Trophic structure and biomass of high-Arctic zooplankton in the Eurasian Basin in 2017

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Nadezhda Zakharova

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Nadezhda Zakharova

Master Program for Polar and Marine Sciences POMOR / 050406 Ecology and environmental management

Supervisors:

Dr. Hauke Flores, Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research

Dr. Vasily Povazhniy, Arctic and Antarctic Research Institute

Prof. Dr. Georgy Cherkashov, Saint Petersburg State University

Трофическая структура и биомасса Арктического зоопланктона в Европейском бассейне в 2017 году

Захарова Надежда

Магистерская программа «Полярные и морские исследования («ПОМОР») / 050406 «Экология и природопользование»

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Научные руководители:

Д-р Хауке Флорес (Dr. Hauke Flores), Институт им. Альфреда Вегенера, Центр полярных и морских исследований в Объединении им. Гельмгольца, Германия

Д-р Поважный Василий, Институт Арктики и Антарктики, Россия

Профессор, Д-р Черкашёв Георгий Александрович, кафедра геологии месторождений полезных ископаемых, Санкт-Петербургский Государственный Университет, Россия

Contents

1. Abstract

Abstract in English

The Arctic Ocean is experiencing some of the most pronounced effects of global climate change. Sea ice coverage and thickness have significantly decreased in the past decades and are predicted to continue in the future. Significant changes in the water column are expected to occur in the environment, such as increases of surface water temperature, ocean acidification, increased stratification, changes in circulation of water. With ongoing climate change, model-based studies indicate a northward migration of Atlantic species with an increased inflow of Atlantic water into the Arctic Ocean. A biogeographical shift in the increasing dominance of warm-temperate-boreal copepod species has been witnessed over the last decade in the Arctic Ocean. The northward expansion of zooplankton communities associated with warm Atlantic waters (AW) leads to a reduction in the number of cold water species. Changes in the zooplankton community will also lead to the changes in its quality as a food source for higher organisms in the Arctic food chain, since zooplankton is one of the main link in the Arctic food web.

In this study pelagic zooplankton collected during the *Polarstern* expedition PS106 from 28 May to 20 July 2017 in the Arctic Ocean, north of Spitsbergen and the Barents sea, were analyzed. The research area comprised stations located on the shelf and slope of the Barents Sea and in the western Nansen Basin. In the sampling area Atlantic inflow from the Fram Strait meets the outflow of the Barents Sea and the southward-moving sea ice and polar surface waters. The Barents Sea shelf slope is a hot spot of atlantification and borealisation. The zooplankton community in this area is highly influenced by all these factors. Therefore, the objectives of this study were to investigate the variability in macrozooplankton species composition, biomass, and size composition of macro- and mesozooplankton across the Barents Sea shelf slope in relation to spatial and water masses influence parameters. In addition, the trophic structure of zooplankton communities was investigated, analyzing the stable isotopic composition and C:N ratio of zooplankton. The AW masses were distributed almost at all stations. To assess the influence of water masses, the stations were divided into two groups: with a smaller and greater influence of AW.

According to the obtained data, the total biomass of zooplankton was highest on the shelf. On the slope, zooplankton biomass was significanly lower than in the Nansen Basin. The smaller size fractions predominated at the stations more exposed to AW. Conversely, the contribution of large fractions in the Nansen Basin was significantly greater. The taxonomic composition of macrozooplankton in the upper 100 m comprised at least 21 taxa. The results indicated a significantly higher number of taxa on the shelf and slope (19 taxa) than in deep-sea areas (15 taxa).

The results of the stable isotope analysis indicated that carbon sources and trophic structure of zooplankton on the shelf slope differed significantly from the zooplankton community in deep-water stations with reduced AW influence. Also, the C:N ratio on the slope was significantly lower than in the Nansen Basin, indicating a lower lipid content in shelf-associated zooplankton. The results obtained for the isotopic composition of the four macrozooplanton species *Themisto libellula*, *Themisto abyssorum*, *Thysanoessa longicaudata*, *Thysanoessa inermis* did not show statistically significant inter-specific differences in trophic level, carbon source and C:N ratio.

In general, the results of the study confirm the changes taking place in the zooplankton community and the impact of the region's atlantification. The unexpected result was that the zooplankton biomass on the slope was no higher than in the deep basin. This is contrary to the general assumption that the zooplankton biomass is higher on the AW-affected slope and will increase in the future. Some of the data require more comprehensive analysis including additional environmental and biological datasets, when they will become available.

Abstract in Russian

На сегодняшний день Северный Ледовитый Океан испытывает наиболее выраженные последствия глобальных климатических изменений. За последние десятилетия толщина морского льда значительно уменьшилась, и по прогнозам, будет уменьшаться в будущем. Так же ожидаются значительные изменения в толщах морских вод: повышение температуры поверхностных вод, закисление океана, усиление стратификации, изменения течений и циркуляции водных масс. В условиях продолжающегося изменения климата, исследования на основе моделей показывают, что с увеличением притока Атлантических вод в Северный Ледовитый океан, происходит миграция атлантических видов на север. В последнее десятилетие в Северном Ледовитом океане наблюдается биогеографический сдвиг в сторону увеличения доли бореальных видов копепод. Расширение сообществ зоопланктона на север, связанное с теплыми Атлантическими водами, приводит к сокращению численности видов, предпочитающих холодные Полярные воды. Изменения в составе зоопланктонного сообщества также приведет к изменению его качества, как источника пищи для организмов высших трофичеких уровней, поскольку зоопланктон является одним из главных звеньев Арктической пищевой сети.

В данной работе были проанализированы образцы зоопланктона пелагиали, отобранного в экспедиции PS106 на исследовательском судне «Поларштерн». Экспедиция проходила с 28 мая по 20 июля 2017 г. в Северном Ледовитом океане, к северу от Шпицбергена и Баренцевом море. В зону исследований входили станции, расположенные на шельфе и склоне Баренцева моря и западной части бассейна Нансена. В зоне отбора проб происходит приток Атлантических водных масс через пролив Фрама и встречается с выносом водных масс с Баренцева моря. В свою очередь, происходит движение морского льда в южном направлении и встречается с Арктическими поверхностными водами. Склон шельфа Баренцева моря является горячей точкой атлантификации и бореализации. Все эти факторы оказывают значительное влияние на сообщество зоопланктона в этом районе. Учитывая важность всего вышесказанного, в рамках данного исследования было проведено изучение видового состава макрозоопланктона, биомассы и размерного состава макро- и мезозоопланктона по склону шельфа Баренцева моря, в зависимости от влияния на них пространственного расположения и водных масс. Кроме того, была исследована трофическая структура сообществ зоопланктона, с

помощью анализа стабильных изотопов и соотношения C:N. Атлантические водные массы были распространены почти на всех станциях. Для оценки влияния водных масс станции были разделены на две группы: с меньшим и большим влиянием Атлантических вод.

Полученные данные показывают, что общая биомасса зоопланктона была высокой на шельфе. На склоне биомасса зоопланктона была значительно ниже, чем в бассейне Нансена. На станциях более подверженных воздействию Атлантических вод преобладали фракции меньшего размера. И, наоборот, в бассейне Нансена вклад крупных фракций был значительно выше. Таксономический состав макрозоопланктона в верхних 100 м составлял 21 таксон. Было показано значительно большее количество таксонов на шельфе и склоне (19 таксонов), чем в глубоководных районах (15 таксонов).

Результаты анализа стабильных изотопов показали, что источники углерода и трофическая структура зоопланктона на шельфовом склоне существенно отличаются от сообщества зоопланктона на глубоководных станциях с пониженным воздействием Атлантических вод. Кроме того, соотношение C:N на склоне было значительно ниже, чем в бассейне Нансена, что свидетельствует о более низком содержании липидов в зоопланктоне, связанном с шельфами. Результаты, полученные для изотопного состава четырех видов макрозоопланктона *Themisto libellula, Themisto abyssorum, Thysanoessa longicaudata, Thysanoessa inermis* не показали статистически значимых межвидовых различий в трофическом уровне, источнике углерода и соотношении C:N.

Подводя итог, можно сказать, что результаты исследования подтвердили изменения, происходящие в сообществе зоопланктона, и подверженность региона исследования атлантификации. Неожиданным результатом стало то, что биомасса зоопланктона на склоне не выше, чем в глубоком бассейне. Это противоречит общепринятому утверждению о том, что биомасса зоопланктона выше на склоне, подверженному повышенному влиянию Атлантических вод, и будет увеличиваться в будущем. Некоторые из этих данных требуют более детального анализа, включая дополнительные экологические и биологические базы данных, когда они станут доступны.

2. Introduction

The Arctic Ocean is the smallest ocean of the five major oceans in terms of area and mean depth, located entirely in the northern hemisphere, between Eurasia and North America. The Arctic Ocean is almost entirely surrounded by land. The average depth is 1225 m. Most of the Arctic Ocean bottom relief is occupied by the shelf (more than 45% of the ocean bottom) and submarine margins of the continents (up to 70% of the bottom area). The Arctic Ocean connects to the Atlantic through the deep gateway of the Fram Strait between Spitsbergen and Greenland with depths up to 2.6 km and a width of 600 km. The Arctic Ocean connects to the Pacific through the shallow Bering Strait (82 km depth). The deep central region of the Arctic Ocean is separated by the Lomonosov Ridge into two major basins, the Eurasian Basin and the Amerasian (Canadian) Basin. The Eurasian Basin, in turn, is divided by the Gakkel Ridge into two basins named Nansen Basin and Amundsen Basin. The Amundsen basin is, on average, the deepest basin in the Arctic Ocean. It lies between the Lomonosov Ridge and the Gakkel Ridge. The Nansen basin is characterized by a predominance of depths of more than 4 km. It is located to the southwest of the Gakkel Ridge. The maximum depth of the Arctic basin is noted here, it reaches 5449 km (Kosobokova 2012).

The waters of the Arctic basin are formed under the influence of the inflow of Atlantic and Pacific waters, river runoff and processes of melting and ice formation (Coachman and Barnes 1961, 1962, 1963; Rudels et al. 1994, 2000, 2004; Schauer et al, 1997; Woodgate et al. 2001). There are three main water masses for the vertical distribution of temperature and salinity in the Arctic basin: Polar Surface Water (PSW), Atlantic Water (AW) and deep water-masses resulting in the mixed products warm Polar Surface Water (wPSW)(Rudels 1987; Rudels et al. 1994, 2004). The layer of PSW stretches from the surface to the depth of 200-250 meters. It is characterized by a relatively low salinity 30-30.5 psu and a negative temperature close to freezing -1.8 °C (Treshnikov 1959; Coachman and Barnes 1961, 1962, 1963; Nikiforov and Shpeikher 1980; Kosobokova and Hirche 2009). In open waters, a warmer version of PSW (wPSW) resides in the very surface layers (around 0°C) (Nicolopoulos et al. 2018). The AW had a mainly positive temperature and a higher salinity than the PSW. It is formed by warm and salty Atlantic waters penetrating the Arctic through the Frame Strait, the Barents Sea and the Kara Sea. According to the data obtained in the middle of the 20th century, the maximum

temperature in the region of Spitsbergen was +2-3 °C, and in Alaska it was +0.5 °C (Coachman and Barnes 1961). The salinity of the Atlantic waters gradually increases with depth to 34.9 psu (Kosobokova 2012).

The Nansen Basin is the most influenced directly by the inflow of AW (Mumm 1993). AW in the Arctic basin move from west to east, forming a cyclonic circulation along the continental slope of Eurasia (Nikiforov and Shpeikher 1980; Rudels et al. 1994, 2000, 2004; Schauer et al. 1997). There are two main branches of AW inflow to the Arctic. The first is through the Fram Strait, where warmer and more salty and dense AW is carried northward through eastern Fram Strait with the West Spitsbergen Current. When entering the Nansen Basin, the AW flows beneath the PSW (Carmack 1990; Nikiforov and Shpeikher 1980; Rudels et al. 1994). The second branch is the inflow of less salty and colder AW across the Barents Sea. Meeting north of the Kara Sea these branches are mixed and form the Atlantic boundary current (Rudels 1987; Rudels et al. 1994). The Atlantic layer can be detected throughout the Arctic Ocean in 200 – 600 m depth below a pronounced halocline. In turn, the PSW moves southwestward across the Nansen Basin in the upper 50 m towards western Fram Strait where it flows into the East Greenland Current (Auel and Hagen 2002).

The ideas about the mechanism of surface water circulation in the Arctic basin were formed mainly on the basis of observations of the Arctic ice drift and hydrographical measurements. Surface circulation is formed under the influence of river runoff and to a greater extent is a result of the action of prevailing winds. General water circulation in the Arctic consists of three parts (Fig.1). The first part is an extensive slowly moving anticyclonic gyre north of the Beaufort Sea. The second is the transarctic current (Transarctic Drift). This is the water flow from the Chukchi Sea through the central part of the ocean. The third is the cyclonic gyre in the Laptev Sea. The sea ice moves with these currents and leaves the Arctic basin through the Fram Strait between Greenland and Spitsbergen (Gorshkov 1983; Nikiforov and Shpeikher 1980; Dunbar and Harding 1968).

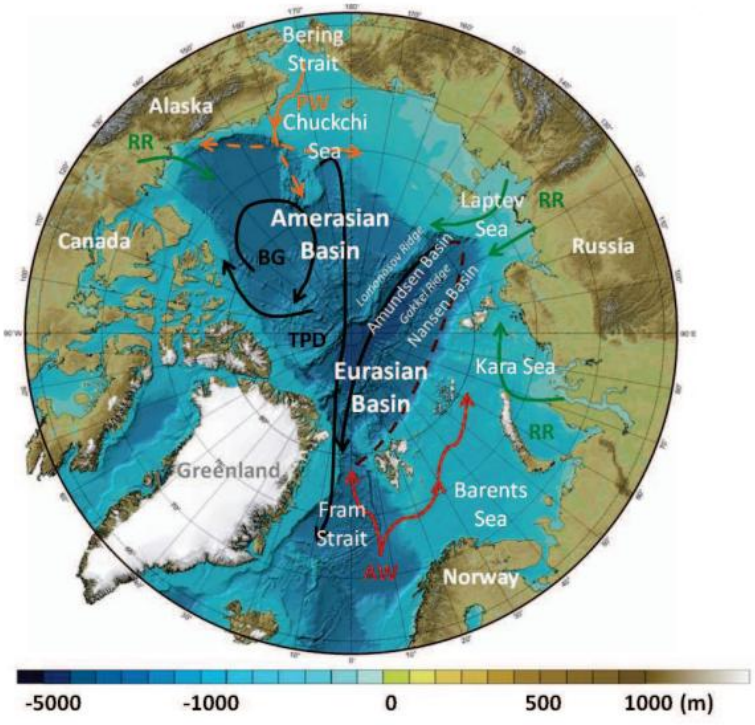

Fig.1. Overview of the Arctic Ocean and its bathymetry with an outline of surface waters circulation. Red lines indicate Atlantic Waters (AW). Orange lines represent Pacific Waters (PW). Black lines represent cold, less saline polar water currents (TPD – Transpolar Drift, BG – Beaufort Gyre). Green lines visualize river runoff inflow (RR). The dashed line indicates the area where polar water is formed (Fernández-Méndez 2014).

Due to the spherical shape and inclination axis of the Earth, the Arctic experiences low exposure to solar energy and is characterized by high seasonality in light conditions. This leads to month-long periods of polar night in winter and midnight sun during summer. Due to the polar geographical position of the ice cover in the central part of the ocean, the ice cover persists throughout the year, although it is in a mobile state. The ice cover of the Arctic Ocean consists of annual and perennial ice. Snow and ice cover control the processes of heat exchange between the ocean and the atmosphere, and determine the amount of light passing into the water (Nicolaus et al. 2012). Thus, sea ice regulates the synthesis of organic matter. Snow and ice cover influence the formation of stable seasonal vertical stratification of surface waters, which is necessary for the development of phytoplankton blooms (Kosobokova 2012).

