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Changes in the abundance, species composition and distribution of the Barents Sea euphausiids (krill)

- with focus on the expansion and reproduction of *Meganyctiphanes norvegica*

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Natural Resource Management

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Summary

Euphausiids (krill) play a key role in the Barents Sea ecosystem, being an important prey for a number of species, and thereby transferring energy from primary producers to higher trophic levels. An unprecedented warming is currently happening in the Barents Sea, diminishing sea ice and affecting the distribution of water masses. As the Barents Sea environment is changing quickly, it crucial to estimate how euphausiid populations will be affected by climate change. The four main species of euphausiids in the Barents Sea are *Thysanoeassa inermis, T. longicaudata, T. raschii* and *Meganyctiphanes norvegica.* The goal of this thesis was to establish the relative species composition, distribution and abundance of the four main euphausiid species in the warm years of 2007-2015. For a reference, the results were compared with data collected in a colder period, during the years 1984-1992. Furthermore, an important part of understanding euphausiid population dynamics is the reproductive cycle. Therefore, this study also investigated the species composition, development and distribution of larvae in the southwestern Barents Sea, May 2015, and sought to compare these to investigations undertaken in 1988 and 1989 (Loftnes, 1993). My results show that there was a significant difference in the total abundance of euphausiids between the two study periods 1984-1992 and 2007-2015, having more than doubled from the first to the second, despite high capelin predation. Total euphausiid abundance was mainly distributed in the southwestern and south-central parts of the Barents Sea, south of 75°N in both study periods. However, *T. inermis*, *T. longicaudata* and the boreal, North-Atlantic species *M. norvegica* seemed to extend their distributional ranges into the northern parts of the Barents Sea during the years 2007-2015. Moreover, the abundance of *M. norvegica* increased from the first to the second study period, constituting a significant part of the species composition in the years 2007-2015. In contrast, abundances of the cold-water species *T. raschii* was significantly lower in the second study period. The distribution and species composition of euphausiid larvae of May 2015 were very similar to what was found in June 1988 and May 1989 with the largest abundances of larvae found in the Atlantic waters south of Bear Island, and the majority of larvae belonging to *T. inermis*. The spawning and development of larvae seemed to be related to water mass, being further developed in Coastal and Atlantic waters. Larvae of *M norvegica* were only found at the southernmost stations, indicating that there is still a thermal constraint on the reproduction of this species in the Barents Sea. However, if the warming continues, *M. norvegica* has the potential of completing a full life cycle in Barents Sea waters, which would highlight the ongoing Atlantification of the Barents Sea ecosystem.

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Introduction

The Barents Sea is home to some of the largest and most economically important fish stocks in the world, as well as rich communities of marine mammals and sea birds (e.g Sakshaug, Johnsen and Kovacs, 2009; Orlova et al., 2010, Dalapadado et al., 2014). Euphausiids (krill) play a key role in the Barents Sea ecosystem, being a link in the energy transfer from primary producers to higher trophic levels (e.g: Orlova et al., 2015; Mehlum, 2001; Dolgov et al., 2011). As one of the most important macrozooplankton group in the Barents Sea (WGIBAR, 2017), they represent a central prey for many fish species and marine mammals (Eriksen et al., 2016; Orlova et al., 2010). Capelin (*Mallotus villosus),* in turn an important prey for North East Atlantic Cod (*Gadus morhua*) (Orlova et al., 2010), relies-heavily on euphausiids as a food-source during summer and autumn (Eriksen and Dalpadado, 2011; Orlova et al, 2010; Zhukova et al., 2009) and can consume up to 30 million tonnes of euphausiids when their stock is high (Drobysheva and Yaragina, 1990; Dolgov et al., 2011).

The Barents Sea is a shallow shelf-sea bordering the Arctic Ocean, and the bathymetry of troughs and banks leads to a complex mixing of cold waters from the Arctic and warm Atlantic waters flowing in from the west (Falk-Petersen et al., 2000; Sakshaug, Johnsen and Kovacs, 2009). These water masses differ in physical properties such as temperature and salinity, which allows for a division into characteristic ecological zones (Sakshaug and Sagstad, 1992). Four species of euphausiids are principally associated with the Barents Sea, each with a defined range connected to water temperature and bathymetry (Einarsson, 1945; Mauchline and Fisher, 1969; Agersted and Nielsen, 2014). These are: *Thysanoessa inermis, Thysanoessa raschii, Thysanoessa longicaudata,* and *Meganyctiphanes norvegica* (Dalpadado and Skjoldal 1991, 1996). *T. inermis* is the most abundant species (Dalpadado and Skoldal, 1991; Zhukova et a., 2009). It is found throughout the Barents Sea but is mainly associated with Atlantic Waters in the south, west and central parts (Dalpadado and Skjoldal, 1991; Zhukova et al., 2009). *T. raschii* is an arctic species mostly found in the colder, shallow parts of the south-eastern Barents Sea where it is abundant in cold years, while *T. longicaudata* is mainly connected to oceanic, Atlantic Waters in the South-West (Dalpadado and Skoldal, 1991; Zhukova et al., 2009). *M. norvegica*, a boreal, North-Atlantic species is usually restricted to the entrance of the Barents Sea (Dalpadado and Skjoldal, 1991), where its occurrence is dependent on the advection from the Norwegian Sea (Dalpadado, 2006).

While the three *Thysanoessa* species are all known to reproduce successfully in the south-western Barents Sea (Drobysheva 1979; Dalpadado & Skjoldal 1991; Loftnes, 1993), it is generally considered that the Barents Sea is too cold for *M. norvegica* to spawn except for in very warm years (Maukhline and Fisher 1969; Siegel, 2000). Einarsson (1945) consider the northern spawning limit of *M. norvegica* up to 70°N, at the continental on the border of the

Norwegian Sea (Dalpadado, 2006). All the Barents Sea euphausiids spawn their eggs freely into the water, from where the larvae pass through a number of larval stages before they develop adult characteristics (Einarsson, 1945; Mauchline and Fisher 1969). A nauplius with swimming abilities hatches from the egg, and develops into a metanauplius stage. Then follow three calyptopes stages where the larvae begin to feed, and lastly up to 14 furcilia stages before entering the juvenile phase (Siegel, 2000; Einarsson, 1945; Mauchline and Fisher 1969). Larvae are subjected to the movements of ocean currents carrying them away from the spawning grounds (Timofeev, 1993), but they depend on a suitable temperature range in order to fulfil the larval cycle and become adult (Einarsson, 1945).

Long-term observations reveal that the Barents Sea has been experiencing dramatic increases in temperature and salinity from the early 2000s and onwards *(*WGIBAR, 2017; Lind, Ingvaldsen and Furevik, 2018). Despite warm periods e.g in the 1950s and early 60s, the warming currently registered is unprecedented (WGIBAR, 2017; Skagseth et al., 2008; Spielhagen et al., 2011). In 2016, an average sea surface temperature (SST) of 1.8°C above the long-term normal (1931-2010) was registered for the whole Barents Sea, whereas the northern and eastern parts showed positive SST-anomalies up to 3.4 °C (WGIBAR, 2017). Climate change seem to increase the temperature and volume of Atlantic water flowing into the Barents Sea (Årthun et al., 2012). In 2016, one of the warmest yeas recorded, saw the lowest area of Arctic water so far registered (WGIBAR, 2017). Moreover, the Barents Sea winter ice cover has been reduced by around 10% per decade since the 1980s (Onarheim et al., 2014), and the loss of fresh melt water from the sea ice causes weaker stratification of the water column. Therefore, the northern parts of the Barents Sea could soon change from a stratified and cold Arctic regime to an Atlantic situation with a well-mixed water column and warm water (Lind, Ingvaldsen and Furevik, 2018).

This rapid change in the Barents Sea environment is expected to greatly impact marine ecosystems (ACIA, 2004). A northward shift in the distribution of many marine species has already been registered (Frainer et al., 2018, Ingvaldsen and Gjøsæter, 2013; Fossheim et al., 2015), and further changes in biogeographic boundaries are expected (Falk-Petersen et al., 2007; Orlova et al., 2011). Euphausiids and other zooplankton groups are known to be impacted by climate variability (Orlova et al., 2010; Richardson, 2008) and respond quickly to changes in the environment (Bucklin et al., 2010). They can therefore be used as a sensitive indicator of water masses and consequently climate change (Richardson, 2008). Furthermore, given their central role in the Barents Sea ecosystem, any change in the euphausiid communities could have direct consequences for higher trophic levels and affect the recruitment of fish stocks (Siegel, 2000; Dalpadado et al., 2014).

