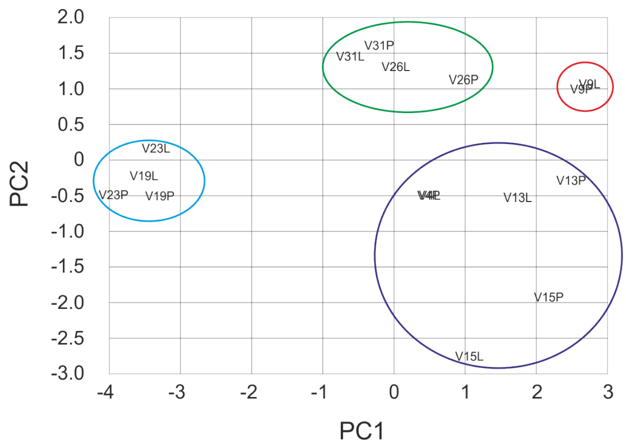

Figure 6

PCA for the calculated ecological indices with applied grouping (marked by circles)

recorded for the Atlantic Water Mass. On the other hand, the number of *Bougainvillia superciliaris* recorded for AtW was considerably lower than for ArW, which underlies its correlation with colder Arctic waters.

Differences in species contribution to general composition of coelenterates, in samples presented in Table 4, were essential for determining their usefulness as indicators. This reasoning included Multidimensional Scaling (MDS) for dissimilarities in the distribution of selected taxa (Fig. 7). This approach resolved the linkages between species and oceanographic features of the region, determining

Table 4

SIMPER cumulative analysis for species composition similarities between AtW and ArW

Group AtW			Group ArW		
Species	Contribution (%)	Cumulative (%)	Species	Contribution (%)	Cumulative (%)
Aglantha digitale	64.44	64.44	*Aglantha digitale*	38.00	38.00
Ctenophora	17.97	82.41	Other	35.49	73.49
Other	12.02	94.43	Ctenophora	9.82	83.31
			Euphysa flammea	5.49	88.80
			Bougainvillia superciliaris	4.25	93.06