The Arctic Ocean is the most poorly studied ocean in the world because of its extreme climate and ice cover, which covers a significant part of the water area. The first hydrobiological studies in its central deep water areas were carried out by the Norwegian Polar Expedition (1893-1896) organized by Nansen on the Fram ship (Nansen

1902). During the first of zooplankton researches, the organisms were collected from drifting ice stations or ships frozen in the ice. Within this period of sporadic data collection, basic knowledge on the major parameters and seasonal dynamics of the zooplankton communities of the Arctic Ocean were obtained. In the first half of the 20th century, Russian expeditions took place in the shelf seas of the Arctic Ocean: the Barents Sea, the Kara Sea, the Laptev Sea and the East Siberian Sea. The expeditions on the ship "Sadko" in 1935-1937 managed to collect zooplankton and in the Arctic abyssal area. One of the deep-water stations was located to the north of Spitsbergen (Yashnov 1940). With the organization of research drifting stations "North Pole" zooplankton collection began to be carried out routinely since 1937. Processing of these collections showed that plankton of the Arctic basin is richer and more diverse than materials from Fram ship suggested (Bogorov 1938; Usachev 1938, 1946, 1949, 1961; Shirshov 1938, 1944; Yashnov 1940). As a result of the materials collected at the "North Pole-2" drifting ice station in 1950, the researchers were able to detect the Pacific zooplankton representatives and it showed the possibility of penetration of the Pacific waters into the central part of the Arctic basin (Brodsky and Nikitin 1955). Also as a result of the work of the "North Pole" stations 3-7 it was found that the number abundance of mesozooplankton is the highest in the narrow surface layer of 0-50 meters, and the greatest diversity of them is typical for the layer of Atlantic waters at a depth of 300-1000 meters (Brodsky 1956, Virketis 1957, 1959).

In the past four decades, biological observations in the Arctic Ocean have increased markedly (Kosobokova et al. 2010). Expeditions of modern ice-breakers can reach even permanently ice-covered regions large-scale and efficient sampling can be accomplished nowadays (Mumm et al. 1998; Kosobokova et al. 2010). The interdisciplinary research brought a breakthrough in understanding of relationships between the structure of pelagic communities with hydrographic processes and environmental factors (Kosobokova and Hirche 2009). The most important factors influencing the formation of the Arctic pelagic biotopes are solar radiation, ice cover and low water temperature. Arctic zooplankton has sophisticated survival and reproduction strategies throughout its life as an adaptation to low temperatures, long-term or seasonal ice cover, limiting the amount of nutrients in the surface layer and an extremely impulsive primary production cycle (Conover and Huntley 1991; Darnis et al. 2012; Kosobokova 2012). Being the major

consumers of primary production (Kosobokova et al. 2010; Kosobokova 2012), zooplankton species are an important component in the Arctic food web since they link primary production with higher trophic levels.

The Arctic Ocean hosts two zooplankton communities: an autochthonous community and an allochthonous community. The autochthonous community consists of species that are resident in the Arctic basin. They can reproduce and maintain populations in Arctic waters. The allochtonous community consists of species advected from surrounding waters that are represented only by older stages of development and adults, they do not reproduce. The absence of young stages in the Arctic regions means that they do not reproduce there or do not survive for some reason. These species are expatriates (Ekman 1953; Beklemishev 1969). There are three groups of allochthonous communities by source of origin: Atlantic, Pacific and neritic origin (Kosobokova 2012; Kososbokova and Hirche 2000). The main expatriates in the Eurasian sector of the Arctic are copepods species - *Calanus finmarchicus, Metridia lucens, Paraeuchaeta norvegica, Rhincalanus nasutus, Pleuromamma robusta, Oithona atlantica*, Euphasiidae spesies - *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, Polychaeta – *Tomopteris septentrionalis* (Kosobokova 2012). North Atlantic zooplankton species are transported through the Norwegian and Greenland Seas towards the Fram Strait and from there into the Barents sea and Arctic Ocean. Copepods *C. finmarchicus* and *O. atlantica* are brought to the Arctic by Atlantic waters in mass quantities (Yashnov 1966; Kosobokova and Hirche 2009; Kosobokova and Hopcroft 2010; Kosobokova et al. 2010). Copepods *Calanus hyperboreus* and *Calanus glacialis* are considered to be of true Arctic origin species (Conover 1988; Auel and Hagen 2002; Hirche and Kosobokova 2007). The contribution of copepods to the total abundance of mesozooplankton in the Eurasian basin is average 94% (Kosobokova 2012). Copepods clearly prevail over all other zooplankton groups and make up about 80% of the total biomass. Other groups that contribute to zooplankton biomass in the Eurasian part of the Arctic basin are Chaetognata (11,9%), Ostracoda (3,4%) , Amphipoda (1,9%), Appendicularia (1,1%), Polichaeta (0,4%), Euphausiacea and Decapoda (0,2%) and Pteropoda (0,2%) (Kosobokova 2012).

Comparison of the composition of zooplankton in open oceanic areas, near-slope water areas and shelf areas shows that the communities of these three areas differ in the

composition of dominant biomass species. In the shelf areas of the Eurasian Arctic, the main contribution to the mesozooplankton biomass is made by *C. glacialis* (up to 82%). The contribution of other species of large ocean copepods *C. hypoboreus* and *Metridia longa* is very small. Further important components of biomass are *C. finmarchicus* (up to 33%), *Pseudocalanus* spp (up to 22%) and neritic Chaetognata *Parasagitta elegans* (up to 25%). In the area of the continental slope, the contribution of *C. glacialis* is decreasing to 67%, but the species still dominates in terms of biomass. Oceanic copepods *C. hypoboreus* (up to 34%), *M. longa* (up to 23%) and Chaetognata *E.hamata* (up to 41%) co-dominate. In the basins deeper 1500 m the contribution of *C. hypoboreus* is increasing up to 41%. The species *C. glacialis* (up to 26%), *M.longa* (up to 26%), *E.hamata* (up to 19%) co-dominate (Kosobokova 2012).

One of the unique characteristic features of the Arctic marine ecosystem is the sea-ice habitat. Snow and sea ice constitute a habitat for autotrophic and heterotrophic microorganisms, bacteria and protozoa (Melnikov 1989; Garrison and Buck 1991; Melnikov et al. 2001; Lizotte 2003; Sazhin et al. 2004), for multicellular animals - nematodes and rotifers (Friedrich 1997; Gradinger 1999) and even for coelenterata (Bluhm et al. 2007; Piraino et al. 2008). As already mentioned above, snow and ice cover control the processes influencing the development of autotrophs - ice algae and phytoplankton. Ice algae are an important component of Arctic ecosystems. These are mainly diatom algae that develop in mass in pores and tubules on the lower surface of the ice. The development of ice algae begins before the phytoplankton vegetation when sufficient light is available (Booth and Horner 1997). In the central Arctic Ocean, most of the primary production is from ice algae rather than phytoplankton (Gosselin et al. 1997; Fernández-Méndez et al. 2015). Recently, it was shown that key species, such as *Calanus* spp. (in some seasons) and juvenile polar cod *Boreogadus saida*, signiicantly depend on carbon produced by ice algae (Budge et al. 2008; Søreide et al. 2010; Wang et al. 2015; Kohlbach et al. 2016, 2017; David et al. 2015). They feed on algae during the mass blooming season (Kosobokova 2012). Sea ice plays an important role as a habitat for zooplankton and higher organisms. The under ice surface serves as a substrate for zooplankton representatives, for example Amphipods: *Gammarus wilkitskii, Onisimus glacialis, O. nanseni, Eusirus holmi, Eusigenes artica*, *Apherusa glacialis* and Copepods: *Jaschnovia tolli, J. breves, Eurytemora richings*i (Melnikov 1989; Carey 1992; Werner

2000; Melnukov et al. 2002; Kosobokova 2012). The ice-associated fauna plays a key role in transmitting carbon from sea ice algae into the pelagic and benthic food webs (Kohlbach et al. 2016, 2017).

The Arctic Ocean is experiencing some of the most pronounced effects of global climate change (Arctic Climate Impact Assessment 2004). The Arctic Ocean is undergoing a rapid decline in sea-ice volume (Laxon et al. 2013). Sea-ice coverage extent over the past two decades have significantly decreased (Stroeve et al. 2012; Simmonds 2015) and are predicted to continue in the future (Johannessen et al. 2004; Laxon et al. 2013). Due to the extremely important role of ice in the functioning of Arctic pelagic ecosystems (Gosselin et al, 1997; Gradinger 2002; Kohlbach et al. 2016), there is a serious risk that the reduction of ice cover and the disappearance of perennial ice may lead to a significant change of the trophic functioning of biological communities in the future Arctic Ocean and productivity of these ecosystems. Zooplankton species are expected to be the first to show a response to climate change because of their short life histories and their sensitivity to environmental changes (Hunt et al. 2014).

Changes in the zooplankton community will also lead to the changes in its quality as a food source for higher organisms in the Arctic food chain, since zooplankton is one of the main link in the Arctic food web.

Significant changes in the water column are expected to occur in the environment, such as increases of surface water temperature, ocean acidification, increased stratification, changes in circulation of water (IPCC 2014; AMAP Assessment 2018; Arctic Climate Impact Assessment 2004; Tremblay et al. 2015). With ongoing climate change, model-based studies indicate a northward migration of Atlantic species with an increased inflow of Atlantic water into the Arctic Ocean (Richardson 2008). The northward expansion of zooplankton communities associated with warm AW leads to a reduction in the number of cold water species (Buchholz et al. 2012; Dalpadado et al. 2012; Woodworth-Jefcoats et al. 2016; Haug et al. 2017). A biogeographical shift in the increasing dominance of warm-temperate-boreal copepod species has been witnessed over the last decade in the Arctic Ocean (Weydmann et al. 2014). The penetration of Atlantic expatriates (*C. finmarchicus*) into the East Siberian Sea is also noted (Ershova and Kosobokova 2019). The distribution, abundance and biomass of zooplankton, the

body size of an organism could change (Heckmann et al. 2012; Trudnowska et al. 2014). Although the total secondary production may increase with higher temperatures (Slagstad et al. 2011), the longer open-water season in the warmer Arctic could potentially drive the zooplankton community towards smaller body sizes and shorter life cycles (Daufresne et al. 2009), resulting in a decrease in the overall zooplankton biomass in the future. While the total abundance of zooplankton is much higher in AW, Arctic waters carry organisms of larger body size and with a higher lipid content, which results in their higher biomass and calorific value (Weslawski et al. 1999, Kwasniewski et al. 2010, 2012). Copepods of the genus *Calanus* have extremely high calorific values (50–70% lipids of dry mass)(Lee et al. 2006) and are key species in the Arctic ecosystems (Frandsen et al. 2014), where they represent significant food items for planktivorous predators from the higher trophic levels, such as birds, fish and mammals (Falk-Petersen et al. 1990).

The three dominant amphipod species found in Arctic waters: the Arctic *T. libellula*, the Arctic-boreal *T. abyssorum*, and the North Atlantic species *T. compressa* (Klekowski and Węsławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002). *T.abyssorum* co-exists with *T. libellula* throughout the Arctic (Klekowski and Węsławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002). However, *T.abyssorum* is more abundant in waters of Atlantic origin (Dalpadado 2002). North Atlantic species *T. compressa* is seldom found, and only in low abundances, in the Arctic marginal seas such as the Barents Sea around Spitsbergen (Dalpadado 2002) and the Greenland Sea (Weigmann-Haass 1997) and was recorded for the first time in the eastern Fram Strait in 2004 (Kraft et al., 2013). Atlantic expatriates krill species *T.Longicaudata* are also often found in samples in the Arctic (Kosobokova 2012). The authors have already observed the shifts in diet composition of the bird black-legged kittiwakes, inhabiting the Spitsbergen area, towards the increase of Atlantic fish species and amphipods (Vihtakari et al. 2018).

Thus, the change in the structure and biomass of the Arctic zooplankton will inevitably lead to the disruption and changing of existing trophic links in the pelagic ecosystem and the natural transfer of energy to higher links in the food chain, for example to birds and higher predators (Kosobokova 2012; Wassmann et al. 2006). There is no doubt that

timely registration of changes in the ice and plankton communities of the Arctic basin requires constant monitoring.

This study is based on pelagic zooplankton samples collected during the *Polarstern* expedition PS106. Expedition was carried out in 28 May to 20 July 2017 in the Arctic Ocean, Northern Spitsbergen area, Barents Sea shelf and western Nansen Basin. The research area comprised stations located on the shelf and slope of the Barents Sea and in the western Nansen Basin. The main feature of the sampling area is the Atlantic inflow from the Fram Strait meets the outflow of the Barents Sea. In addition, the Barents Sea shelf slope is a hot spot of atlantification and borealisation, where the zooplankton community is highly influenced by climate change factors. During the *Polarstern* cruise, PS106 AW was present at all locations, with the maximum temperatures decreasing with distance from the Fram Strait. The overall maximum temperature of AW observed during PS106 was 4.67°C near Spitsbergen (80.095°N 9.622°E, at 35 m depth). Moving away from the continental slope and into the Nansen basin or the Barents Sea, the AW successively loses its heat and the maximum temperatures are found deeper in the water column. Over the north-eastern parts of the Yermak Plateau, the maximum AW temperatures averaged 2.3°C at an average depth of 195 m. Similar AW temperatures were observed further east along the shelf-slope (Nicolopoulos et al. 2018).

During PS106, the physical and biogeochemical habitat properties and biodiversity of the sea-ice associated habitat were sampled, with an emphasis on polar cod and its ice-associated and pelagic prey species. The studies conducted in this area are unique, as they provide an opportunity to quickly track changes in the biological systems of the Arctic Ocean in changing climatic conditions. Therefore, the **objectives** of this study were:

- Investigate the variability of macrozooplankton taxonomic composition across the Barents Sea shelf slope and the western Nansen Basin in relation to spatial and water masses influence parameters;
- Investigate the variability in biomass, size composition of meso- and macrozooplankton across the Barents Sea shelf slope and the western Nansen Basin in relation to spatial and water masses influence parameters;

- Investigate the variability of the trophic structure and the carbon sources of macro- and mesozooplankton, analyzing the stable isotopic composition and C:N ratio of zooplankton across the Barents Sea shelf slope.

Based on the literature data and own assumptions, the following **hypotheses** were formulated within the framework of the present research and set objectives:

- The taxonomic composition in upper 100 m is more diverse at the shelf and shelf slope then in the Nansen basin;
- Zooplankton biomass is higher on the shelf and slope and decreases in the Nansen basin;
- Smaller fractions predominate at the stations more exposed to Atlantic Waters. Biomass at these stations may be higher;
- The bigger size-class of zooplankton have a higher trophic level;
- Carbon source may change from phytoplankton to ice-algae in the deep water community;
- The species in the Nansen basin have more lipids and higher C:N ratio.

3. Material and Methods

3.1. Sample collection

Samples of pelagic zooplankton used in this study were collected during the *Polarstern* expedition PS106 from 28 May to 20 July 2017 in the Arctic Ocean, north of Spitsbergen and the Barents sea. The research area comprises stations located on the shelf and slope of the Barents Sea (stations 52, 64, 65, 83) and in the Nansen Basin (stations 67, 70, 71, 72, 73, 74, 75, 76, 77, 78, 80). The most northern station 73 was located at 83,71°N. An overview of the sampling stations is given in Figure 2. A summary of stations considered in this study is given in Table 1 (Flores et al. 2018).