Based on sampling conducted in the years 1984-1992, Dalpadado and Skjoldal (1991; 1996) published detailed descriptions of the species composition, distribution, abundance and maturation of euphausiids in the Barents Sea. Also, from data collected during May 1989 and June 1988, Loftnes (1993) gave an extensive account of euphausiid larvae in the southwestern Barents Sea. Both these studies were conducted just after the cold period in the early 1980s (PINRO, 2018) Given the recent warming conditions, it would be interesting to investigate the changes in the euphausiid populations from the colder 80s to the warmer 2000s.

Over the recent years euphausiid biomass has been observed to increase, even in periods with high capelin predation, indicating that higher temperatures and increased primary production (Dalpadado et al., 2014) may be favourable for euphausiid biomass (Eriksen and Dalpadado, 2011). It has also been shown that the relative species composition of Barents Sea euphausiids changes with climatic variability and the inflow of Atlantic water (Zhukova et al., 2009; Eriksen and Dalpadado, 2011). There is evidence suggesting that the neritic, cold-water species *T. raschii* decreases in warm years, while *M. norvegica* expands its distribution and abundance (Zhukova et al., 2009). This was the case for the warmer 1950-60s and the early 2000s when temperatures were around 0.5°C above the long-term average (Zhukova et al., 2009; PINRO, 2018). Since then, temperatures have continued to rise and further changes in the euphausiid species composition are important to quantify. Furthermore, after investigations undertaken in 1988 and 1989 (Loftnes, 1993), little information has been available on euphausiid larvae in the Barents Sea. It is therefore important to study how the euphausiid population dynamics responds to warmer temperatures, and if any changes in development, distribution and species composition of the larvae can be seen.

In this thesis, I explored to what degree the relative species composition and abundance of the four main euphausiid species of the Barents Sea: *T. inermis, T. longicaudata, T. raschii* and *M. norvegica*, have changed from the colder period in the 80s to the warmer 2010s. In order to do so, I have compared euphausiid data collected during the period 2007-2015 with data from the years 1984-1992 (previously published by Dalpadado and Skjoldal, 1991;1996), and studied changes in species composition, distribution and abundance. I have also analysed larvae specimens collected in May 2015 and compared the results of distribution, species composition and development with the situation found in May 1989 by Loftnes (1993). A special focus was given to the boreal, North-Atlantic species *M. norvegica*. The following questions were addressed in this thesis:

(Q1) Did the total euphausiid abundance increase from the years 1984-1992 to 2007-2015, and could any changes be related to sea temperature?

(Q2) Did the species composition and distribution of Barents Sea euphausiids change between the two time periods?

(Q3) Which species of euphausiid larvae were present in the southwestern Barents Sea in May 2015, and had the species composition changed compared to the previous study of Loftnes (1993)?

(Q4) How was the distribution of euphausiid eggs and larvae?

(Q5) How was the distribution of larval developmental stages in the different water masses?

Methods

Geography and hydrography of the Barents Sea

The Barents Sea is the deepest of the many shelf areas that encircle the Arctic Ocean (Ozhigin et al., 2011). It stretches an area of approximately 1600 000 km^2 (Ozhigin et al., 2011) and has an average depth of 230 m (Sakshaug, Johnsen and Kovacs, 2009). The maximum depth of 500 m is found in the Bear Island Trough at the western entrance of the Barents Sea (Figure 1), while the many banks ranges depths of 50-200 m (Ozhigin et al., 2011). Lying at the western edge of the Eurasian shelf, the Barents Sea is bordered by the continental slopes that stretches from Norway to Svalbard in the west, and from Svalbard to Frank Josef's Land in the north. The eastern border is marked by Novaya Zemlya while the Russian and Norwegian coasts borders the Barents Sea in the south (Ozhigin et al., 2011).

The Barents Sea is one of the major pathways for Atlantic Water entering the Arctic Ocean, and in this way act as a transition zone where cold Arctic Waters mixes with the warm and saline Atlantic Water (Figure 1) (Ozhigin et al., 2011). These water masses meet at the Polar Front, and are separated by strong gradients of temperature and salinity (Loeng, 1991, Skagseth et al., 2008). While the Polar Front has a defined border in the West around the Svalbard Bank, the eastern parts of the front are marked by a large zone of mixed water (Sakshaug and Sagstad, 1992; Loeng, 1989, 1991). In the south, fresher Coastal Waters that are influenced by seasonal temperature fluctuations flows along the Norwegian and Russian coastlines (Loeng, 1991).

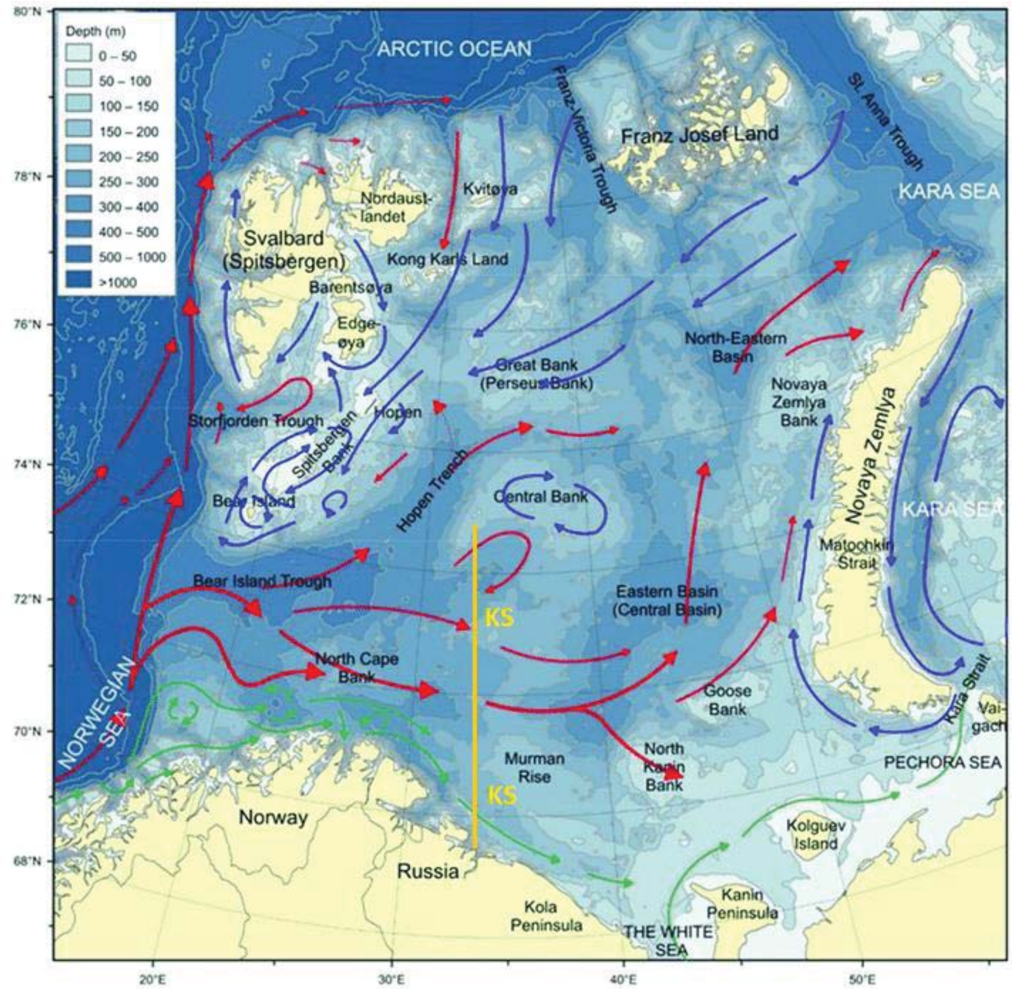


Figure 1: The Barents Sea bathymetry and prevailing currents. Red arrows show Atlantic Waters, blue arrows Arctic, and green arrows Coastal Waters (Figure from Eriksen et al., 2017, used with permission). The Kola Section is marked with a yellow line demarked “KS”.