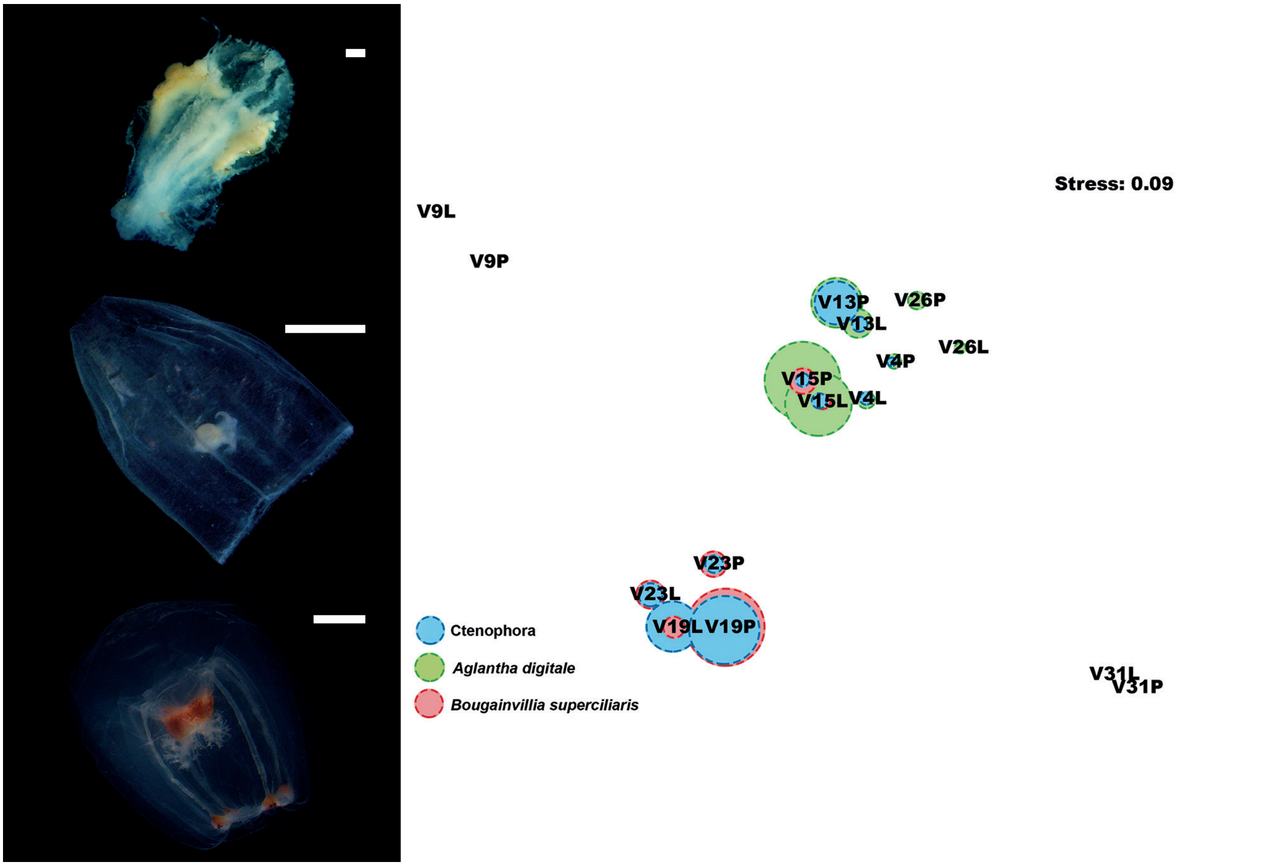

Figure 7

MDS of distribution of Ctenophora undet., *Aglantha digitale* and *Bougainvilla superciliaris* respectively from top

Scale bar: 1 mm

three possible indicators of water masses: *Aglantha digitale* for AtW, *Bougainvilla superciliaris* and large numbers of ctenophores for ArW.

Discussion

Hydrological conditions

The study area, which mostly comprised the Barents Sea, is the region assumed to be the most productive and diverse area of the western Arctic Ocean (Arashkevich et al. 2002). The most reasonable justification for this belief is the presence of separate water masses in this area. Their coexistence and mixing is characterized by high variability, in both physical and chemical water parameters. Moreover, this area is characterized by great seasonal diversification, and perceptible climatic variations, which are the consequences of the variable influx of the Atlantic Water Mass, and the properties of inflowing water (Loeng 1991). This influx was estimated at about 2 Sv (1 Sverdup =

10^6 m^3 s^{-1}) (Adlansdsvik & Loeng 1991). Most recent studies suggest that this number is now higher. See, for example, the results of Maslowski et al. (2004) – 3.27 ±0.58 Sv, or Smedsrud et al. (2013) – 2.3 Sv.

The purpose of this study was to connect the diversity and distribution of coelenterates with water mass fluxes in the investigated area, rather than the other way around. The reason for this approach is the scarcity of the collected environmental data, the narrowness of the investigated area, and the lack of comprehensive inquires on Coelenterates in this specific region. However, the inability to distinguish between those two aspects (biodiversity and hydrology) emerges from the presented data, because they are influencing each other to a significant degree (e.g. Lan et al. 2004).

CTD probe results, combined with coelenterate species diversity and distribution, lead to a hypothesis of the increasing width of the main flow of the Atlantic Water Mass. Changes in the Atlantic influx and the observed decrease in the sea ice range seem to be an example of a hydrological positive feedback loop (Smedsrud et al. 2013). According to Ikeda (1990), substantial increases in the inflow of warmer waters (AtW) cause warming of the surface layer in the Arctic waters, and therefore sea ice melting (Adlandsvik & Loeng 1991). As a result of the sea ice decline, waters in the study area are cooling more slowly, and henceforth the possibility of AtW flow expansion (Ikeda 1990; Smedsrud et al. 2013).

The previously mentioned increase in the water volume transport from the Atlantic Ocean to the Barents Sea, and in general to the Arctic Ocean is followed by the heat transfer (Maslowski et al. 2004). The hydrological positive feedback loop, developed by Smedsrud et al. (2013), relies on this heat supply, which was the object of numerous scientific studies, including those of Walczowski and Piechura (2006, 2007) or Holliday et al. (2008). Maslowski et al. (2004) estimated the heat influx along the Svalbard-Norway transect at 78.38 ±14.55 TW for the 23-year period (1979-2001), which means that the amount of heat delivered by this area to the Arctic Ocean is two times higher compared to the Fram Strait. It means that the marginal seas from the investigated area could be highly responsible for shaping the climate of the subarctic region. Therefore, their susceptibility to thermal changes may induce ecological restructuring of the food web in this region.