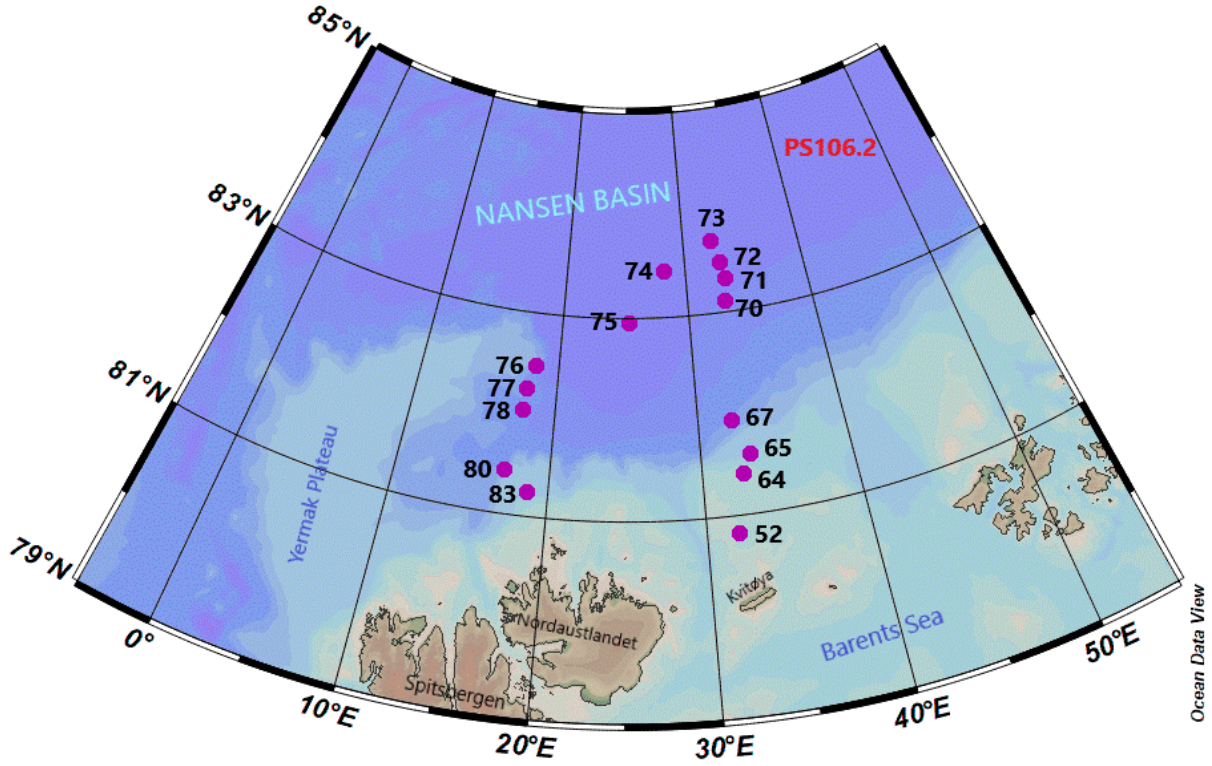

Fig. *2. Overview of the RMT stations during the Polarstern expedition PS106.*

In order to investigate the pelagic zooplankton communities in the study area, a Rectangular Midwater Trawl (RMT) was used. The RMT consist of pair of rectangular midwater trawls combined within the same frame – an RMT 1 of 1m^2 nominal mouth area and mesh size 320 µm, and an RMT 8 with an 8 m^2 nominal mouth area and a mesh size of 4,5 mm (Baker et al. 1973). The nets are opened and closed using an electrical signal transmitted release gear with a cable. The scheme of the RMT1+8 is given in Figure 3.

Table 1. Summary of RMT hauls conducted during PS106 expedition (Flores et al. 2018).

Station	Date	Time	Latitude	Longitude	Depth (m)
52	2017-06-29	14:33	80,83113	31,95887	139
64	2017-07-01	14:53	81,41144	32,6221	197
65	2017-07-02	04:33	81,59458	33,24857	532
67	2017-07-03	12:08	81,94919	32,31414	2815
70	2017-07-05	20:49	83,12072	32,96476	3806
71	2017-07-06	05:23	83,33891	33,25254	3907
72	2017-07-06	12:31	83,50209	33,02191	3984
73	2017-07-07	10:29	83,71652	32,38325	4022
74	2017-07-08	12:18	83,46498	28,11783	4049
75	2017-07-09	09:58	82,96027	25,17511	4045
76	2017-07-10	08:14	82,48855	18,27031	2460
77	2017-07-10	17:05	82,25152	17,79139	2003
78	2017-07-11	03:24	82,05086	17,67925	3176
80	2017-07-12	19:16	81,43975	17,02899	1818
83	2017-07-13	12:15	81,24548	18,60551	472

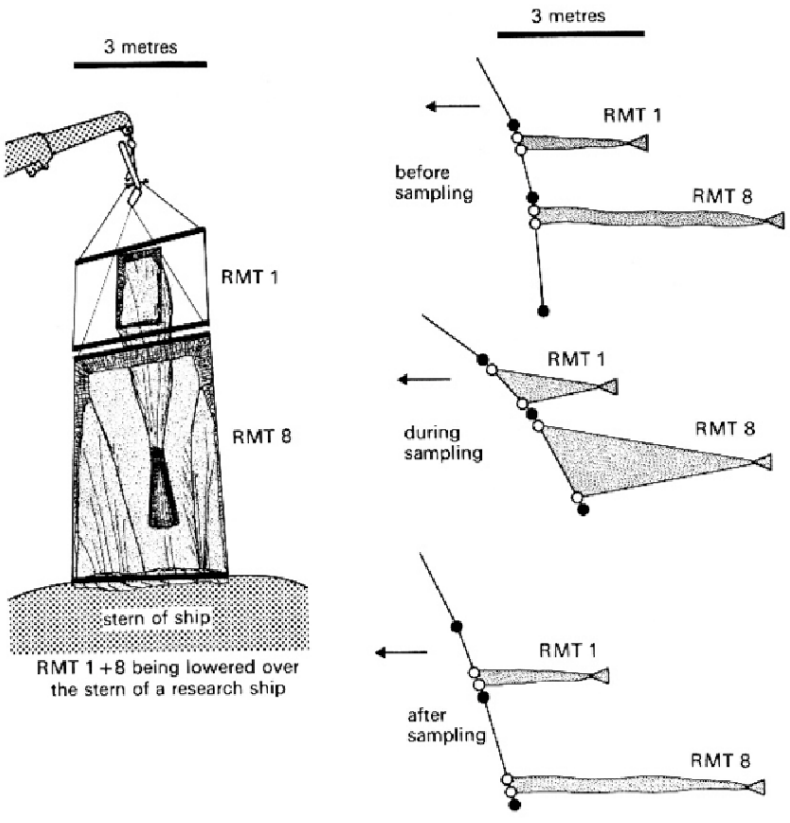

Fig. 3. The scheme of Rectangular Midwater Trawl (RMT 1+8). Left: the nets being lowered over the stern of a research vessel. Right: diagrams of the nets before, during, and after sampling at the depth (Baker et al. 1973)

Zooplankton was collected during oblique hauls between 0 m and 100 m depth. The speed of research vessel was from 1 to 3 knots. The volume of water filtered by the RMT net was estimated by multiplying the distance sampled (estimated by the ship`s speed, vertical depth and duration of the trawl) with the mouth area of the net, estimated after (Roe and Shale 1979). The catches of the mesozooplankton net of 320 µm mesh size were split in two halves (split factor = 0.5), after which one half was size-fractioned by sequentially sieving them through sieves of 4, 2, 1, 0.5, 0.25, 0.125 and 0.063 mm mesh directly on board of the research vessel (Flores et al. 2018). The fractioned samples were transferred into Petri dishes and frozen at -20 °C. The samples were transported to the Alfered-Wegener-Institute and stored in a freezer at -20°C for the later analysis in the laboratory. For this study, mesozooplanton samples of 12 stations were analyzed (52, 64, 65, 67, 70, 71, 72, 73, 74, 76, 77, 78). Samples of three stations (75, 80, 83) were contaminated with sand and particles of the ship, and therefore it was impossible to estimate the real biomass.

The catches of the shrimp net of 4,5 mm mesh size were also split in two halves (split factor = 0.5). One half was preserved in 4% formaldehyde/seawater solution immediately after catch the (Flores et al. 2018). The samples were transported and stored at room temperature for later analysis of specie composition, abundance and biomass estimation in the laboratories of the Alfered-Wegener-Institute. From the second half, jellyfish were extracted and counted, and their volume was determined. Various other species were collected for further analysis. For this study, frozen (-20°C) samples of *Themisto libellula*, *Themisto abyssorum*, *Thysanoessa longicaudata*, *Thysanoessa inermis* were used to establish length-weight relationships. From the RMT 8 net, all 15 stations were analyzed.

Hydrographic data was recorded with a Conductivity Temperature Depth probe with attached water sampler rosette (CTD/RO; Sea-Bird Electronics Inc) near almost every RMT station. The CTD (SBE911+) was equipped with duplicate temperature (SBE3; SN2460/2417) and conductivity sensors (SBE4; SN2055/2054), a pressure sensor (SBE9+; SN0485), an altimeter (Benthos; SN1228), sensors for fluorescence (WETLabs ECO-AFL/FL; SN1670), and a dissolved oxygen probe (SBE43; SN0880). Content of chlorophyll A in water was calculated from fluorescence data from CTD by Anna Nikolopoulos (Nikolopoulos, unpublished data). Content of chlorophyll A in surface water were also

measured by sensors of Surface and Under-Ice Trawl A Surface and Under-Ice Trawl (SUIT) (SUIT: van Franeker et al. 2009; Flores et al. 2018).

3.2. Species identification

For analyzing the species composition and distribution patterns of macrozooplankton, the catch of the RMT 8 shrimp net from 15 stations was analyzed. Samples were preserved in 4% formaldehyde/seawater solution immediately after catch and stored at room temperature. Originally the split-factor of all samples was 0,5 (Flores et al. 2018). In the laboratory, each sample was rinsed with water carefully and sorted by different groups of organisms with the naked eye in a sorting tray. All copepod organisms were not counted from these samples. Highly abundant samples were split into an aliquot of at least ¼ using a plankton splitter (Motoda 1959). However, all rare species were picked up from whole samples.

Zooplankton was identified under a binocular (LEICA M205C). Individuals were identified based on morphological features (Klekowski and Weslawski 1991). *Themisto libellula*, *Themisto abyssorum*, *Thysanoessa longicaudata*, *Thysanoessa inermis, Apherusa glasialis, Clione limacina* and some rare species were identified to the species if it was possible. All other organisms (*Beroe* spp., *Sagitta* spp., Chaetognatha etc.) and larvae were determined to phylum or class level due to time restrictions. The taxon "Chaetognata" was defined in this study as species ranging from 8 to 30 mm, with average lengths ranging from 12 to 22 mm. Based on this size range, it can be assumed that these chaetognaths were predominantly *E. hamata.* All chaetognaths which were larger than *E.hamata* and had eyes were attributed to *Saggita* spp. Representative subsamples were analyzed to a minimum of 30 individuals of each taxon. All organisms were counted, and the length was measured.

Length measurements were carried out under a stereo microscope (LEICA M205C) connected to a personal computer with the software Leica Application Suite (LAS) (version 4.12.0 [build:86]) (Amphipods, Chaetognatha ect.). If the body of organism was larger than 32 mm, the organism was measured with a ruler (*Themisto* spp*., Sagitta* spp. ect.). All measured organisms were photographed (magnification 0,5x), and measurements were stored in the personal computer. All counted numbers and length of bigger organisms were noted in data sheets and transferred later into an Excel file. The organisms of *Thysanoessa* spp. were measured from the front of the rostrum to the

tip of the telson. The organisms of *Themisto* spp. were measured from the front edge of the eye to the tip to the telson, and other Amphipods were measured from the front edge of the head to the tip of the telson. Chaetognatha, *Sagitta* spp., and fish larvae were measured from the front edge of the head to the end of the tail. Specimens of *C. limacine* were measured from the mouth to the tip of the mantle. In *Beroe* spp., the length and width of the body were measured. The cephalopod were measured the length of the body.

3.3. Length-weight relationships

Frozen samples collected from the RMT 8 were used to establish length-weight relationships for four species: *T.libellula, T.abyssorum, T.longicaudata and T.inermis*. Zooplankton was collected during onlique hauls between 0 m -and 100 m depth. The speed of research vessel was from 1 to 3 knots. After the size measurement, each organism was placed in a separate vial, and an individual sample ID was assigned to it. All vials were placed in a freeze drier (Sublimator VaCo5 4024, Zirbus Technology). Each dried organism was weighed on a calibrated analytical scale (Satorius Genius ME 2355) with an accuracy of 0.01 mg. For length-weight regression, 41 specimens of *T. inermis*, 67 specimens of *T.longicaudata*, 26 specimens of *T.abyssorum*, and 60 specimens of *T.libellula* were analyzed. For length-weight regressions, I used nonlinear model nlm ($y = b1 \times x^{b2}$) using R version R-3.5.2. To check fitting of regression model were used coefficient of goodness of fit (Table 2).

Visual inspection of the plotted data indicated that, data from *T.inermis* and *T.longicaudata* could be combined in one regression to increase the statistical power of the regression model. To build the regression for *A.glacialis* the data obtained in the laboratory Ice Flux in AWI from Mai Apasiri Klasmeier based on samples from the same expedition were used.

3.4. Biomass

The size-fractioned samples from the RMT 1 mesozooplankton net were stored in Petri dishes in a freezer at -20°C. Samples were defrosted at +2°C in the laboratory. Excess water was gently removed from Petri dish with paper tissue, and afterwards the fresh biomass was measured on a calibrated analytical scale (Satorius Genius ME 2355) with an accuracy of 0.01 mg. Afterwards, each size fraction sample was freeze-dried for 48 hours in a freeze drier (Sublimator VaCo5 4024, Zirbus Technology). Each Petri dish with

dried biomass was subsequently weighed to the nearest microgram. Dried biomass of each sample was ground in a mortar and moved to a prepared vial for subsequent preparation for stable isotope analysis. The Petri dishes were cleaned and weighed on the same analytical scale. The dry biomass of each size fraction on each station was calculated by subtracting the weight of the petri dish from the dry weight with Petri dish. In total I analyzed size-fractionated mesozooplankton biomasses of 12 stations.

The biomass of samples from the RMT 8 net (4,5 mm mesh size) calculated using macrozooplankton abundances and size distributions in combination with length-weight relationships of the most abundant species. At each station, I counted the number of each macrozooplankton taxon from samples preserved in 4% formaldehyde/seawater solution. The abundance of each taxon was calculated with formula (1):

$$Abundance\left[\frac{ind}{m^3}\right] = \frac{number\ \ of\ organisms\ \times split-factor}{filtred\ \ volume\ [m^3]} \qquad (1)$$

I used the length measurements of the animals to calculate the mean individual length of each taxon at each station. I then estimated the mean individual weight of each taxon at each station by applying length-weight regressions from this study and other sources in most taxa (Table 2).

Table 2. Summary of Length-weight regressions for macrozooplankton taxa. (DW- dry weight, x – mean length)

Taxon	Length-weight regression Parameters	R^2/ goodness of fit	sample size	Source
A. glacialis	$DW = 0.013892 \times x^{2.4397}$	0.91591	70	Data from M. A. Klasmeier unpublished
T. abyssorum	$DW = 0.01970 \times x^{2.29976}$	0.90548	26	This study
T. libellula	$DW = 0.002654 \times x^{3.00226}$	0.962793	60	
E. holmi	$DW = 0.0106 \times x^{2.5234}$	-	-	Flores et all. 2019
O. glacialis	$DW = 0.004 \times x^{2.8983}$			
Gammarus wilkitzkii				
Gammarid amphipod				
T. inermis	$DW = 0.0002905 \times x^{3.5451962}$	0.932437	108	This study
T. longicaudata				
Zoea larvae				
Furcilia larvae				
Chaetognata	$DW = 0.0008401 \times x^{2.6571322}$	0.9968066	220	Immerz 2016
Sagitta spp.	$DW = 0{,}3471e^{0{,}0645x}$	0.9411	27	Data from Mizdalski 1988
Clione limacina	$DW = 1.6146e^{0.088x}$	0.748	-	Böer 2005
Beroe spp.	$DW = 47.611 \times V(jelly\ fish)[ml] + 54.899$	0.9435	24	C.David unpublished

In cephalopods, individual dry mass was calculated assuming that 1,5 ml of squid contain 80% of water (Schaafsma 2018), volume of squids were calculated assuming a cylindrical body shape. In *Limacina* spp., dry weight was calculated assuming that the animals had a mean diameter of 2 mm and weighed on average 0,272 mg (Mizdalski 1988). For the calculation of Jellyfish biomass I added the volume from formaldehyde samples, to the volume of jellyfish measured directly on board from fresh sample. In jellyfish observed in the formaldehyde samples, I used the measured length and width of each animal to estimate the volume, Data of the volume of jellyfish *Beroe* spp. and *Mertensia* spp. measured on board were taken from stations protocols. The mean biomass of Jelly fish was calculated according to Carmen David (unpublished) formula.