Temperature data

Yearly and monthly average sea temperatures used in this thesis were collected by the Russian Institute of Marine Research (PINRO), along the Kola monitoring transect (70°30´N to 72°30´N along 33°30´E) (Figure 1). The Kola monitoring transect is the longest series of temperature data from the Barents Sea, and has more or less continuous observations of temperature and salinity since 1900, and with regular collections every month starting from the 1960s (Tereshchenko, 1996). The Murman current flowing through the Kola section has been shown to be representative for the temperature and salinity of Atlantic Waters elsewhere in the Barents Sea (Tereshchenko, 1996) and represents a local manifestation of the larger climatic fluctuations of the North Atlantic Ocean (Skagseth et al., 2008). The Kola section is divided into three parts, the northernmost having generally colder temperatures as it measures Arctic water at the Central Bank. The southernmost part is influenced by coastal waters, while the central part measures the main Murman Current temperatures. In this study the temperatures from the central part has been utilized. All temperatures used in this study are measured from 0-200 meters depth. The Kola temperature data in this thesis are used with permission from PINRO (Russian Institute of Marine Research), and was obtained from their website. The data can be accessed at: http://www.pinro.ru/.

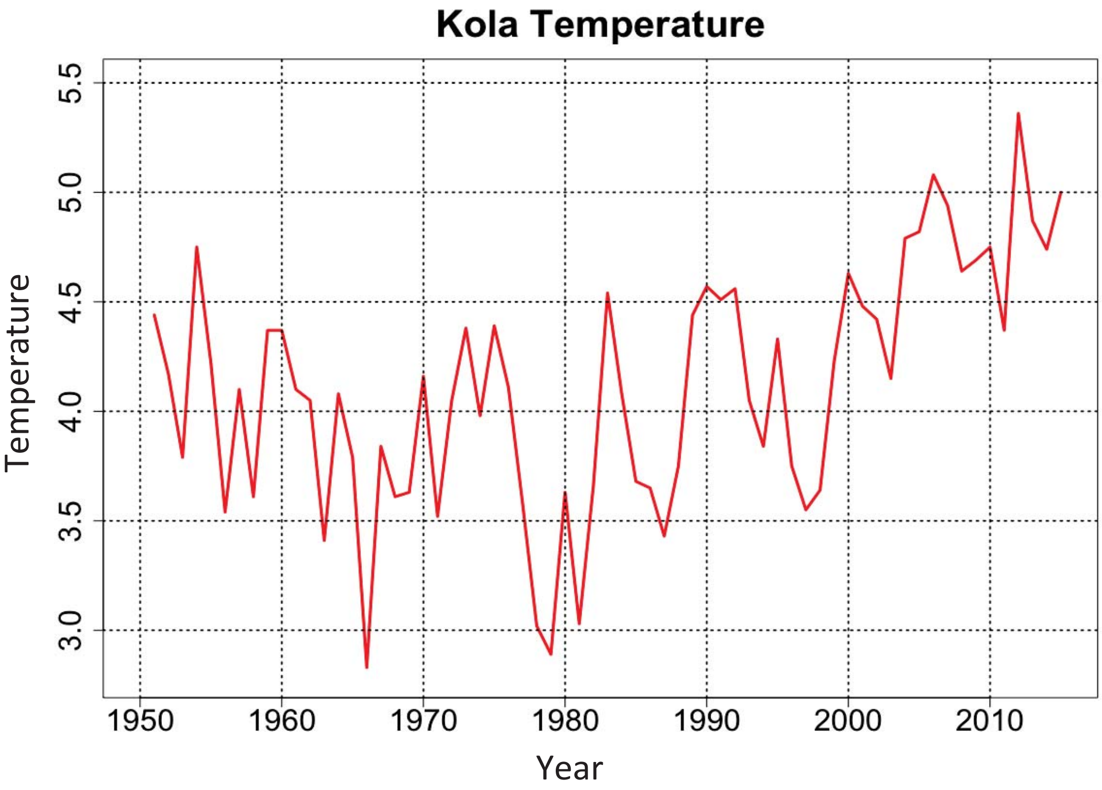


Figure 2: Kola temperatures from 1950-2015 in°C (Data from: http://www.pinro.ru/). Monthly measurements have been taken from 1960 and onwards.

Temperatures of the study periods

The average Kola temperature of the years 1984-1992 was 4.07°C (SD = 0,45°C) (Figure 2), lying close to the long-term average (1931-2010) of 3.94°C. The first part of the period (1985-1988) was on average one degree colder than the latter part (1989-1992). The years 2007-2015 had an average Kola temperature of 4.81°C (SD = 0.27°C) with the highest temperatures measured in 2012 and 2015 with yearly averages of 5.36°C and 5°C respectively (SD not available).

Euphausiid data

The findings in this thesis stem from data sets collected during the periods 1984-1992 and 2007-2015 (no data are available from 2009) and from formalin-preserved samples collected in May-June 2015 (Table 1). The data from 1984-1992 are previously published by Dalpadado and Skjoldal (1991, 1996) and are used with permission in this thesis for comparison purposes only. All the data have been collected on surveys carried out by the Institute of Marine Research, Bergen, Norway. There are differences in the number of stations sampled per year, the area covered, the sampling season and gear used.

Data from 1984-1992 were sampled from 103 stations, in an area ranging from 73-78°N and 10-45°E (Table 1, Figure 3a) (Dalpadado and Skjoldal, 1996). The sampling was conducted during the months January, February, March, May, June, August, September and October (specifics are given in Table 2). All samples were collected with a MOCNESS plankton sampler with a $1m^2$ opening and a mesh size of 180 µm (Figure 5a) (Wiebe et al, 1976;1985). Samples were collected at varying times both day and night. Data from 2007-2015 were sampled from 142 stations, in an area ranging from 70-81°N and 30-43°E (Figure 3b). The sampling was conducted in August only (Table 2), and all samples were collected using a MOCNESS plankton sampler at varying times during both day and night.

Data from May 2015 were sampled at 8 stations, in an area ranging from 72-75°N and 20-29°E (Figure 4). Three of the stations were located along the shallower bank south of Spitsbergen bank and Bear Island and the (St. I, II, III (Table 3, Figure 1) while four stations were located at the deeper Bear Island Trough and Hopen Trench (IV, V, VI, VII, Figure 1, Figure 4). Station VIII was located at the shallower vicinities of North Cape Bank (Table 3). The sampling was undertaken from May 26th to June 4th for the "TIBIA" project. Five stations were collected with a MOCNESS, and three stations with a WP2 plankton sampler (Anonymous, 1968) with a 0,25 m^2 opening and 180 µm mesh (Figure 4, Figure 5b,). Samples were collected at varying times during both day and night.

On board the cruises, all samples were preserved in a 4% formalin and seawater solution, and later analysed for species composition and relative abundance (N/m^2) of adult euphausiids. Data from 1984-1992 and 2007-2015 were analysed by staff at the Institute of Marine Research (IMR), Bergen, Norway, while I analysed the 2015 samples at the research facilities of the IMR in Bergen.

Table 1: Euphausiid data used in this thesis and the respective sampling periods, number of stations, gear and type of data available.

Years	Time of sampling	N. Stations	Previously published	Gear	Type of data
1989-1992	January February March May June August September October	103	(Dalpadado and Skjoldal 1991, 1996)	MOCNESS	Previously analyzed data of: -Species composition -Abundance (N/m2)
2007-2015 (not 2009)	August	142		MOCNESS	Previously analyzed data of: -Species composition -Abundance (N/m2) -Relative biomass (g/m2)
2015	May 28th - June 4th	8	-	MOCNESS WP2	Formalin-preserved samples of euphausiid adults and larvae

Table 2: Overview of the sampling periods during the years 1984-1992 and 2007-2015. Number of sampling stations per month in 1984-1992 are given in parenthesis.