Biologically speaking, such fluctuations in the delivery system of warmer waters may accelerate the arrivals of warmer-water species, prolong their stay, and facilitate their accommodation (Błachowiak-Samołyk et al. 2007). Besides crustaceans associated with the Atlantic waters, like *Calanus finmarchicus, Themisto abyssorum, Thysanoessa inermis,* and *T. longicaudata,* brought to the Barents Sea and the westerly adjacent seas in the Arctic Ocean, the majority of incoming predatory zooplankton are represented by specimens of *Aglantha digitale* (Arashkevich et al. 2002; Błachowiak-Samołyk 2008).

Species composition

Coelenterata distribution across the investigated transect represents a significant water mass association and therefore, latitudinal variability. General species composition altogether comprised 21 taxa. Higher species diversity was associated with the Atlantic Waters, but higher abundance was observed for colder Arctic Waters. Such a distribution is expected according to literature resources (e.g. Wiborg 1955; Kosobokova & Hirche 2000; Raskoff et al. 2005; Błachowiak-Samołyk 2008). There is, however, an immense deficiency of information about the assumed increase in the species abundance in the Polar Front area, which has been confirmed in the collected samples. For example, sites V19 and V26, categorized as ArW-affected, slightly differ in the abundance of coelenterates from V23, a site also classified as ArW-influenced. It can be assumed that the background for this situation is the existence of mixing zones on the border of both water masses, resulting in the creation of the Polar Front Water Mass. As evidenced for the Antarctic Convergence Zone, in areas assumed to be polar fronts, primary production, and therefore abundance and species diversity are increased (Owen 1981). Thus, the presence of the Polar Front can be confirmed for the slopes of the Spitsbergen Bank, i.e. a region in the center of the investigated area.

Also worth mentioning is the observable progression in the species abundance. When comparing the results obtained by Żmijewska (1976) from a similar transect with the results of our work, all species showed noticeable, significant expansion in the population size. For example, the frequency of *Aglantha digitale* increased 15 times compared to its original frequencies at sites resembling those presented in our study area. Therefore, it appears that the distribution patterns have changed.

As discussed above, sampling sites V31 and V9 are clearly different from other sites. The northwesternmost site – V31 – exhibits features typical of the AtW influence (Loeng 1991). This raises the question of what kind of water movement is affecting the engulfment of the Atlantic current, just after crossing the Spitsbergen Bank? One possible answer was introduced by Mitchelson-Jacob (1993) who used infrared radiometry to detect mesoscale eddies in this region. It is highly probable that mesoscale eddies are the factor affecting the warmer water delivery to V31, thus bringing the species diversity and abundance typical of the sites affected by the Atlantic (Muench 1990).

Another site presenting a convincing level of distinctiveness is site V9. The hydrological and topographical features of this sampling site cannot explain the data collected here. Site V9 is located on a plateau that is higher than the Spitsbergen Bank area (Waage 2012). Such a location contributes to Atlantic current splitting, which, with the arrival of the Coastal Current, causes the unique conditions of site V9. Moreover, the dichotomous division of the Coastal Current and eddy formation alters the biological characteristics of site V4. Therefore, those two cannot be considered as typical AtW-affected or CW-affected locations, as they have a natural mixing system in the form of eddies, which disturbs the characteristics of coastal areas in terms of depth stratification, and demonstrate neither coastal nor Atlantic water temperature ranges (Mitchelson-Jacob 1993; Cottier & Venables 2007).

At this point, understanding the similarities in both the hydrological and biological aspects of sites V4 and V26 is helpful. Both sampling sites are situated in the vicinity of abnormal water mass/current distribution and consequently, they exhibit characteristics that derive from all of the involved parameters (Harris 1996; Ingvaldsen et al. 2003). Coelenterates at these sites are only partially distributed according to water mass influence, and therefore their contribution as indicator species was diminished (Bieri 1959).

Coelenterates' potential as water mass indicators

Planktonic animals are perceived as good indicators of water mass distribution, ocean climate variability, and seasonal timing of species arrivals (Edwards & Richardson 2004; Hays et al. 2005). Recently many studies focus on the use of pelagic coelenterates as indicators (Pagès & Gili 1991; Pagès 2001). Although they have been conducted in different regions, they provided similar conclusions to those of Zelickman (1972) – i.e. based on the research conducted in the Barents Sea, the author explained the versatile adaptation system of gelatinous animals to variable environmental conditions and prey availability. The above-mentioned adaptation system consists in the capability of adjusting the timing, rates, and types of reproduction, withstanding long periods of starvation and forming aggregations (Arai 1992; Mills 1995; Zelickman 1972).