The total biomass of each taxon at each station was estimated by multiplying the mean individual biomass with the abundance:

$$Biomass[taxon] = mean\ Biomass[ind] \times abundance[taxon] \qquad (2)$$

The mean individual dry weights of *T.libellula*, *T.abyssorum*, *T.longicaudata*, *T.inermis, A. glacialis* were calculated using the length-weight regressions described above in chapter 3.4 (Table 2). Dry biomass of furcilia and zoea larval was calculated using the *Thysanoessa* spp. formula obtained in this study, assuming that the regression is similar and larval abundance and biomass are not large. Dry biomass of fish larvae was calculated according to David et al. (2015). The length-weight regression for *Sagitta* spp. was built based on data for *Sagitta gazellae* from Mizdalski (1988). Calculation of dry biomass for Chaetognata were carried out using length-weight relationships obtained from expedition PS92, which was largely situated in the same area and took place at the same season as PS106 after Immerz (2016). Calculation of dry biomass for *C. limacina* were carried out after Böer (2005)**.** Dry biomass calculation of the rare amphipod species *Eusiris holmii, Onisimus glacialis*, *Gammarus wilkitskii* and other gammarid amphipods were carried out according to Flores et al. (2019).

Organisms from the RMT 8 were divided into size fractions of 4000 µm, 8000 µm, 16000 µm, 32000 µm, 64000 µm according to organism length. Then, the biomass for each fraction at each station was calculated and combined with the biomass of mesosooplankton from the RMT 1 to obtain biomass spectra.

3.5. Bulk Stable Isotope Analysis (BSIA)

All samples for isotope analysis were prepared in Alfered-Wegener-Institute and processed by LIENSs Stable Isotope Facility laboratory, University of La Roshelle in France.

Samples were prepared according to instructions given by the laboratory. The freeze-dried size-fractioned samples of biomass from the RMT-1 mesozooplankton net were homogenized in a mortar and moved to prepared clean glass vial. From freeze-dried macrozooplankton organisms of *T.libellula*, *T.abyssorum*, *T.longicaudata*, *T.inermis* 9 - 10 organisms of approximately the same length from different stations were selected and homogenized. From the material of mesozooplankton three replicates of 0.3-1.0 mg were taken. From the material of macrozooplankton one replicates of 0.3-1.0 mg were taken. For further analysis, each replicate was placed in a tin capsule and carefully closed and a ball made. Each sample ball was placed in a separate cell in a specially prepared

96-well trays for the analysis and movement of samples. The replicates were analyzed for %C, %N, $\delta^{13}C$ and $\delta^{15}N$ the LIENSs stable isotope facility. The C:N ratio was calculated from obtained data with division %C by %N. Samples and 96-well trays were stored in desiccators at room temperature to avoid of humidity.

Elemental analyzer Flash 2000 (Thermo Scientific, Milan, Italy) and Isotope ratio mass spectrometer Delta V Plus with a Conflo IV interface (Thermo Scientific, Bremen, Germany) were used for analysis. **$\delta^{13}C$:** USGS-61, USGS-62, **$\delta^{15}N$:** USGS-61, USGS-62 were used the for calibration of the stable isotope measurements. Analytical precision: **$\delta^{13}C$:** <0.10 ‰, **$\delta^{15}N$:** <0.15 ‰ . Results are expressed in the δ unit notation as deviations from standards (Vienna Pee Dee Belemnite) for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula:

$$\delta 13\mathrm{C} \text{ or } \delta 15\mathrm{N} = [\frac{\mathrm{Rsample}}{\mathrm{Rstandard}} - 1] \times 10^3 \quad (3)$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively.

Bulk stable isotope analysis

The δ13C value was used to analyse the dependency of mesozooplankton on ice algae. In the sea-ice environment, carbon availability is often limited and then results in a higher proportion of the heavy 13C isotope over the lighter 12C isotope (Kohlbach et al. 2016). Thus, the zooplankton which is feeding on the sea ice (ice-algae) has a higher δ13C than zooplankton feeding only on phytoplankton (Kohlbach et al. 2016). The dominant source of nitrogen in marine organisms is dietary protein. Both δ15N and δ13C values increase with increasing trophic level (Tarling et al. 2012; Newsome et al. 2010). The δ15N was used to indicate trophic level differences between the size fractions, because increasing of δ13C can also be due to ice-algae feeding.

C:N ratios

The protein/lipid ratio in the body of each size fraction could be determined by analyzing the C:N ratio. The C:N ratio is often used as an indicator of the protein/lipid ratio in the body (Donnelly et al. 1994). Proteins have a C:N ratio around 3, which increases with increasing lipid content. As lipids have a higher energetic value than proteins, lipid rich food is considered as high quality food. Furthermore, as high lipid content is an indicator

of a fat reserve, used to overcome periods of food scarcity, high lipid content suggests that the organism is in good condition (Harris et al. 1986).

3.6. Data analysis

For comparison of data related to the distribution, the following groups of stations were identified: "Shelf" (station 52), "Slope" (stations 64, 65, 67, 83), "Nansen Basin" (stations 68-78). In order to consider the impact of Atlantic Waters on distribution by stations, the stations were divided into two groups: stations with the highest impact of AW (AW was present in the upper 400 m) and stations with lower impact (AW was lower than 400 m) based on data of Anna Nikolopoulos (Nicolopolous, unpublished data).

Before statistical analysis, the suitability of the data for parametric statistics was plotted as raw data and as histograms and visually assessed for homogeneity of data and normal distribution. For data which were not normally distributed I applied non-parametric tests. The Wilcox runk sum test was used to estimate the significance of differences between two groups of stations (slope and basin) for different parameters: abundance, biomass, d13C, d15N and C:N. The summary of obtained parameters of Wilcox test is shown in Table 4.

Two-Way ANOVA test was used to evaluate the influence of various factors (Station, size fraction) on the values of d13C, d15N and C:N ratio for mesozooplankton and macrozooplankton (*Themisto libellula, Themisto abyssorum, Thysanoessa longicaudata, Thysanoessa inermis*). The summary of obtained parameters of ANOVA test is shown in Table 5. If $p < 0.05$, the differences among the results were considered significant.

Subsequently, Analysis of Variances (ANOVA) was used to estimate the significance of differences in the isotope composition of $d^{13}C$, $d^{15}N$, and in the C:N ratio between the four macrozooplankton species *T.libellula*, *T.abyssorum, T.longicaudata, T.inermis*. The summary of obtained parameters of ANOVA test is shown in Table 6.

The software R version R-3.5.2 was used for statistical analysis.

4. Results

During the expedition PS106 pelagic zooplankton was collected in the upper 100 m in May-July 2017. Four stations were located at the shelf and shelf slope – 52, 64, 65, 83 with depth from 139 m to 532 m. Station 67 was at the very edge of the slope, but was groupped to the slope because it showed similar species composition and mesozooplankton size composition. Stations from 70 to 80 were located in the Nansen basin between 2003 m and 4049 m ocean depth. Distribution of water masses was typical for this region of Arctic Ocean and reflects the interactions between the main components Polar Surface Water (PSW), Atlantic Water (AW) and deep water-masses resulting in the mixed products warm Polar Surface Water (wPSW) and Modified Atlantic Water (MAW) (Nicolopoulos et al. 2018).

4.1. Taxonomic composition and abundance of macrozooplankton

In total 15 stations were analysed for the taxonomic composition and abundances of macrozooplankton (Table 3). The total number of taxa was the highest at station 52 (14) and station 83 (12), which were located on the shelf and slope. A high number of taxa was at the deep-sea station 80 (11), which was located near station 83. Acording to the data obtained on board by SUIT (Flores et al. 2018) and CTD (Nikolopoulos, unpuplished data) a phytoplankton bloom was observed at stations 80 and 83. At the other stations the number of taxa ranged from 7 to 9. The number of taxa on the shelf and slope was significantly higher than in the basin (Wilcox test: $W=40$, $p=0.01709$, $\alpha=0.05$).

T.libellula and Chaetognata were recorded at all stations. *T. longicaudata* was recorded at all stations except station 76. *T.abyssorym. T.inermis. Sagitta* spp. *Beroe* spp and *Mertensia* spp were also common at almost all stations*. A.glacialis. E.holmii*. zoea and furcilia larvae and Sepiida were rare. *G. wilkitsi* and undetermined Gammuarid Amphipoda were found only one at station 83. *Limacina* spp was found once at station 52, undetermined Hyperiid organism at station 64. Fish larvae were recorded at stations 52 and 64. In total of 21 taxa were recorded on the transect, 19 taxa were found on the shelf and slope and 15 in the Nansen basin (Table3, Fig.4).

Table 3. Taxonomic composition of macrozooplankton across the Barents Sea shelf slope and Nansen basin

		Shelf and slope				Nansen basin										
	Station number	**52**	**64**	**65**	**83**	**67**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**80**
Taxon	**Total number of taxa**	**14**	**9**	**9**	**12**	**8**	**8**	**9**	**8**	**7**	**9**	**8**	**8**	**7**	**8**	**11**
Amphipoda	A. glacialis	+			+				+							
	T. abyssorum	+			+		+	+	+	+	+	+	+		+	+
	T. libellula	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	O.glacialis															+
	E. holmi					+					+				+	
	G.wilkitzkii				+											
	Gammuarid amphipod				+											
	Hyperiid		+													
Euphausiacea	T. inermis	+	+	+	+	+	+	+			+	+	+	+	+	+
	T. longicaudata	+	+	+	+	+	+	+	+	+	+	+		+	+	+
	Zoea larvae	+			+											+
	Furcilia larvae				+											+
Chaetognata	Chaetognats	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Sagitta spp	+		+			+	+	+	+	+	+	+	+	+	+
Pterapoda	C. limacina	+	+	+	+	+	+						+	+		+
	L. helicina	+														
Cnidaria+ Ctenophora	Beroe spp	+	+	+	+	+		+	+	+	+	+	+	+	+	
	Mertensia spp	+	+	+		+	+	+	+	+	+	+				+
	Hydromedusae	+														
Sepiida	Sepiida			+				+					+			
Fish larvae	Fish larvae	+	+													

Results of macrozooplankton abundance and contribution of the main groups to the total number are shown in Figure 4. The highest abundance of macrozooplankton was at station 80 (0.35 ind. m^{-3}) (see appendix 1), wich was located in the Nansen basin close to shelf slope. The lowest total abundance was at station 67 (0.01 ind. m^{-3}), wich was located also in the Nansen basin close to the shelf slope. On the shelf and slope group of stations abundance ranged from 0.03 to 0.07 ind. m^{-3}. The highest abundance in this group of statons was at station 83 (0.07 ind. m^{-3}), wich was located to the west (Fig. 2) and phytoplankton bloom was noticed there (Flores et al. 2018; Nikolopoulos,

unpublished data). On avarage total abundance on the slope and in Nansen Basin was not sagnificanly different (Wilcox test: W=11, p=0.2398, α=0.05) (Table 4).

Chaetognata were the dominant group of macrozooplancton at almost all stations except stations from 52 to 67, which were located at the Barents sea shelf slope and near to slope. The contribution of Chaetognata ranged from 3% to 54 % at shelf and from 5% to 94% in the Nansen basin (see appendix 2). The contribution of Amphipoda was low at all stations and ranged from 1% to 18%. The contribution of Euphauseacea ranged from 2% to 70%. The highest contribution of Euphauseacea was at stations 65 (62%) and 67 (70%). The stations were located on the shelf slope and near to the slope were influenced by Atlantic Water (AW) masess. At station 67 AW even reached the upper 100 m. The taxonomic composition of the shelf and slope was very diverse. Different groups of macrozooplanton have made different contributions, therefore it is difficult to identify the dominant group in terms of number. Not a small contribution was made by Eaphuseacea from 4% to 62 % and Cnidaria and Ctephanophora from 1% at station 83 to 56% at station 64. Contribution of Pterapoda was quite large at stations 64 (32%) and 65 (25%). Some organisms of Sepiida were noticed at stations 65, 71, 76 with very tiny contributions. Fish larvae were noticed at station 52 (15%) and 64 (2%).

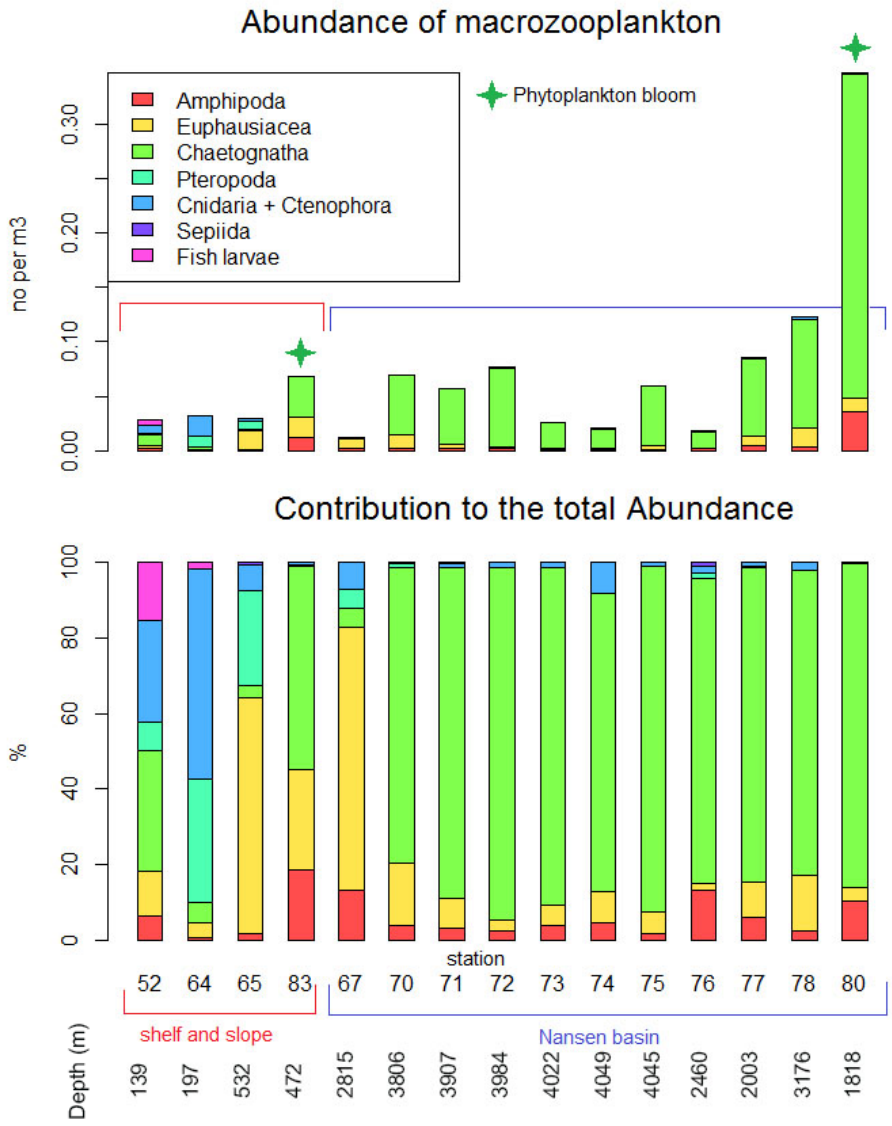

Fig. 4. Abundance and contribution to the total abundance of the main macrozooplankton groups along the RMT transect at shelf and slope of the Barents sea and the Nansen Basin.