	Month	N.St.		Month	N.St.
1984	June (6), August (21)	27	2007	August	28
1985	January (7), August (19)	26	2008	August	24
1986	April (4), May (2)	6	2009	-	-
1987	February (2), March (5), May (2), June (8)	17	2010	August	28
1988	March (8), September (3), October (5)	16	2011	August	16
1989	May (5)	5	2012	August	14
1990	September (5), October (1)	6	2013	August	31
1991	January (2), February (1), June (6)	9	2014	August	49
1992	September (21), October(2)	23	2015	August	47
Total		103			142

Table 3: Depths sampled at each station during May-June 2015.

Station	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Depth (m)	188	131	139	360	385	440	323	460

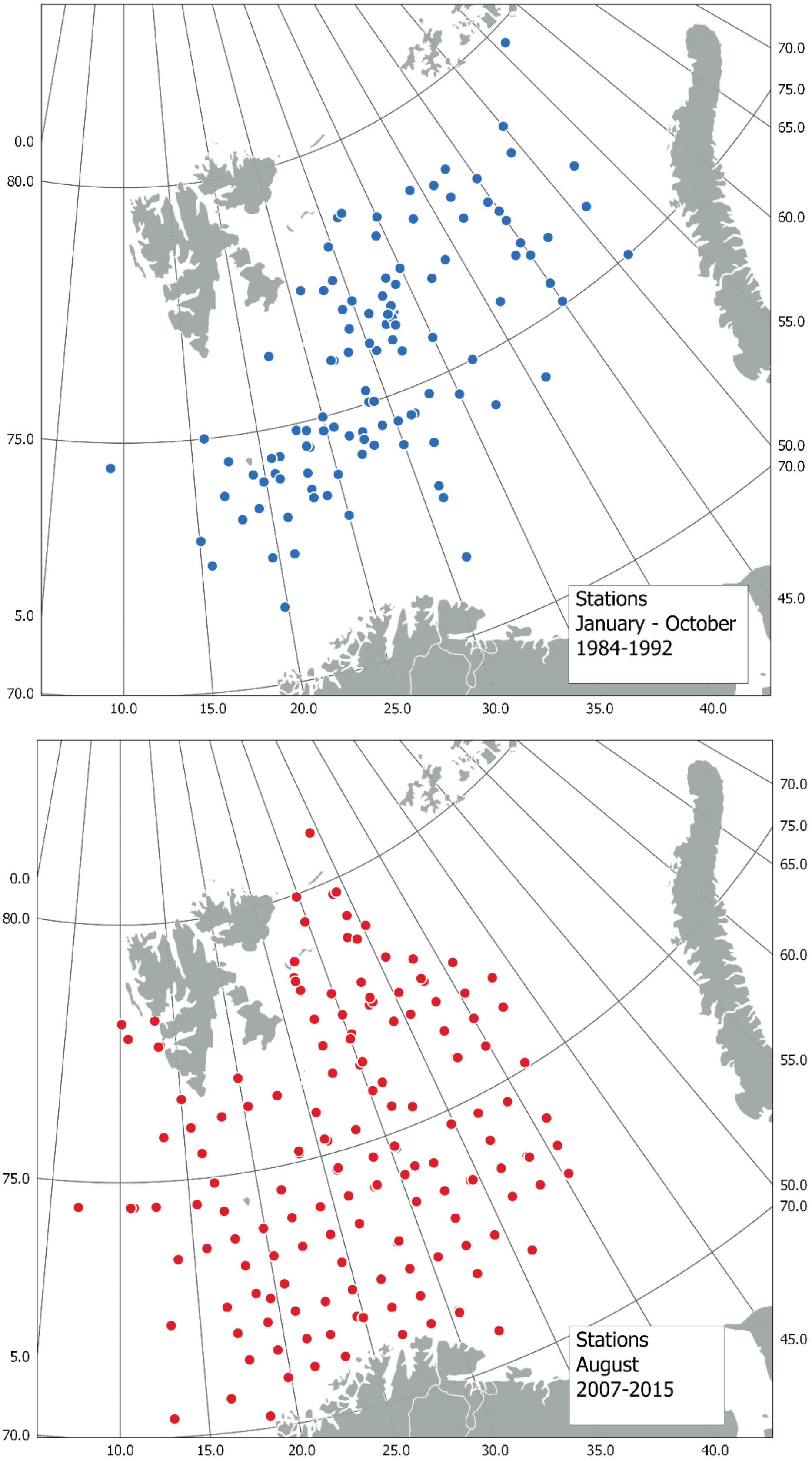


Figure 3: Sampling stations during the years 1984-1992 (above) and 2007-2015 (below). Note that some stations are stacked on the map due to sampling at the same coordinates over several years.

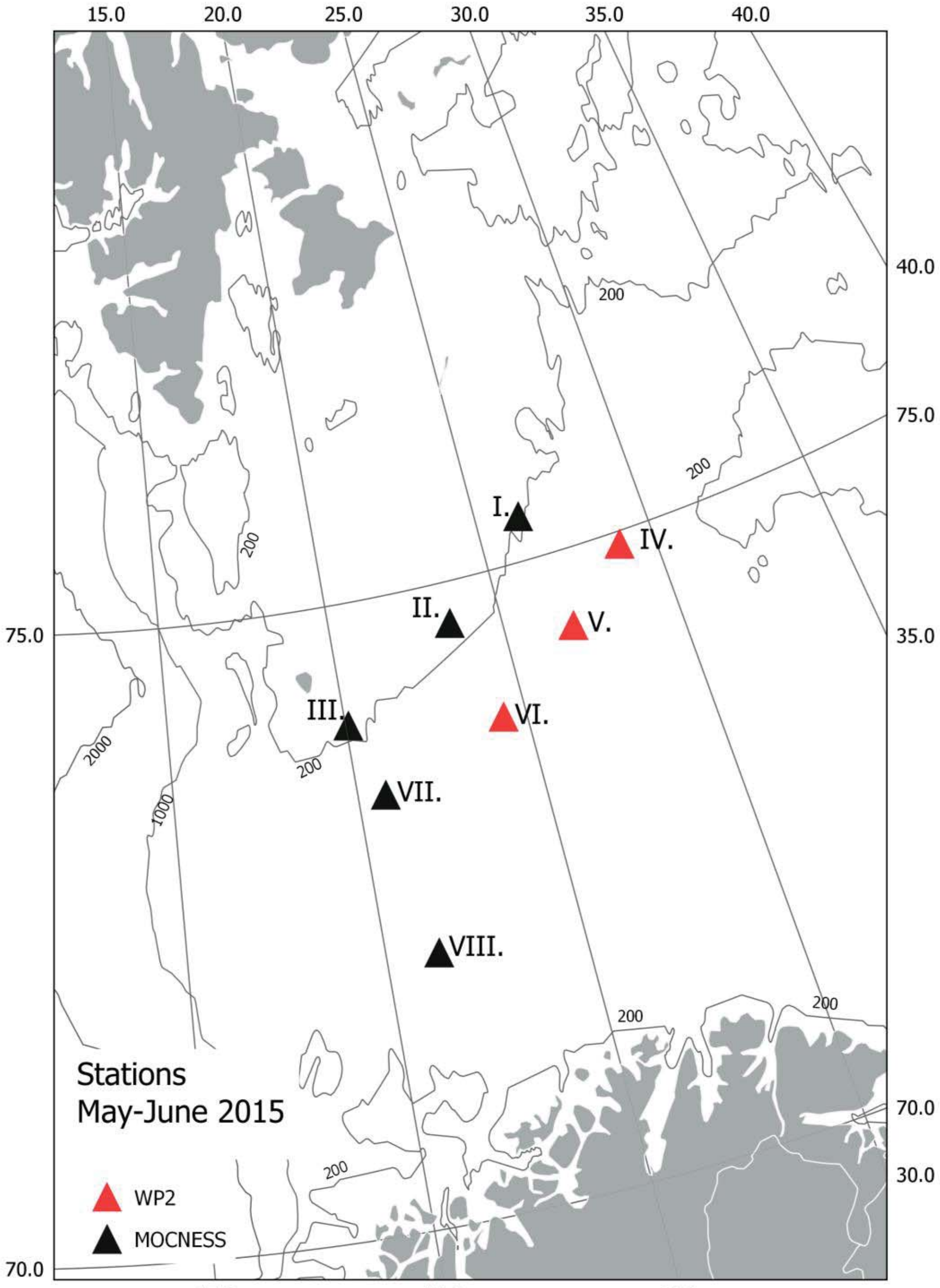


Figure 4: Sampling stations during May-June 2015. Bathymetry from Naturalearth.com.