Our study implies that certain Arctic Ocean species have a solid physiological background for becoming water mass indicators. *Aglantha digitale*, whose abundance is associated in our study with the Atlantic Water Mass, is an example of Trachymedusae with a varied feeding pattern (Pagès et al. 1996). Juvenile individuals feed primarily on microplankton (diatoms and ciliates), while adult forms prey on copepods and even chaetognaths (Williams & Conway 1981). This feeding pattern was used by Shiota et al. (2012) to understand the latitudinal and seasonal variation in the reproduction of this species, which remains holoplanktonic through the life cycle. Moreover, as Williams & Conway (1981) proved, *A. digitale* has the ability to perform multiple reproductions within one generation. The arguments listed above, together with the number of *A. digitale* (adult form) being strongly correlated with water temperature (Pedersen & Smidt 2000), justifies the use of the species in water mass detection.

Other choices of taxa associated with the Arctic Water Mass can also be validated by reviewing their physiology. *Bougainvillia superciliaris* distribution is limited to the circumpolar region (Arai & Brinckmann-Voss 1980; Zelickman 1972). Although the polyp of this Anthomedusae species is an eurytherm (2-15°C), the lethal water temperature for an adult medusa is over 10°C (experimental studies, *in situ* presumably lower) (Werner 1961). Therefore, the existence of *B. superciliaris* is feasible only in cold Arctic waters. Aggregations of these hydromedusae are a common phenomenon in the researched areas with low temperatures (Zelickman et al. 1969), and consequently we believe they may be used as ArW indicators. One can also develop a similar ecological reasoning for the number of recorded ctenophores with ArW-affiliation. Ctenophora in this region are mainly dominated by *Mertensia ovum* and *Beroe cucumis* (Swanberg & Båmstedt 1991). Those highly carnivorous planktonic predators are known for their ability to rapidly increase in numbers (Zelickman 1972; Haddock 2007; Purcell et al. 2010). As the population size and the reproduction rate are environmentally variable, and in general positively correlated with a temperature decrease (Błachowiak-Samołyk 2008), aggregations of Ctenophora in the Barents and its adjacent seas may be used as an ArW presence indication (Zelickman 1972; Swanberg & Båmstedt 1991).

Conclusions

- Physiology, ecology, and life history of pelagic Coelenterata may lead to their better fitting into the role of water mass indicators in comparison to "hard-bodied" plankton species.
- Coelenterates species may serve as water mass indicators. In the Arctic Ocean, *Aglantha digitale* is an indicator of the Atlantic Water Mass, while *Bougainvillia superciliaris* and high abundance of ctenophores are associated with the Arctic Water Mass.
- Both hydrology and bottom topography of the investigated area affect the species distribution and diversity of pelagic Coelenterates, creating boundaries to their population expansion.
- The pattern of water mass distribution in the study area of the Arctic Ocean has changed over the past years, enabling larger amounts of Atlantic waters to enter this polar region.
- Atlantic Water Mass engulfment into the Barents Sea explains the presence of boreal species and their wide distribution.

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Suplementary materials

Online Resource 1

Specific information on the sampling method

Site	Net type and size (µm)	Date	Hour	Longitude	Latitude	Maximum depth (m)	Trawling length (min)	Trawling velocity (knots)
V31	Bongo 500	10.08.2011	06:04	75° 42.002' N	017° 32.797' E	218	15	1.5
V26	Bongo 500	10.08.2011	12:50	74° 57.001' N	018° 25.047' E	71	15	1.5
V23	Bongo 500	10.08.2011	15:30	74° 41.972' N	018° 39.208' E	82	15	1.5
V19	Bongo 500	10.08.2011	20:00	74° 09.897' N	019° 09.453' E	65	15	1.5
V15	Bongo 500	11.08.2011	01:00	73° 29.932' N	019° 19.694' E	480	15	1.5
V13	Bongo 500	11.08.2011	06:10	73° 00.056' N	019° 27.466' E	410	15	1.5
V9	Bongo 500	11.08.2011	15:10	71° 59.990' N	019° 41.012' E	310	15	1.5
V4	Bongo 500	11.08.2011	20:00	70° 59.997' N	019° 53.924' E	186	15	1.5