4.2. Length-weight relationships

In order to calculate the macrozooplankton biomass for the most common species *T.libellula*, *T.abyssorum*, *T.longicaudata*, *T.inermis, A.glacialis* length-weight relationship models were established. To improve the regression model of *Thysanoessa* spp. species, data on two species *T.inermis* and *T.longicaudata* were used together. The obtained regressions are shown in Figure 5.

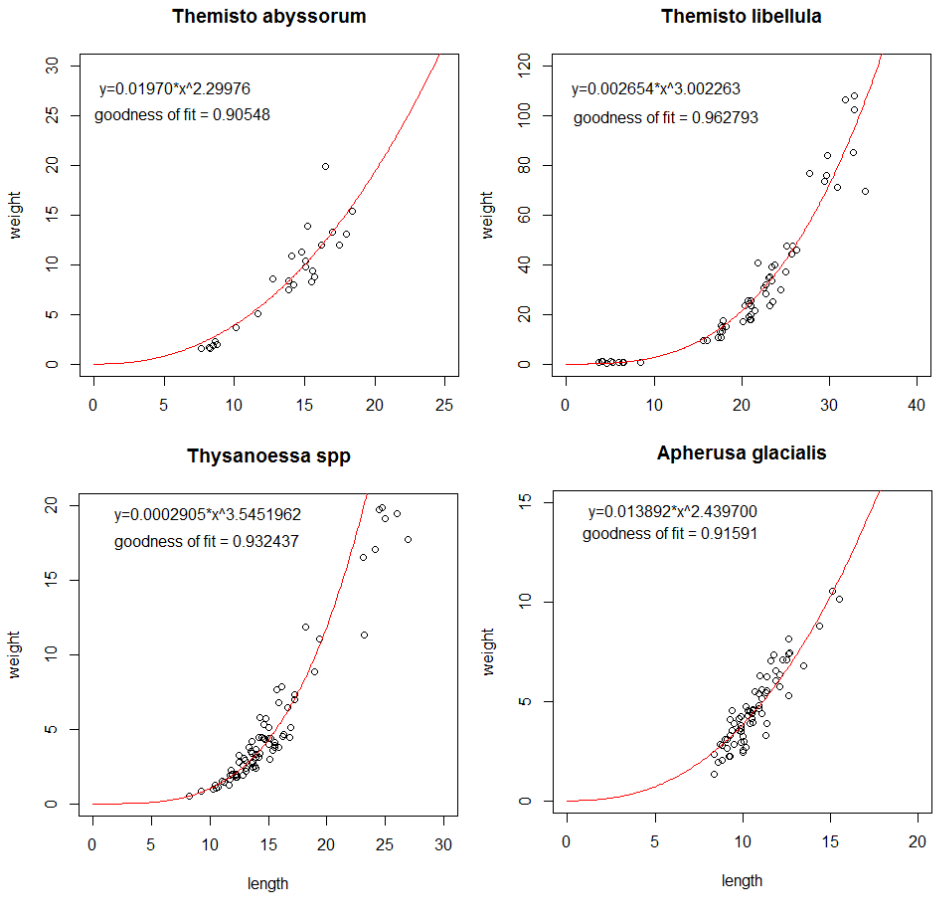

Fig.5. Length-weight relationships for Themisto abyssorum, Themisto libellula, Thysanoessa spp, Apherusa glacialis.

4.3. Biomass of macrozooplankton

Biomass of macrozooplankton was calculated from RMT8 net formoldehyde samples. In total 15 stations were analysed. Results of macrozooplankton biomass and contribution of the main groups to the total biomass are shown in Figure 6.

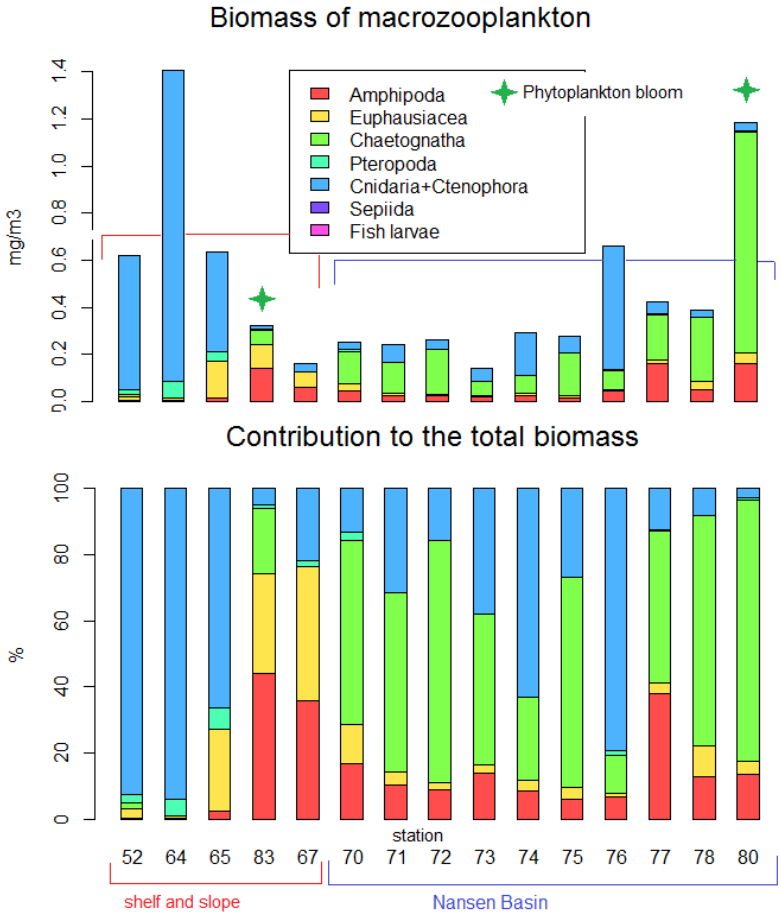

Fig.6. Biomass and contribution to the total biomass of the main macrozooplankton groups along the RMT transect at shelf and slope of the Barents sea and the Nansen Basin.

The highest biomass of macrozooplankton was at station 64 (1.4 mg m^{-3}) (see appendix 3), wich was located on the shelf. The lowest biomass was at the most nothern station 73 (0.1 mg/m^3). The lowest biomass on the shelf and slope group of stations was at station 83 (0.3 mg/m^3). However, at another station 80 where there was a phytoplankton bloom (Flores et al. 2018; Nikolopoulos, unpublished data),there was a high biomass (1.2 mg/m^3). Relatively high biomass was at station 76 (0.7 mg/m^3). On average the biomass on the shelf and in the Nansen Basin was not sagnificanly different (Wilcox test: W=25, p=0.5395, α=0.05)(Table 4).

Contribution of the main groups of macrozooplankton varied at different stations. Contribution of Chaetognata ranged from 0.2% to 79% (see appendix 4). Contribution of Chaetognata was very low at stations of the Barents sea shelf and slope 52, 64, 65, 67. Contribution of Cnidaria and Ctenophora was quite large and varied from 3% (station 80) to 94% (station 64). Contribution of Amphipoda varied from 0.3% to 44% and was very

low at stations 52, 64 and 65 on the shelf. Contribution of Euphausiacea was quite big on the shelf and slope station 65 (25%), station 83 (30%) and station 67 (41%). At station 67 AW even reached upper 100 m. Contribution of Pterapoda, fish larvae and Sepiida to the biomass was very small.

4.4. Biomass of mesozooplankton

The dry weight of mesozooplankton biomass was measured for each size fraction (Fig. 7). In total, 12 stations were analyzed. Stations 52, 64, 65, 67 were located on the shelf and shelf slope between 2003 m and 4049 m ocean depth. Results of mezooplankton biomass and are shown in Figure 7.

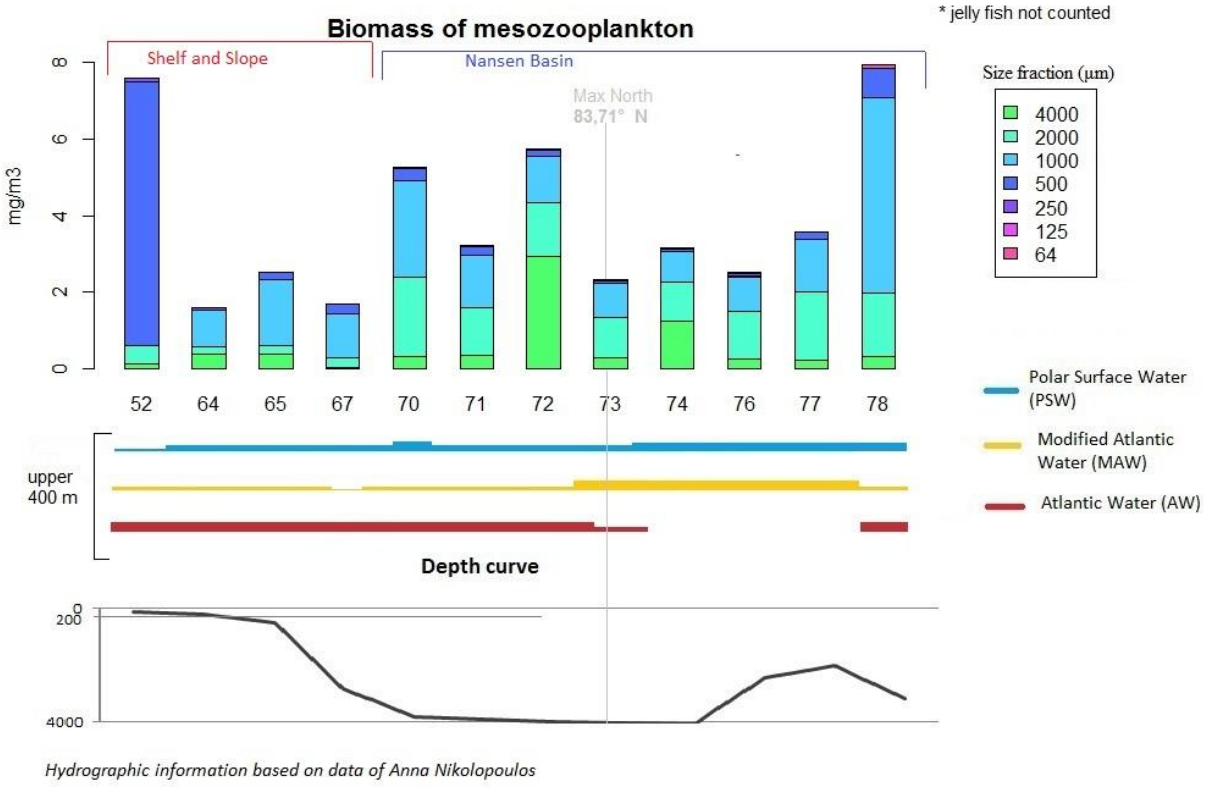

Fig. 7. Comparison of mesozooplankton biomass along the RMT transect. Water mass influence and depth profile. Hydrographic information based on data of Anna Nikolopoulos (Nikolopoulos unpublished).

The highest total mesozooplankton biomass was found at station 78 (7.9 mg/m^3) (see appendix 5), which was located in the Nansen basin. In total, there was a high rate of biomass on the shelf station 52 (7.6 mg/m^3). Relatively high biomasses were observed at stations 70 and 72 (5.3 and 5.8 mg/m^3, respectively). The lowest biomass were observed at station 64 (1.6 mg/m^3).The mesozooplankton biomass at the other stations varied

from 1.7 to 3.6 mg/m^3. On average, the biomass on the slope was significanly lower than in the Nansen Basin (Wilcox test: W=2, p=0.04848, α=0.05)(Table 4). The biomass at the stations influenced by AW and at stations not influenced by AW was not significanly different (Wilcox test: W=12, p=0.8636, α=0.05)(Table 4).

Zooplankton of bigger size fractions (4000 µm and 2000 µm) were present at all stations. The highest amount of the 4000 µm fraction biomass was observed at deep-sea station 72, the lowest amount was found at station 67. At the other stations, the biomass of this size classes varied. The biomass of the 2000 µm fraction was highest at station 70 and was approximately the same at the stations from 71 to 78, and higher than at stations 52 to 67, which were located on the shelf and slope and near to it (Fig 2). The 1000 µm fraction was present at all stations except of station 52, and was higher in station 78. Relatively high biomasses of 1000 µm were observed at stations 70. At the other stations, the biomass of this size class varied. The highest quantity of biomass of the 500 µm fraction was found at station 52. It was only one station with dominant fraction 500 µm. At the same time, the fraction 1000 µm was absent, and the contribution of the fraction 2000 µm was very small. At other stations, the fraction 500 µm contribution was very small and varied. The smaller size fractions from 250 to 64 µm were present in very small amounts. Fraction 64 µm was absent or was lower than the detection of scales at stations 64, 67, 71, 74.

4.5. Biomass distribution in size fractions (meso- and macrozooplankton)

The Figure 8 shows the combined biomass of macro- and mesozooplankton. The macrozooplankton biomass was low except station 72 (Fig. 9), so the total biomass did not change significantly when summing up. Jellyfish biomass was not counted in the distribution by fractions, as it is difficult to classify them by fractions.

The total biomass was highest at the deep-sea station 78 (8.3 mg/m^3)(see appendix 6) and at the shelf station 52 (7.6 mg/m^3). Relatively high biomass was at the deep-sea stations 72 (6.0 mg/m^3) and 70 (5.5 mg/m^3). The lowest biomass was at station 64 (1.7 mg/m^3) and 67 (1.8 mg/m^3). The total zooplankton biomass at the other stations varied from 2.6 to 4.0 mg/m^3. On average, the biomass on the slope was significanly lower than in the Nansen Basin (Wilcox test: W=2, p=0.04848, α=0.05)(Table 4). The biomass at the

stations influenced by AW and at stations not influenced by AW was not significanly different (Wilcox test: W=12, p=0.8636, α=0.05)(Table 4).

The contribution of the fractions is shown in Figure 9. The main contribution was made by fractions from 500 µm to 4000 µm. At almost all stations, the fraction 1000 µm contributed greatly from 20.3% to 63.0% (see appendix 7), except station 52, where the fraction 500 µm dominated (90.2%). The fraction 1000 µm was absent at station 52. At other stations, the contribution of size fraction 500 µm 1.4% (station 74) to 9.2% (station 78). The fraction contribution of 2000 µm ranged from 6.4% (station 52) to 46.4% (station 76). The contribution of 2000 µm was relatively high at station 77 (45.7%), station 73(43.7%), 70 (37.7%), 71 (36.4%). The contribution at other stations varied from 8.3% to 30.8%. The contribution of the 4000 µm fraction was 1.2% to 49.2% and was the lowest at station 67 and highest at station 72. The contribution was relatively high at station 74 (37.8%), station 64 (21.3%). The contribution at other stations varied from 1.6% to 13.7%. The contribution of the 8000 µm was not high and varied from 5% (station 77) to 0.2% (station 52). The contribution at other stations varied from 1.6% to 13.7%. The contribution of the 16000 µm was also not high and varied from 6.4% (station 67), 6.1% (station 64) to 0.4% (station 52). Smaller fractions from 64 µm to 250 µm contributed very little as well as large fractions from 320000 µm. The biggest fraction 64000 µm was present only at station 74.