Sampling gear

The two plankton nets MOCNESS and WP2 are differently constructed (Figure 5, a and b) (Gjørsæter et al., 2000). The MOCNESS (Multiple Opening/Close Net and Environmental Sensing System) consists of long funnel nets that can be automatically opened and closed, sampling the whole water column in 3-8 depth intervals depending on the bottom depth (Eriksen et al., 2016). The net normally samples some meters above the sea floor (10-20 m) and is towed obliquely at low speed. The WP2 (Working Party 2) is a funnelled ring net that is immersed vertically into the water and samples the water column in vertical hauls from the sea bottom (Gjøsæter et al., 2000). For this study, vertical stratifications were not registered by the WP2 net. Gjøsæter et al. (2000) found that the WP2 tends favour the smallest size fraction, while the MOCNESS overall gave higher values for the largest fractions. However, this difference was not significant and they concluded that data from both gear types can be used for estimation of mean biomass (Gjøsæter et al., 2000). Data from both these nets have therefore been used for comparisons in this thesis.

Quantitative sampling of euphausiids by nets or trawls is inherently difficult as large individuals can see and actively avoid plankton nets, while the smaller individuals are not properly sampled by traditional pelagic trawls (Eriksen et al., 2017). Therefore, smaller nets like WP2 and MOCNESS tend to underestimate the total euphausiid biomass and especially the abundance of larger specimens (Eriksen et al., 2017). Abundances (numbers per square meter: no.m^{-2}) given in this thesis should therefore be considered as relative estimates.

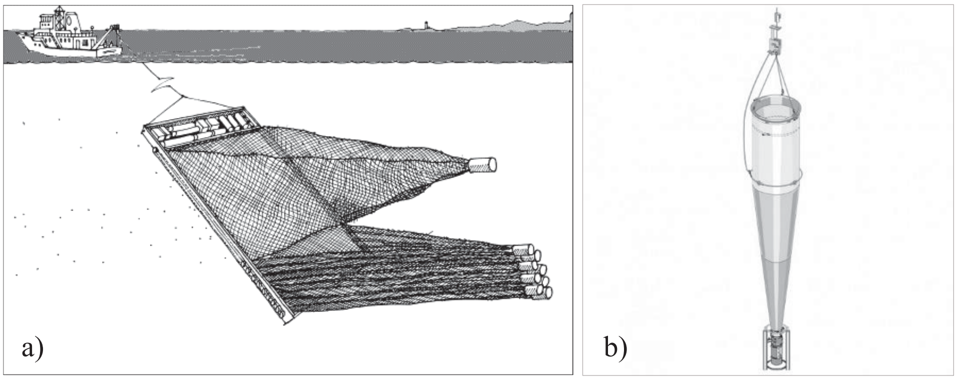


Figure 5: a) MOCNESS (Gulf of Marine Research Institute, 2012) b) WP2 net (HydroBios, 2018).

Estimation of abundance (no.m^{-2})

The MOCNESS is equipped with flowmeters that measures the exact volume of water filtered through the net, and the estimation of euphausiid concentration (no.m^{-3}) was based upon the total number of euphausiids caught within each net and the volume of water filtered. The relative abundance (no.m^{-2}) was found by multiplying numbers per m^3 with the depth interval of each net. The WP2 used in this study did not have any flowmeters mounted and the volume filtered was calculated by multiplying the opening area of 0,25 m^2 with the vertical hauling distance, assuming 100% filtering efficiency.

Sample analysis

The preserved May-June samples from 2015 were analysed at the lab-facilities at the Institute of Marine Research in Bergen. Firstly, each sample was filtered through a 180 µm mesh, and all euphausiid specimens were sorted. Samples with large numbers of specimens were divided using a Motoda splitter (Motoda, 1959). Adult euphausiids were determined to species, sex, and maturation using a microscope. Sex was determined using secondary sexual characters: “thelycum” for females and “petasma” for males (Einarsson, 1945; Makarov and Denys, 1980; Dalpadado and Skjoldal, 1996). Four maturity stages were identified using the descriptions summarized by Dalpadado et al. (2008a). These stages are assigned based on the development and colouring of the petasma and the thecylum (Dalpadado et al., 2008a), and individuals with spermatophores are identified to stage four. Some of the specimens did not have any visual sexual characteristics. This could be due to: a) the individual being immature b) the individual already having spawned and sexual characteristics regressed, c) the individual may not be able to mature due to non-optimal conditions such as temperature (Dalpadado, 2018). Such individuals were registered as “non-identifiable”.

Morphological identification of larvae

Egg and larvae were sorted to stage (egg, nauplii 1-2, metanauplii, calyptopis 1-3, furcilia 1-14) and length measured to the nearest 10 µm using the eyepiece reticule of a microscope. Diameter of both the outer and inner capsules of the egg were measured, and all larvae were length measured from the tip of the rostrum to the end of the telson, not including the terminal spines (Figure 6). Egg and larvae were identified to species level following descriptions by Einarsson (1945), Mauchline (1971), Lebour (1926; 1924), MacDonarld (1928), Sars (1898), and Loftnes (1993). A compilation of these characteristics can be found in Appendix II. It should be noted that some of the larval stages are practically indistinguishable (Einarsson, 1945) (Appendix II). This applies to nauplii-calyptopes stages of *T. raschii*, which is considered by Einarsson (1945) to be indistinguishable from *T. inermis*, and subsequently not identified in this thesis. In other difficult cases such as the nauplii of *T. longicaudata*, species were determined based on length measurements given by Loftnes (1993), or in the case of *M. norvegica* eggs, by the presence of early larval stages exclusively belonging to *M. norvegica*.

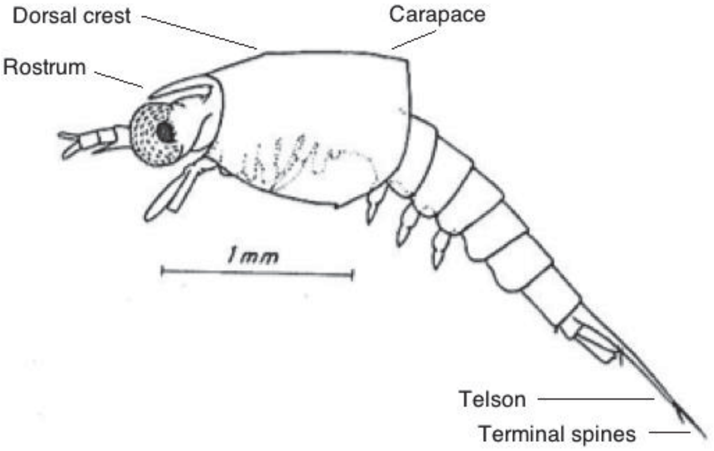


Figure 6: Example of *M. norvegica* larvae, calyptopis 1 (drawing from Einarsson, 1945).

Verification of morphological identification

Following the morphological identification of the larvae, the DNA of 12 individuals of furcilia and metanauplii were sequenced to verify the results. The larvae were collected in the Norwegian Sea (GPS: 70.79483, 16.7087 and 74.53017, 16.875) in May 2015 under the COPECLAD Project and preserved in 96% alcohol.

DNA isolation, PCR amplification and sequencing

DNA was isolated from the eyes of the furcilia and from the whole specimen of the metanauplii larvae. The eyes were then deposited in 1.5 mL Eppendorf tubes with 75 µL of a solution containing 5% Chelex 100 Resin (BioRad, CA, USA) and 15 µL of Proteinase K (Qiagen, Germany), and incubated for 1 hour at 56°C followed by 10 min at 96°C. After a brief centrifugation the supernatant containing the nucleic acids were transferred into new tubes. Following DNA isolation, Polymerase Chain Reaction (PCR) was performed targeting the mitochondrial cytochrome c oxidase subunit I (COI) gene. The COI gene has been widely used as a molecular marker, for species identification (Herbert et al., 2004). The PCR was performed in 20 µL containing 4 µL of the 5x buffer, 1.6 µL of a 25 mM solution of $MgCl_2$, 4.8 µL of a solution 1.25 mM of the dNTPs, 0.6 µL of each primer LCO1490 / HCO2198 (Folmer *et al.,* 1994), 6.2 µL of the dsH_2O, 0.2 µL of the 5 units GoTaq G2 DNA polymerase (Promega, WI, USA) and 2 µL of the template. The PCR conditions were i) an initial denaturation of 2 min at 94°C, followed by ii) 40 cycles of amplification (denaturation 40 s at 94°C, annealing at 40°C for 40 s and an extension of 1 min at 72°C), and iii) a final extension of 10 min at 72°C. Amplicons were visualized in a 1% agarose gel stained with GelRed (ThermoFisher Scientific, MA, USA).