In total, contribution of fraction bigger 2000 µm was more than half at station 74 (71.9%), station 72 (76.6%), station 76 (61%), station 77(60.1%), station 71(51.6%). The contribution of fractions bigger 2000 µm was significantly higher in the Nansen Basin than on the shelf (Wilcox test: W=2, p=0.04848, α=0.05)(Table 4)

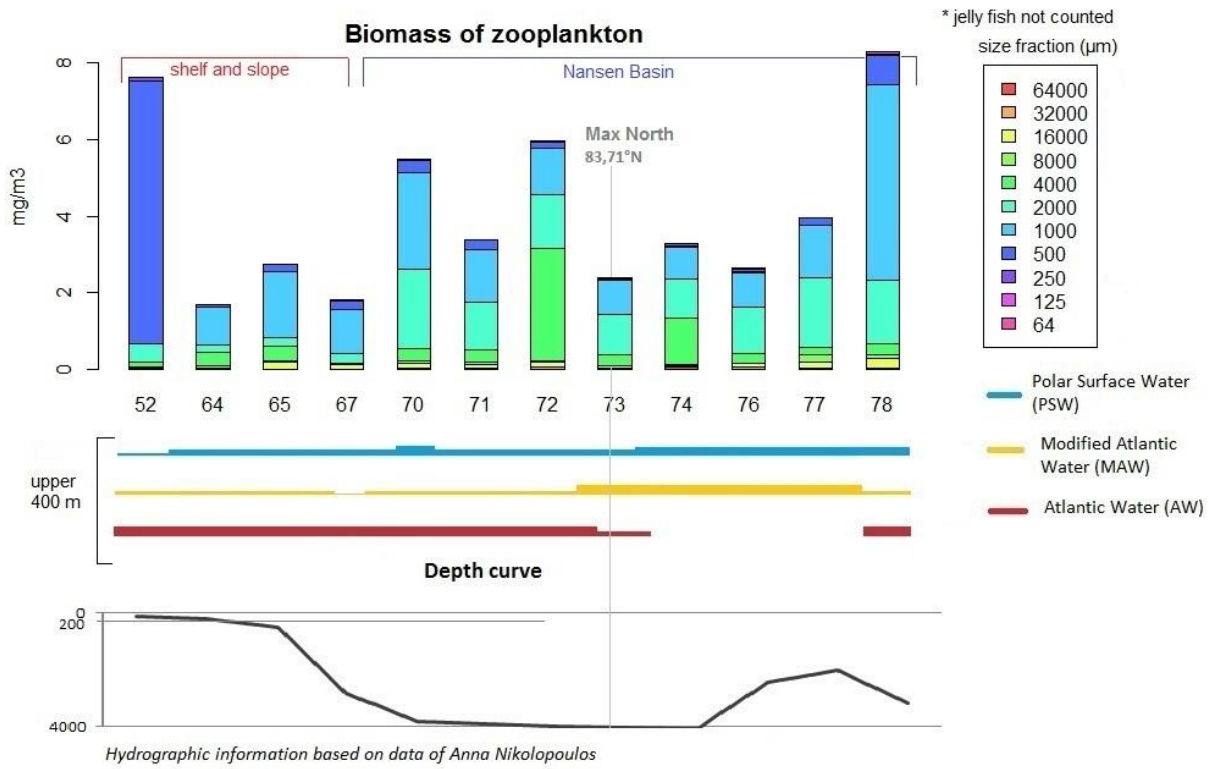

Fig. 8. Biomass distribution in size fracrions along the RMT transect at shelf and slope of the Barents sea and the Nansen basin. Water mass influence and depth profile. Hydrographic information based on data of Anna Nikolopoulos (Nikolopoulos, unpublished).

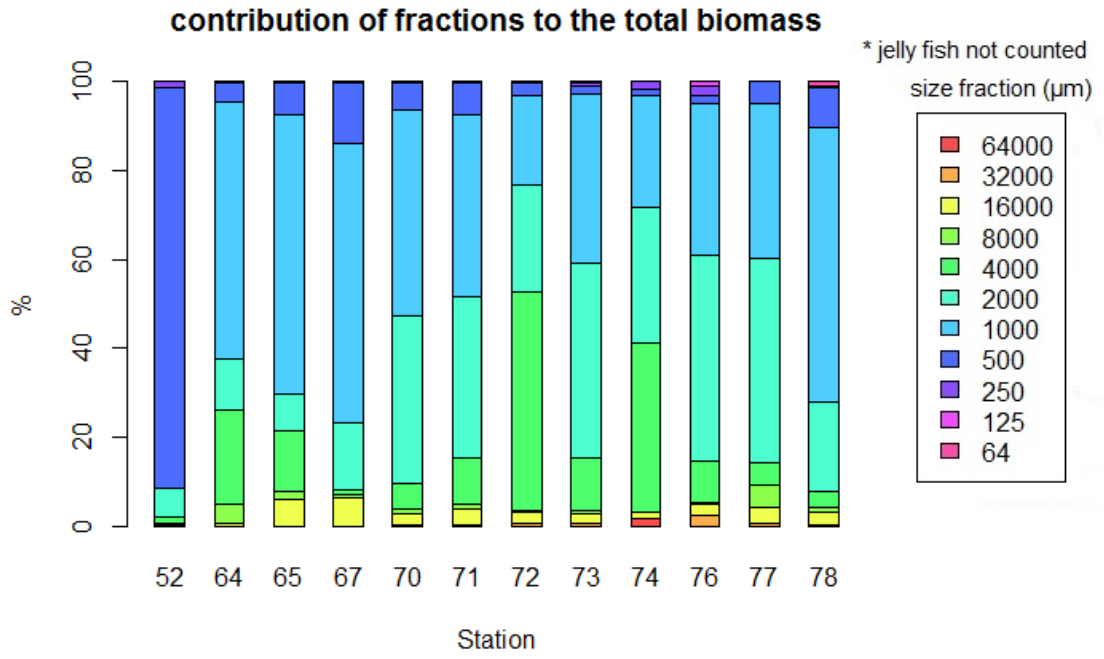

Fig. 9. Contribution of fractions of zooplankton to the total biomass along the RMT transect at the shelf and slope of the Barents sea and the Nansen basin.

4.6. Isotope analysis of $d^{13}C$, $d^{15}N$ and C: N ratio of mesozooplankton

Isotopes $d^{13}C$, $d^{15}N$ and C:N ratio were determined in mesozooplankton samples by fractions. The distribution of isotopes by fractions and stations is shown in Figure 10.

In all fractions, the median of $d^{13}C$ ranged from -25.57 ‰ to -26.58 ‰ (Fig.10). Fraction 4000 µm had the highest $d^{13}C$. Fractions 2000 µm and 64 µm were lowest $d^{13}C$. According to Two-Way ANOVA test the fraction had a significant effect on $d^{13}C$ (df=1, F=5.530, p=0.0214, α=0.05)(Table 5). The distribution of $d^{13}C$ varied at different stations in the different size fractions, but the variability was not statistically significant (Two-Way ANOVA test: df=1, F=0.176, p=0.6840, α=0.05)(Table 5). Slope stations 64, 65, 67 had significantly higher $d^{13}C$ than stations in the Nansen Basin (Wilcox test: W=24, p=0.01212, α=0.05)(Table 4).

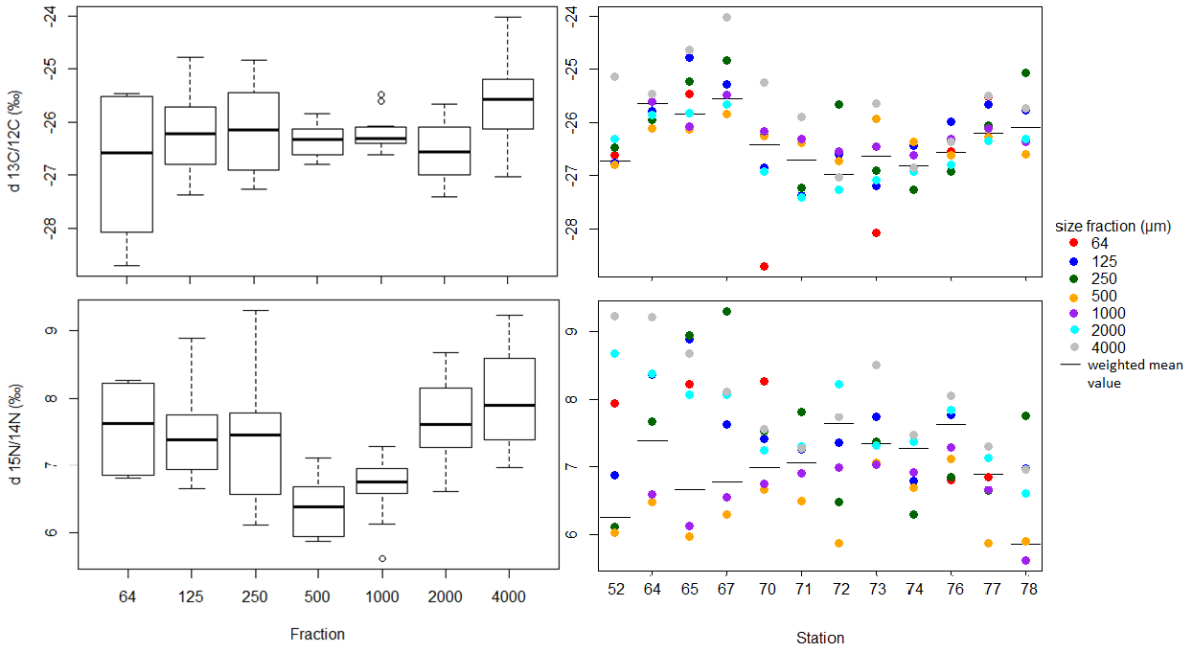

Fig.10. Distribution of isotopes $d^{13}C$ and $d^{15}N$ for the different size fractions and stations in mesozooplankton samples along the RMT transect at the shelf and slope of the Barents sea and the Nansen basin. The mean value is expressed taking into account the contribution of the biomass of each fraction.

The distribution of $d^{15}N$ varied with different fractions. The lowest fraction was 500 µm (6.39 ‰)and grew from 500 µm to 4000 µm fraction.The highest $d^{15}N$ was in the fraction 4000 µm (7.89‰). Smaller fractions also had relatively high median $d^{15}N$ - 64 µm (7.6‰), 125 µm (7.4‰), 250 µm (7.45‰). The distribution of $d^{15}N$ varied in relation to the stations and different fractions were more scattered in values at stations 52 - 67. According to

Two-Way ANOVA test the fraction had a significant effect on $d^{15}N$ (df=1, F=7.734, p=0.00689, α=0.05)(Table 5), and station had no significant effect (df=1,F=0.672, p=0.4210, α=0.05)(Table 5). It is difficult to trace any patternts in the distribution of mean values of $d^{15}N$ by stations. According to Welcox test the weighted mean values of $d^{15}N$ at slope stations was not different from deep-sea stations (W=8, p=0.497, α=0.05)(Table 4). One can trace that stations 72-76 had significantly higher mean values of $d^{15}N$ than the other stations (Wilcox test: W=30, p=0.01616, α=0.05)(Table 4).

The figure 11 shows that the shelf stations (green) was grouped together and had viriability in $d^{13}C$ and $d^{15}N$. The Stations of Nansen Basin (blue) was grouped together, exept station 78, which was located seperatly. Station 52 (red) was located separately.

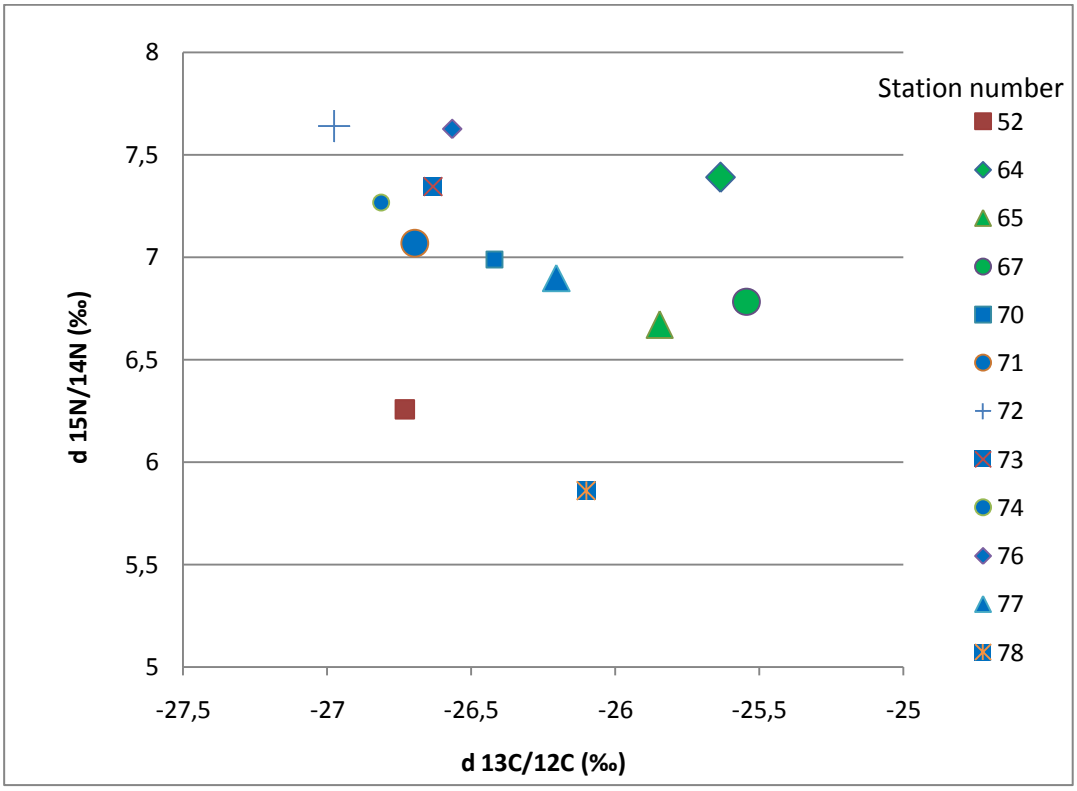

Fig. 11. Scatterplot of the combined $d^{13}C$ and $d^{15}N$ for the weighted mean value of each station in mesozooplankton samples along the RMT transect at the shelf and slope of the Barents sea and the Nansen basin. The mean value is expressed taking into account the contribution of the biomass of each fraction. Red color – shelf, Green color – slope, Blue color – Nansen Basin.

The distribution of C:N ratio for the different size fractions and stations is shown in Figure 12. The median of C:N in fraction 64 µm was high as well as variability. Smaller size fractions 64 µm - 250 µm had higher variability within fraction then bigger fractions

500 µm - 4000 µm. The median of C:N was highest in fraction 2000 µm (5.9) . The median of 4000 µm (5.3) fraction was lower than for 2000 µm (5.9). The C:N varied with the stations. According to Two-Way ANOVA test the fraction (df=1, F=0.424, p=0.517, α=0.05)(Table 5) or station (df=1, F=0.247, p=0.148, α=0.05)(Table 5) had no significant effect on C:N ratio. However, it is possible to trace that shelf and slope stations 52-67 had significanly lower C:N ratio then other stations in Nansen Basin (Wilcox test: W=0, p=0.00404, α=0.05)(Table 4).

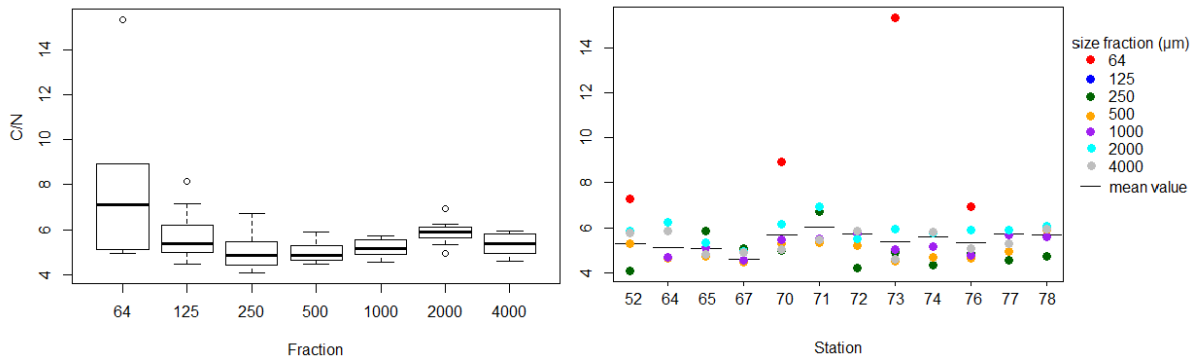

Fig.12. Distribution of C:N ratio for the different size fractions and stations in mesozooplankton samples along the RMT transect at shelf and slope of Barents sea and the Nansen basin. The mean value is expressed taking into account the contribution of the biomass of each fraction.

4.7. Isotope analysis of d^{13}C , d^{15}N and C: N ratio of macrozooplankton

Isotopes d^{13}C , d^{15}N and C:N ratio were determined in four species of macrozooplankton *Themisto libellula*, *Themisto abyssorum*, *Thysanoessa longicaudata*, *Thysanoessa inermis*. The distribution of isotopes by specie is shown in Figure 13.

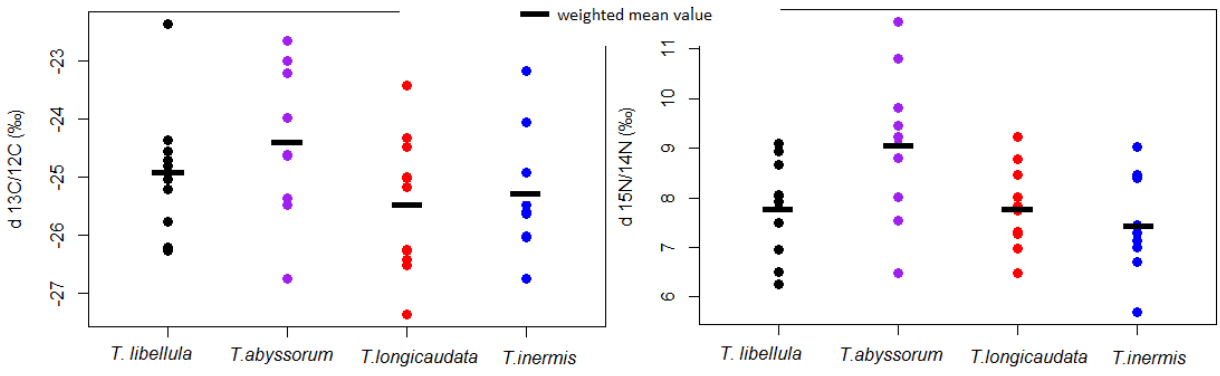

Fig.13. Distribution of isotopes d^{13}C and d^{15}N for T.libellula, T.abyssorum, T.longicaudata, T. inermis. The mean value is expressed taking into account the contribution of the biomass of each fraction.

The mean value of $d^{13}C$ and $d^{15}N$ varied in different species. The mean value of $d^{13}C$ was highest for *T.abyssorum* and lowest for *T.longicaudata*. The mean value of $d^{15}N$ was highest for *T.abyssorum* and lowest for *T.inermis*. Acording to ANOVA test there was no significant difference between species in $d^{15}N$ (df=1, F=1.497, p=0.229, α=0.05)(Table 6) and in $d^{13}C$ (df=1, F=1.57, p=0.218, α=0.05)(Table 6). According to Two-Way ANOVA test size of the *T.libellula* organism had effect on $d^{13}C$ (df=1, F=11.000, p=0.01607, α=0.05)(Table5) and $d^{15}N$ (df=1, F=10.193, p=0.0188, α=0.05). The size range of *T.libellula* was 20.7 mm ($d^{13}C$ = -24.28‰, $d^{15}N$ = 7.93‰) to 34.10 mm ($d^{13}C$ = -22.35‰, $d^{15}N$ = 8.93‰), and one organism was 6.5 mm ($d^{13}C$ = -24.36‰, $d^{15}N$ = 6.96‰). According to Two-Way ANOVA test size of the *T.abyssorum* organism had effect on $d^{15}N$ (df=1, F=16.204, p=0.0101, α=0.05)(Table 5) and had no effect on $d^{13}C$ (df=1, F=0.127, p=0.736, α=0.05)(Table 5). The size range of *T.abyssorum* was 13.9 mm ($d^{15}N$ = 10.81‰) to 18.0 mm ($d^{15}N$ = 9.82%), and one organism was 7.6 mm ($d^{15}N$ = 6.48‰). For other two specie *T.longicaudata* and *T. inermis* there was no spatial or size effect (Table 5).

The distribution of C:N ratio for species of macrozooplankton and stations is shown in Figure 14. The mean values of C:N ratio for T*.libellula, T.abyssorum, T.Longicaudata* were relatively on the same level. Acording to ANOVA test there was no significant difference between species in C:N ratio (df=1, F=3.966, p=0.0539, α=0.05). An increased mean value for *T. inermis* was observed, but not statistically confirmed. The distribution of values by stations showed that the values for *Thysanoessa* spp and *T.libellula* grew to the last transect stations (78, 80, 83) where phytoplankton bloom was noted (Flores et al. 2018; Nikolopoulos, unpublished data). According to Two-Way ANOVA test spatial effect was only for *T.libellula* (df=1, F=7.350, p=0.0350, α=0.05).

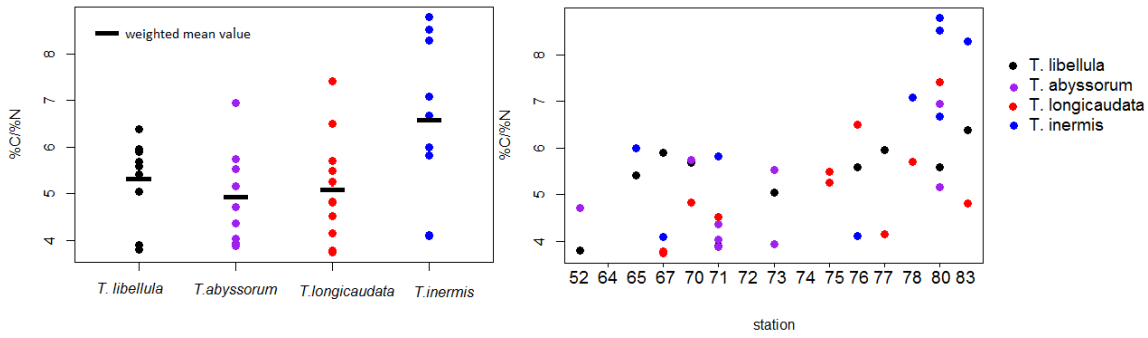

Fig. 14. Distribution of isotopes of C:N ratio for Themisto libellula. Themisto abyssorum. Thysanoessa longicaudata. Thysanoessa inermis and for stations along the RMT transect at the shelf and slope of the Barents sea and the Nansen basin. The mean value is expressed taking into account the contribution of the biomass of each fraction.

4.8. Data analisis

The summary of obtained parameters of Wilcox test is shown in Table 4. The summary of obtained parameters of Two-Way ANOVA test is shown in Table 5. The summary of obtained parameters of ANOVA test is shown in Table 6.

Table 4. Summary of Wilcox tests (n=sample size, W- Wilcoxon statistical criterion, p-value)

Parameter	Stations	n	W	p
Total Abundance of Macrozooplankton				
Slope	64-67,83	4		
Nansen Basin	68-80	10	11	0.2398
Total Biomass of Macrozooplankton				
Slope	64-67,83	4		
Nansen Basin	68-80	10	25	0.5395
Total Biomass of Mesozooplankton				
Slope	64-67	3		
Nansen Basin	68-78	8	2	0.0485
influenced by AW	52-73,78	9		
not influenced by AW	74-77	3	12	0.8636
Total Biomass of Zooplankton				
Slope	64-67	3		
Nansen Basin	68-78	8	2	0.0485
influenced by AW	52-73,78	9		
not influenced by AW	74-77	3	12	0.8636
Contribution of fractions >2000 µm to the total biomass				
Slope	64-67	3	2	0.0485
Nansen Basin	68-78	8		
Weighted means of d13C for Mesozooplankton				
Slope	64-67	3		
Nansen Basin	68-78	8	24	0.0121
Weighted means of d15N for Mesozooplankton				
Slope	64-67	3		
Nansen Basin	68-78	8	8	0.4970
influenced by AW	72-76	4		
not influenced by AW	52-71,77,78	8	30	0.0162
Weighted means of CN ratio for Mesozooplankton				
Shelf and slope	52-67	4		
Nansen Basin	68-78	8	0,0	0.0040

Table 5. Summary of Two-Way ANOVA test (n=sample size, Df -degrees of freedom, F- Fisher criterion, p-value). Weighted means were used to analyse the influence of factor Station on parameters.

	Parameter	Factor	N	Df	F	p
Mesozooplankton	d 13C (‰)	Station	12	1	0.176	0.6840
		Size Fraction	7	1	5.53	0.0214
	d 15N (‰)	Station	12	1	0.672	0.4310
		Size Fraction	7	1	12.27	0.0008
	C: N ratio	Station	12	1	0.247	0.1480
		Size Fraction	7	1	0.424	0.5170
Themisto libellula	d 13C (‰)	Station	10	1	1.375	0.2853
		Size	10	1	11	0.0160
	d 15N (‰)	Station	10	1	1.387	0.2835
		Size	10	1	10.193	0.0188
	C: N ratio	Station	10	1	11.703	0.0141
		Size	10	1	1.081	0.3385
Themisto abyssorum	d 13C (‰)	Station	9	1	0.54	0.4950
		Size	9	1	0.127	0.7360
	d 15N (‰)	Station	9	1	16.204	0.0101
		Size	9	1	4.47	0.0881
	C: N ratio	Station	9	1	0.692	0.4430
		Size	9	1	0.223	0.6570
Thysanoessa longicaudata	d 13C (‰)	Station	11	1	3.448	0.1060
		Size	11	1	1.071	0.3550
	d 15N (‰)	Station	11	1	3.706	0.0956
		Size	11	1	1.484	0.2626
	C: N ratio	Station	11	1	4.364	0.0751
		Size	11	1	0.017	0.8988
Thysanoessa inermis	d 13C (‰)	Station	9	1	3.361	0.1260
		Size	9	1	0.295	0.6100
	d 15N (‰)	Station	9	1	3.698	0.1125
		Size	9	1	4.152	0.0972
	C: N ratio	Station	9	1	5.096	0.0736
		Size	9	1	0.355	0.5770

Table 6. Summary of ANOVA tests to estimate the significance of differences between the four species of macrozooplankton T. libellula, T. abyssorum, T. longicaudata, T.inermis (n=sample size, Df -degrees of freedom, F- Fisher criterion, p-value)

Parameter	n	Df	F	p
d 13C/12C (‰)	39	1	1.57	0.2180
d 15N/14N (‰)	39	1	1.497	0.2290
C: N ratio	39	1	3.966	0.0539

5. Discussion

5.1. Taxonomic composition and abundance of macrozooplankton across the Barents Sea shelf slope and Nansen basin.

The taxonomic composition of macrozooplankton in the upper 100 m comprised at least 21 taxa (Table 3). The results indicated a higher number of taxa on the shelf and slope (19 taxa) than in deep-sea areas (15 taxa) (Wilcox test: W=40, p=0.01709, α=0.05), which confirm the first hypothesis.

Chaetognata were a dominant group of macrozooplankton almost at all stations of PS106. Most chaetognaths were not identified to species in this study due to time constraints. According to the literature, the most common species in the study area are *Parasaggitta elegans* and *Eukrohnia hamata*. *P. elegans* dominates in the shelf zone and is rare in areas outside the continental slope (Kosobokova et al. 2010; Kosobokova 2010). *E. hamata* is common in deep-water areas (Kosobokova 2012). In the study area, both taxa were distributed almost at all stations, but the contribution to the abundance and biomass was the largest in the Nansen Basin. It is mentioned that the surface waters are dominated by immature individuals (3-22 mm long) of *E.hamata* and they reproduce in AW, usually at a depth of about 700 m (Richter 1994; Timofeev 1998). In this study, individuals of more than 22 mm have been observed in upper 100 m and AW have been reported to rise higher (Nikolopouos, unpuplished data). Therefore, with the rise of the AW, reproduction may not be as deep, within the upper 400 metres. Although chaetognaths are associated with AW (Kosobokova 2012), they strongly dominated even at stations with weak AW influence in the study area.

T.inermis and *T.longicaudata* were observed almost at all stations. *T.longicaudata* is a common expatriate in the Eurasian sector of the Arctic advected with AW into the Nansen Basin (Kosoboova et al. 2010; Auel and Hagen 2002; Kosobokova 2012). Accordingly, the abundance and biomass was the highest at the slope stations experiencing the strongest influence of AW. This species were observed in the upper 100m, even at those stations where the AW influence was less. This indicates that *T.longicaudata* migrate to the upper layers to a certain extent. However, the preferred depth range of this species is between 200 and 1000 m (Kosobokova et al. 2010), indicating that the major part of the population may not have been captured with the

RMT during PS106. However, presence of *T.longicaudata* at the northernmost stations of the transect in the Nansen Basin indicates the atlantification of the area.

T.libellula and *T.abyssorum* are two widely distributed northern hyperiid amphipods (Koszteyn et al. 1995, Klekowski and Węsławski 1991; Weigmann-Haass 1997; Dalpadado et al. 2001; Dalpadado, 2002) were identfied in samples of RMT8. The typical Arctic amphipod *T.libellula* was found at each station of transect of RMT8 in this study. The authors also confirm the occurrence of the species in the Central Arctic Ocean (Auel and Hagen 2002; Kosobokova et al. 2010) and in the Nansen Basin (Kosobokova et al. 2010) with depth preference 0-200m. *T.libellula* was more abundant than *T.abyssorum*. The Arctic-boreal specie *T.abyssorum* was found even at most northern station 73 in Nansen Basin. *T.abyssorum* abundance was higher at the shelf, which may confirm the increased impact of AW. However, presence of *T.abyssorum* at the northernmost stations of the transects in the Nansen Basin may indicate the atlantification of the area.

The pteropods *Clione limacine* and *Limacina helicina*. are widely distributed in the Arctic Ocean (Mumm 1993; Kosobokova and Hirche 2000; Auel and Hagen 2002; Hopcroft et al. 2005; Kosobokova and Hopcroft 2010). They are found in both the Eurasian and Canadian basins, both shelf and deep-sea. *L.helicina* in our study was found at only one shelf station and had a very small size of about 2 mm. Since the net was 4.5 mm in size, it is likely that most of these small *L. helicina* were not caught in the samples. *C.limacina* was found on the shelf and at deep-sea stations, except the stations north of 83.3°N latitude. The largest contribution of Pteropods to the abundance was found on the shelf and on the slope (Fig. 4). *C.limacina* is assumed to feed on *L.helicina* in the polar waters (Böer 2005), therefore *L.helicina* were possibly present at all stations where *C.limacina* was found.

Organisms associated with the sea ice *G.wilkitzkii*. *A. glacialis* and *O.glacialis* were observed singly and predominantly on the shelf. *O.glacialis and A. glacialis* were also recorded in the Nansen Basin. The literature also mentions that organisms are found everywhere in the Arctic basin (Kosobokova et al. 2010; Hop et al.2000; David et al. 2015). The *E. holmi* was recorded at the stations near the slope and at the northern station 83.46°N. Literary data also confirm the occurrence of this specie in the Nansen basin as well as throughout the Arctic, but the preferred ocean depths of this species are

1000-3000 m (Kosobokova et al. 2010). Since abundance of ice-associated organisms in RMT pelagic samples was low and I found only a few organisms in the samples, it can be assumed that they were accidently falling from the ice during hauling.

It is worth noting that Cnidaria and Ctenophora were in a good condition in the samples preserved in formaldehyde. It have been counted in addition to counted directly on board the ship. Different taxa have been recorded at almost every station and the literature confirms their widespread distribution (Kosobokova et al. 1998; Kosobokova and Hirche 2000; Shirley and Leung 1970).

It's important to mention that the abundance of macrozooplankton was greatly higher on the slope station 80, where phytoplankton bloom was noted (Flores et al. 2018, Nicolopolous, unpublished data). On avarage, total abundance on the slope of the Barens sea and in the Nansen Basin was not significanly different (Wilcox test: $W=11$, $p=0.2398$, $\alpha=0.05$).

As a summary, it can be said that AW bring species related to them far north to the Nansen Basin and the greatest amount of them was observed on the slope, where the impact of boundary current likely increased.