Clean-up of the PCR products was performed by mixing 5 µL of the PCR product and 2 µL of the ExoSap-IT PCR product cleanup (ThermoFisher, MA, USA) followed by an incubation at 37°C for 15 min and 80°C for 15 min. Finally, Sanger sequencing was performed using the Big Dye Terminator kit (v3.1 ThermoFisher Scientific) at the sequencing facility at the University of Bergen (http://www.seqlab.uib.no). Sequence analysis was performed in Geneious v8.0.5 (Kearse *et al.,* 2012). Sequence identity was determined according to the best hits when using Basic Local Aligment Tool (BLAST) (Altschul *et al.,* 1990) against the NCBI database (http://www.ncbi.nlm.nih.gov/blast).

Phylogenetic tree construction

The obtained sequences as well as similar sequences downloaded from GenBank, were used to construct a phylogenetic tree. The phylogenetic tree is a visualization of the relationship between the species and their ancestors, and gives an estimate of the certainty of the results. All the sequences were first aligned using the MUSCLE algorithm in MEGA 7 (Kumar *et al.,* 2016). This alignment tool organizes the sequences so that nucleotides of common origin are found in the same position. Once the sequences were aligned a phylogenetic analysis was performed using the Maximum Likelihood method based on the Jukes-Cantor model and 500 bootstraps.

Data analyses

A Mahn-Whitney test was used to determine whether there was a significant change in the abundance and biomass of euphausiids from the years 1984-1992 to 2007-2015, while correlation analyses were done in order to check the relationship between euphausiid abundance and Kola-temperature. Statistical analyses were performed in R version 1.0.136 (Rstudio Team, 2016), while mapping of stations and visualizations of spatial patterns in euphausiid abundance were done in QGIS 2.18 and 3.2 (QGIS, 2016;2018). Bathymetry layers used in the analysis were accessed from Natural Earth (naturalearthdata.com).

Due to the stations being unevenly positioned in the two sampling periods1984-1992 and 2007-2015, analyses of distribution were performed within an area that is approximately evenly sampled for both periods (Figure 7). From here on referred to as the “restricted area”.

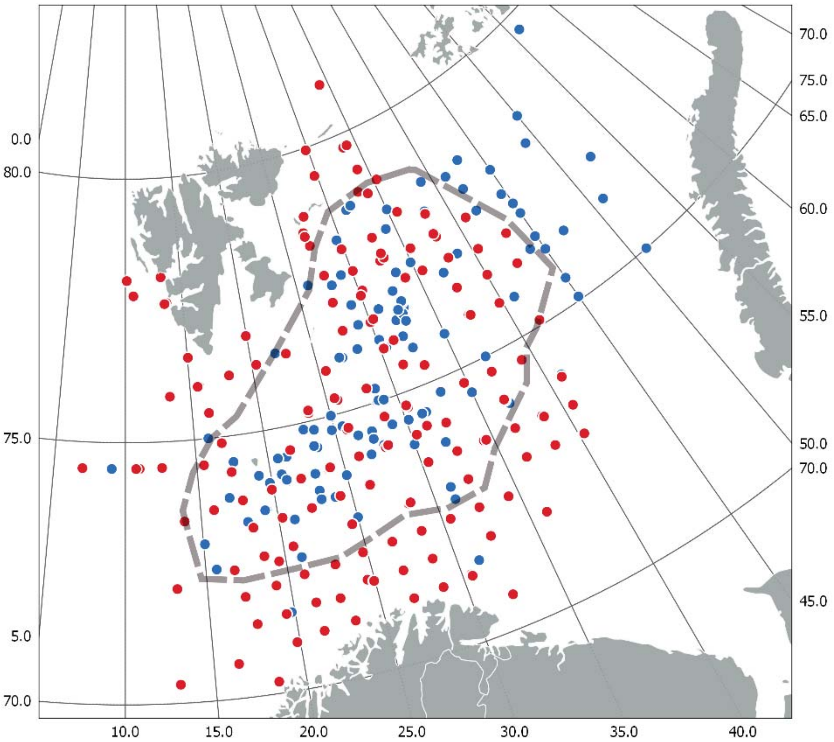


Figure 7: The area sampled with approximately equal frequency in the two time periods is given within the grey border. Blue dots represent stations of 1984-1992, red dots stations from 2007-2015.

Chlorophyll a data

Remotely sensed imagery on chlorophyll-a concentrations averaged for the months April, May and June 2015 were used in this thesis. These images are a courtesy from the Norwegian Research Council project "Trophic interactions in the Barents Sea—steps towards an Integrated Ecosystem Assessment (TIBIA-NRC Project No. 228880)" in collaboration with Prof. Kevin Arrigo and Gert van Dijken from Stanford University, USA. The images can be found in Appendix I (Figure A1).

Results

Abundance

Euphausiid average abundance per station for each of the study periods are shown in Figure 8 and Table 4. There was a significant increase in euphausiid abundance ($p < 0,001$) from the years 1984-1992 to 2007-2015. The average abundance per station was 27,3 no.m^{-2} (SD = 29,72) in the first study period, and 44,8 no.m^{-2} (SD = 15,19) for the second (Table 4) (Including the number of euphausiids not identified to species), corresponding to a 64% increase from the years 1984-1992. The first study period was characterized by an abundance peak in 1987-1989 where average abundance per station reached 60-85 no.m^{-2} (Figure 8), but else low abundances. The yeas 2007-2015 saw less inter-annual differences, with 2012 being the year of highest abundance (77,8 no.m^{-2}). Excluding the stations outside the restricted area, the increase in average abundance per station was found to be the same as above. However, when excluding all samples not collected during autumn 1984-1992 (August, September and October) the average abundance was significantly ($p < 0,001$) three times higher in the second study period compared to the first (Table 5). No significant relationship between Kola temperature and euphausiid abundance could be found during the years 1984-1992 ($r^2 = -0,13$, $p = 0,72$) (Figure A2, Appendix I), but a strong positive relationship was apparent for the years 2007-2015 ($r^2 = 0,54$, $p = 0,046$, Figure 9).

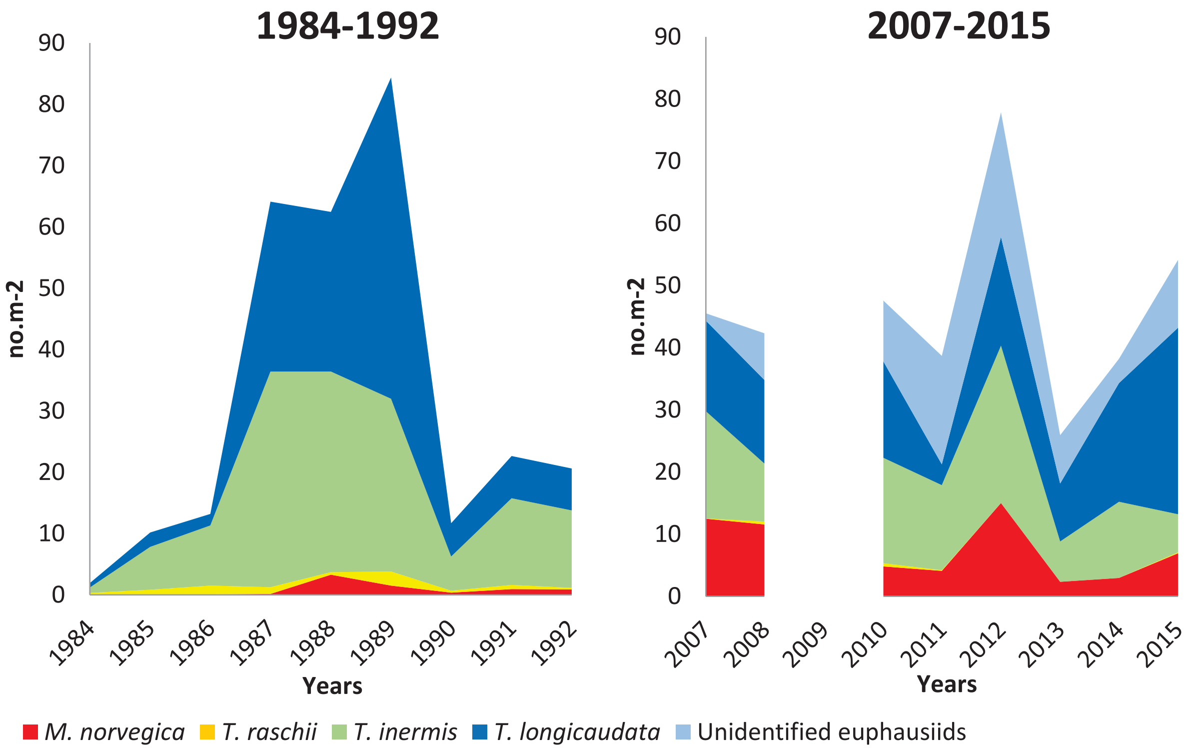


Figure 8**:** Average euphausiid abundance (no.m^{-2}) per station for the each of the four euphausiid species in the periods 1984-1992 and 2007-2015.

The average abundances (no.m^{-2}) per station for *T. inermis, T. longicaudata, T. raschii* and *M. norvegica* are shown in Figure 8 (average abundances for the four species with standard error of mean (SEM) are given in Figure A2, Appendix I). *T. inermis* and *T. longicaudata* dominated in the years 1984-1992, and averaged for the entire period, 14,7 no.m^{-2} of *T. inermis* and 11 no.m^{-2} of *T. longicaudata* were sampled at each station (Table 4). During the years 1986-1989 these species mainly constituted the abundance peak. *T. raschii* and *M. norvegica* were both recorded in low numbers during the 1984-1992 period with *M. norvegica* barely being present before 1988 and *T. raschii* fluctuating between 0 and 2 individuals per station. However, both species showed slight increases during the peak period of *T. inermis* and *T. longicaudata*.

During 2007-2015, interannual fluctuations were similar for the three species *T. inermis, T. longicaudata* and *M. norvegica* (Figure 8). Numbers of these three species were all lower in 2011 and 2013, and peaked in 2012. From 2014 to 2015 the numbers of *T. longicaudata* increased substantially while *T. inermis* decreased. Overall, *T. inermis* and *T. longicaudata* were the dominating species, with averages of 12 and 17,3 no.m^{-2} per station for the entire period (Table 4), while *M. norvegica* showed an average of 6,7 no.m^{-2} per station. Abundances of *M. norvegica* fluctuated between peaks of 14.87 no.m^{-2} in 2007 and 15 no.m^{-2} in 2012 and with lower abundances of ca 2.5-5 no.m^{-2} in the years 2010, 2011, 2013 and 2014. In the period 2007-2015, abundances of *T. raschii* were stable and low with an average of 0,16 individuals per m^2 at each station.

Table 4**:** Average number of individuals per station (no.m^{-2}) for each of the two periods 1984-1992 (all months) and 2007-2015 (August). All stations are included. The respective percentage of each species in the total abundance of each period is given in parenthesis. A complete data set can be found in Table A1, Appendix I. Note that the species composition in percent for 2007-2015 does not include the unidentified species (Unid.).

	T. inermis	*T. longicaudata*	*M. norvegica*	*T. raschii*	Unid.	Tot
1984-1992	14,7 (54%)	11,2 (41%)	0,72 (2,4%)	0,65 (2,6%)	-	27,3
2007-2015	12 (33%)	17,3 (48%)	6,7 (18,43%)	0,16 (0,45%)	8,4	44,8

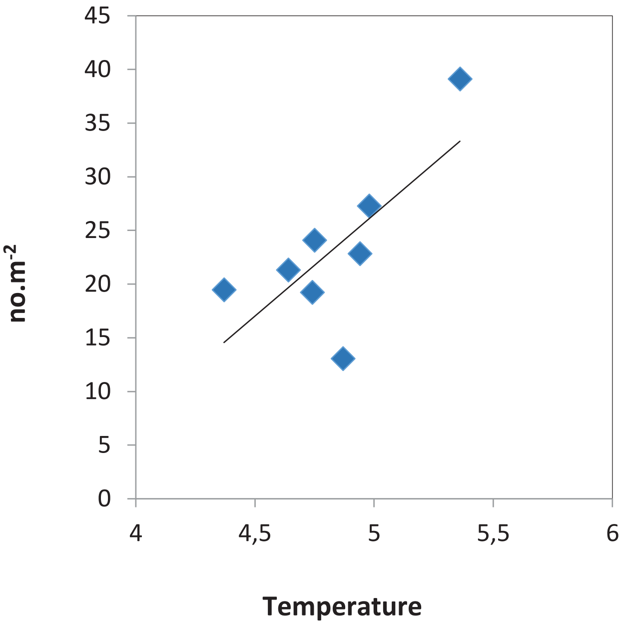


Figure 9: Total euphausiid abundance vs. Kola-temperature during 2005-2015.

Species composition

There was no significant difference in the abundance of *T. inermis* ($p = 0,81$) and *T. longicaudata* ($p = 0,30$) between the two study periods. However, the abundance of *T. raschii* was significantly lower in the period 2007-2015 than in 1984-1992 ($p < 0,001$), while the abundance of *M. norvegica* significantly increased ($p < 0,001$). In result, the percentage of *T. raschii* in the species composition of Barents Sea euphausiids decreased from 2,65% in the first to 0,45% in the second study period. *T. inermis* decreased from 54% to 33%, *T. longicaudata* remained relatively stable, while the percentage of *M. norvegica* rose from 2,63% to 18,43% (Table 4).

Distribution

The total euphausiid abundance was mainly distributed south of 75°N in both study periods (Figure 10, Table A2, A3, Appendix I). Inside the restricted area, the abundance increased with 46% both south and north of 75°N from the years 1984-1992 to 2007-2015. However, the abundance increase was only significant south of 75°N ($p = 0,002$) (north of 75°N: $p = 0,37$). *T. inermis* was the most widely distributed species, dominating the species composition north of 75°N in both study periods (Table A2, Appendix I). Abundances of *T. inermis* north of 75°N were not significantly different in 2007-2015 compared to 1984-1992 ($p = 0,17$ (restricted area)). However, relatively large abundances (95 no.m^{-2}) of *T. inermis* were found as far north as 78,9°N, outside the restricted area (Figure A4, Appendix I).

T. raschii was distributed in the central parts of the study area in both periods, however with a tendency to being more easterly distributed in the second study period (Figures A5 and A6, Appendix I). Both *T. raschii* and *T. longicaudata* increased significantly ($p < 0,00$ and $p = 0,00$) north of 75°N, although in small numbers. In 1984-1992 there were only two observations of *M. norvegica* specimens north of 75°N, both made around 75-76°N. In 2007-2015 *M. norvegica* were found at one third of the stations in the restricted area north of 75°N, representing around 1 no.m^{-2} on average per station and having significantly increased from the first to the second period ($p < 0,00$). Outside the restricted area, observations of *M. norvegica* were made as far north as 80°N (Figure 11).