5.2. Biomass distribution, size composition of meso- and macrozooplankton across the Barents Sea shelf slope and Nansen Basin.

In the Arctic Ocean, zooplankton biomass is often dominated by Calanoid copepods (Auel and Hagen 2002; Hop et al. 2019), mostly contributing about 80% of the mesozooplankton biomass (Kosobokova 2012; Kosobokova and Hirche 2000). With a mesh size of 0.33 mm in the RMT1 small copepod species (e.g. *Oithona* spp.) were probably not sampled quantitatively. Copepods > 0.3 mm would be mainly expected in the fractions of 500 µm and 1000 µm. Females of large species (*Calanus* spp.) would be expected in the 2000 µm fractions, and even larger species (*Pareuchaetha, Calanus hyperboreus*) in the 4000 µm size fraction.

The contribution of the 500 µm fraction was the highest on the shelf (about 90%). It should be noted, that the fraction of 1000 µm was absent. It can be assumed, that the Barents sea outflow brought very small species in large abundance on the end of shelf. At the other stations, the fraction 1000 µm contributed greatly from 20.3% to 63.0%. This size fraction could be attributed to the copepod species *C. glacialis.* Northward, in

Nansen Basin, the contribution of fraction >2000 µm was significantly higher than at shelf (Wilcox test: W=2, p=0.04848, α=0.05). In this size fraction females of large species (*Calanus* spp.) would be expected. And even larger species *C. hyperboreus* in the 4000 µm size fraction could be. According to the literature, contribution of *C.hyperboreus* is increasing in the deep water areas (Kosobokova 2012).

Previously, the ARK IX/4 and ARK XI/1 expeditions also recorded high biomass values on the slope of the continental shelf near Spitsbergen due to the influence of young AW masses (Kosobokova 2012, Kosobokova et al. 2010). The data of my study shows the low biomass values on the slope, but high in shelf station 52. However, the highest biomass was oserved at the station 78 in Nansen Basin. This station was located close to the slope area where phytoplankton bloom was observed (Flores et al. 2018; Nikolopoulos ., unpublished data). It is possible that blooming was also present at this station before sampling and zooplankton consumed primary products, increasing biomass. Unfortunately, there were no results in this study of mesosooplankton for this stations, it was not possible to calculate total biomass. However, based on the high biomass of macrozooplankton, it is possible to assume an overall high biomass at these stations. On average, the total biomass of zooplankton on the slope was significanly lower than in the Nansen Basin (Wilcox test: W=2, p=0.04848, α=0.05), without taking into account the stations with phytoplankton bloom.

In order to consider the impact of Atlantic Waters on biomass distribution, the stations were divided into two groups: stations with the highest impact of AW (AW was present in the upper 400 m) and stations with lower impact (AW was lower than 400 m). The biomass at the stations influenced by AW and at stations not influenced by AW was not significanly different in this study (Wilcox test: W=12, p=0.8636, α=0.05). At the same time, at the station 67, where AW reached even the upper 100 m, the contribution of fractions <1000 µm was great, except for the only station situated in waters < 200 m deep (52), where the fraction 500 µm dominated. The increased influence of AW on station 67 and stations on the shelf near the station 67 was also confirmed by the high abundance and biomass of Euphausiacea in comparison with the other stations.

In the beginning of the study, it was assumed as a hypothesis that zooplankton biomass is higher on the shelf and slope and decreases to the Nansen basin. According to the

obtained data, the total biomass of zooplankton on the slope was significanly lower than in the Nansen Basin, and was high at the shelf. The hypothesis was not confirmed. And the data do not coincide with the literature data, where zooplankton was collected in August and September using Midi and Maxi Multinets (Kosobokova 2012, Kosobokova et al. 2010). The difference with the obtained data of this study may be due to differences in sampling methods and time of haul. Furthermore, a patchy distribution of zooplankton in the Arctic Ocean, which can be related to different climate conditions, phytoplankton blooming, influence of water masses and ice or other parameters, may have introduced a high variability in my dataset.

The following hypothesis: “smaller fractions predominate at the stations more exposed to Atlantic Waters. Biomass at these stations may be higher”, was partially confirmed. Indeed, the contribution of smaller fractions at the slope stations was significantly higher where the influence of boundary current increased.

5.3. Variability of the trophic structure and the carbon sources of macro- and mesozoplankton across the Barents Sea shelf slope and Nansen Basin.

According to Two-Way ANOVA test the fraction had a significant effect on $d^{13}C$ (df=1, F=5.530, p=0.0214, α=0.05). In all size fractions, the median of $d^{13}C$ ranged from -25.57 ‰ to -26.58 ‰ and there was almost no variability between different size classes. Fraction 4000 µm had the highest median of $d^{13}C$, this could be due to the trophic enrichment according to high median of $d^{15}N$ and potentially presence of ice amphipods in the sample. Size fraction 2000 µm had lowest median of $d^{13}C$ but at the same time lower median of $d^{15}N$ compared to 4000 µm. These differences could be due to the lower dependency of organisms from the fraction on ice-algae. High median and viriability within the smaller size fractions 125 µm and 64 µm could be because of presence of small particles of higher fractions, which can penetrate during sifting.

Slope stations 64, 65, 67 had significantly higher mean weighted $d^{13}C$ than stations in the Nansen Basin (Wilcox test: W=24, p=0.01212, α=0.05), at the same time, mean weighted $d^{13}C$ was high on the shelf (station 52). According to Welcox test, the weighted mean values of $d^{15}N$ at slope stations was not different from deep-sea stations (W=8, p=0.497, α=0.05), so there was no differences in triphic level at the stations. The variability of $d^{13}C$ data can be correlated with the different compositions of the meso- and

macrozooplankton communities. According to the ratio of the fractions contribution to the total biomass (Fig. 9), the shelf (Station 52), slope and the Nansen Basin can also identified. Different carbon sources could be advected with AW, which have more influence on the slope. Reasons for similar values on the shelf and in the Nansen Basin, probably, are different. On the shelf it could be the predominant influence of coastal waters, as well as it can influence on the zooplankton community composition. In the Nansen Basin it could be the higher influence of Polar Waters. The effect of Ice algae on d13C is difficult to disentangle because the trophic baseline of ice algae and phytoplankton is not known. The Ice algae chlorophyll was generally low in the study area, with lowest values (< 0.2 mg chlα*m^{-2}) between stations 70 and 78. At the all other stations the Ice algae chlorophyll was around 0.2 mg chlα*m^{-2}(G. Castellani, unpublished data). Low ice algae biomass could have caused the lower $d^{13}C$ values in the Nansen Basin than to be expected. The data of this study showed that $d^{13}C$ values in the different size fractions of mesozooplankton ranged from -24 ‰ to -28 ‰. The literature shows from -21.9 ‰ to -25.6 ‰ for copepods in Chukchi Sea (Schell et al 1998), -24.1 ‰ to -31.2 ‰ in Barents sea shelf and slope (Kohlbach et al. 2016). The differences in values, probably, very strongly influenced by different conditions, geographical location. It is likely that individual values for all organisms will be observed for each location.

According to Two-Way ANOVA test the fraction had a significant effect on $d^{15}N$ (df=1, F=7.734, p=0.00689, α=0.05), and station had no significant effect (df=1,F=0.672, p=0.4210, α=0.05)(Table 5). The distribution of $d^{15}N$ varied with different fractions. The lowest fraction was 500 µm (6.39 ‰) and grew from 500 µm to 4000 µm fraction.The highest $d^{15}N$ was in the fraction 4000 µm (7.89‰). This is expected, as the trophic level should increase too, from the small herbivorous copepods (*Pseudocalanus spp*., *C.finmarchicus*) to the more omnivorous *M.longa* to the predatory copepods (*Pareuchaeta* spp.) and amphipods (*Themisto* spp.). Smaller fractions also had relatively high median $d^{15}N$ - 64 µm (7.6‰), 125 µm (7.4‰), 250 µm (7.45‰). The differences could be because of presence of omnivorous organisms. Size classes < 250 µm probably under-sampled, and body parts of higher fractions could have influenced these values.

The distribution of $d^{15}N$ varied in relation to the stations and different fractions were more scattered in values on the shelf and slope stations 52 - 67. It is difficult to trace any patternts in the distribution of mean values of $d^{15}N$ by stations. According to

Welcox test the weighted mean values of $d^{15}N$ at slope stations was not different from deep-sea stations (W=8, p=0.497, α=0.05). One can trace, that stations 72-76 had significantly higher mean values of $d^{15}N$ than the other stations (Wilcox test: W=30, p=0.01616, α=0.05). The elevated $d^{15}N$ mean values to the north of Nansen Basin could be because of the lack of primary production as a food source. The community could switch to the more heterotrophy regime (Flores et al. 2019).

The data shows that the shelf stations was grouped together and had viriability in $d^{13}C$ and $d^{15}N$. The Stations of Nansen Basin was also grouped together, exept station 78, which was located separatly. It could be because station 78 was located near to stations, where phytoplankton bloom was observed (Nicolopolous, unpublished data). I can assume that at the stations where blooming was dominated by the herbivorous community. Station 52 was located separately also lower in $d^{15}N$, it could be the same reason.

According to Two-Way ANOVA test the fraction (df=1, F=0.424, p=0.517, α=0.05) (Table 5) or station (df=1, F=0.247, p=0.148, α=0.05)(Table 5) had no significant effect on C:N ratio. However, it is possible to trace that shelf and slope stations 52-67 had significanly lower C:N ratio then other stations in the Nansen Basin (Wilcox test: W=0, p=0.00404, α=0.05). It's possible that on the shelf the bigger organisms contain more lipids in a body.

The mean value of $d^{13}C$ and $d^{15}N$ varied in different species. The mean value of $d^{13}C$ and $d^{15}N$ was the highest for *T.abyssorum.* However, according to ANOVA test there was no significant difference between species in $d^{15}N$ (df=1, F=1.497, p=0.229, α=0.05) and in $d^{13}C$ (df=1, F=1.57, p=0.218, α=0.05). Two-Way ANOVA test showed that size of the *T.abyssorum* organism had effect on $d^{15}N$ (df=1, F=16.204, p=0.0101, α=0.05) and had no effect on $d^{13}C$ (df=1, F=0.127, p=0.736, α=0.05). The size range of *T.abyssorum* was 13.9 mm ($d^{15}N$ = 10.81‰) to 18.0 mm ($d^{15}N$ = 9.82%), and one organism was 7.6 mm ($d^{15}N$ = 6.48‰). In the study of the macrozooplankton length of *T.abyssorum* ranged from 7.5 mm to 18.5 mm, so they mostly contribute to the 4000 µm – 8000 µm fraction. The data for this organism are related to the results for the 4000 µm fraction.

According to Two-Way ANOVA test size of the *T.libellula* organism had effect on $d^{13}C$ (df=1, F=11.000, p=0.01607, α=0.05) and $d^{15}N$ (df=1, F=10.193, p=0.0188, α=0.05). The

size range of *T.libellula* was 20.7 mm ($d^{13}C$ = -24.28‰, $d^{15}N$ = 7.93‰) to 34.10 mm ($d^{13}C$ = -22.35‰, $d^{15}N$ = 8.93‰), and one organism was 6.5 mm ($d^{13}C$ = -24.36‰, $d^{15}N$ = 6.96‰). In the study of the macrozooplankton length of ranged from 5.5 mm (only at station 52) to 24.0 mm. The data for this organism are also related to the results for the 4000 µm fraction.

For other two specie *T.longicaudata* and *T.inermis* there was no spatial or size effect. Unfortunately, it is difficult to assess the reliable differences for these four species of macrozooplankton and to say, which of them is more or less predatory, due to the different influence of factors on each individual species. Probably, a large sample should have been made for a more reliable comparison. This may be a separate topic for a study.

It is also difficult to assess the variability of the probability dependence on ice-algae of this four species. The ice-dependent organism *A.glacialis* had $d^{13}C$ -20.0 ‰ to -23.3 ‰ (Kohlbach et al. 2016) and -21.03 ‰ to 26.62 ‰ at the same study area (Klasmeier M., unpublished data). Data of this study showed the same ranges.

The mean values of C:N ratio for T.*libellula, T.abyssorum, T.Longicaudata* were relatively on the same level, the highest was for *T.inermis*, but not statistically confirmed. According to ANOVA test there was no significant difference between species in C:N ratio (df=1, F=3.966, p=0.0539, α=0.05). The distribution of C:N ratio for species of macrozooplankton by stations showed that the values for *Thysanoessa* spp. and *T.libellula* grew to the last transect stations (78, 80, 83) where phytoplankton bloom was noted (Flores et al. 2018; Nikolopoulos, unpublished data). It is probably the grassing effect. According to Two-Way ANOVA test spatial effect was only on *T.libellula* (df=1, F=7.350, p=0.0350, α=0.05), that can confirm the stations differences in C:N ratio of the specie. For a more statistically significant result, it is likely that a wider sample at the stations and one size of organisms should be selected.

As a result of the study, the hypothesis formulated in the beginning were partially confirmed. The trophic level of zooplankton increased from 500 µm to 4000 µm, but it was also increasing in smaller fractions of 64 µm to 250 µm, which may be a mistake and needs additional testing. There was a noticeable difference between the carbon source at deep-water stations and the shelf, but it was not possible to say that deep-water

communities were strongly attached to the ice community. On average, the lipid content at the Nansen Basin stations was slightly higher than on the shelf.

6. Conclusions

The study of variability of taxonomic composition of macrozooplankton in the upper 100 m across the Barents Sea shelf slope and western Nansen Basin comprised at least 21 taxa. The results indicated a significantly higher number of taxa on the shelf and slope (19 taxa) than in deep-sea areas (15 taxa). The data of this study confirms that taxonomic composition in the upper 100 m is more diverse at the shelf and shelf slope then in the Nansen basin. I would like to mention, that the study noted the presence of high abundance of Atlantic and boreal expatriates on the shelf slope. These data reflect the well-known assumption that the Barents Sea shelf slope is a hot spot for atlantification and borealisation.

The study of zooplankton biomass showed unexpected results that the zooplankton biomass on the slope was significantly lower than in the deep-sea basin. This is contrary to the general assumption that the zooplankton biomass is higher on the AW-affected slope and will increase in the future. The difference in total biomass in relation of the influence of Atlantic Waters was not statistically confirmed. However, the influence of Atlantic Waters on the contribution of smaller fractions of organisms on the shelf of the Barents Sea, which is under increased influence of the boundary current, was confirmed.

The results of the stable isotope analysis indicated that carbon sources and trophic structure of zooplankton on the shelf slope differed significantly from the zooplankton community in deep-water stations with reduced AW influence. Isotopic analysis suggests that a more herbivorous community dominates the shelf and stations where phytoplankton bloom has been observed. In general, data confirmed the statement that with the increasing of size classes of zooplankton the trophic level was also increasing. But it was also increasing in smaller fractions of 64 µm to 250 µm, which may be a mistake and needs additional testing. Also, the C:N ratio on the slope was significantly lower than in the Nansen Basin, indicating a lower lipid content in shelf-associated zooplankton.

The results obtained for the isotopic composition of the four macrozooplanton species *Themisto libellula*, *Themisto abyssorum*, *Thysanoessa longicaudata*, *Thysanoessa inermis* did not show statistically significant inter-specific differences in trophic level, carbon source and C:N ratio.

7. Literature

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Appendix

The appendix can be viewed on the CD attached to the master thesis.

The list of appendix is presented below.

1. Abundance of the main macrozooplankton groups
2. Contribution to the total abundance of the main macrozooplankton groups
3. Biomass of macrozooplankton
4. Contribution to the total biomass of the main macrozooplankton groups
5. Biomass of mesozooplankton
6. Total biomass of zooplankton
7. Contribution of different size fractions to the total biomass of zooplankton

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Statement on the thesis originality

Herewith I, Nadezhda Zakharova, declare that I wrote the thesis independently and did not use any other resources than those named in the bibliography, and, in particular, did not use any internet resources except for those named in the bibliography. The master thesis has not been used previously as part of an examination. The master thesis has not been previously published.