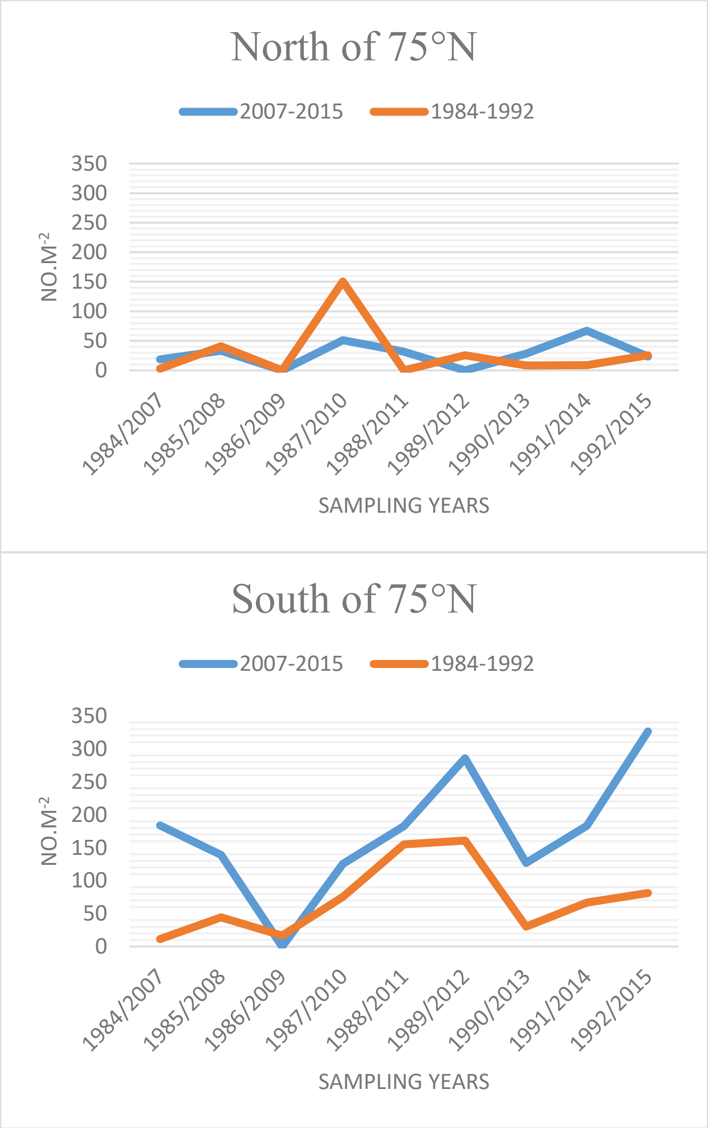


Figure 10: Abundance (no.m^{-2}) north (above) and south (below) of 75°N in the years 1984-1992 and 2007-2015.

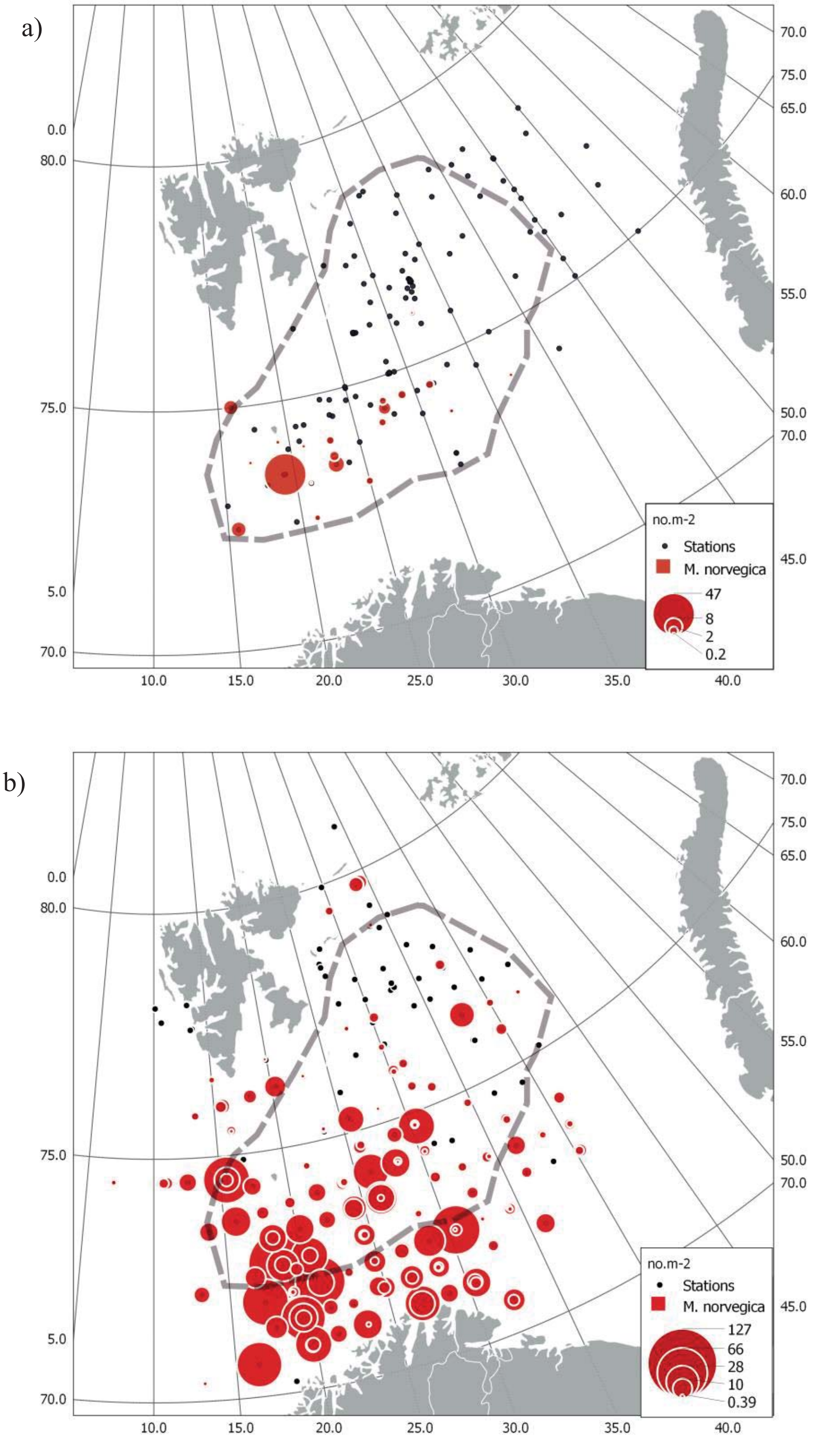


Figure 11: Distribution of *M. norvegica* in a) 1984-1992 and b) 2007-2015

Maturity

A total of 490 adult euphausiids were collected in the 2015 TIBIA cruise, sampling from 28th of May until the 4th of June. Of these, 39% were males, 24% were females and 37% had no identifiable sexual characters (Table A4, Appendix I). Most of the euphausiids that could be identified by sex were in stage 3 or 4 of maturation (87% of the males and 80% of the females) and around 67% of both sexes carried spermatophores.

138 individuals of adult *T. inermis* were found, all (except three) at stations on the slope of the Bear Island and Svalbard Banks (stations I, II and III (Figure 4, Table A4, Appendix I)). At station III, the adults were either mature (stage 3-4) or had no identifiable sexual characters. At station I and II, almost all of the adults had no identifiable sexual characters. Out of 334 individuals of *T. longicaudata*, 83% were found at station III and I; the rest at the southernmost stations VII and VIII (Table A4, Appendix I). Most of *T. longicaudata* were ready to spawn but around 30% had no identifiable sexual characters. In total, two mature (stadium 4, but no spermatophores) individuals of *M. norvegica* were found at station VIII, while eight individuals of *T. raschii* were found at station III, all mature and half of them carrying spermatophores.

Abundance of eggs and larvae in 2015

About 25 000 eggs and larvae were collected at 8 stations in 2015. Of these, *T. inermis* was the dominating species with 93,8% of the total abundance. *T. longicaudata* and *T. raschii* constituted 2,9% and 0,013% respectively while *M. norvegica* represented 3,3% of the total abundance (Table 5). The lowest abundances (no.m^{-2}) of eggs and larvae were found at two of the stations located at the slope of the Bear Island bank and south the Spitsbergen bank (stations III and II, Figure 12) while the highest abundances appeared at the stations located in Bear Island Trough and Hopen Trench (Table 5). Larvae of *T. inermis* were found at all stations with abundances varying from 270-6528 individuals per m^2 (Table A5, Appendix I). *T. raschii* larvae were only found in very low numbers at the two southernmost stations, VIII and VII (Table A6, Appendix I), while *T. longicaudata* egg and larvae were found at all stations except V and VI (Table A7, Appendix I). Eggs and larvae of *M. norvegica* were present at both of the two southernmost stations, with the highest numbers at station VIII (Figure 12, Table A8, Appendix I).

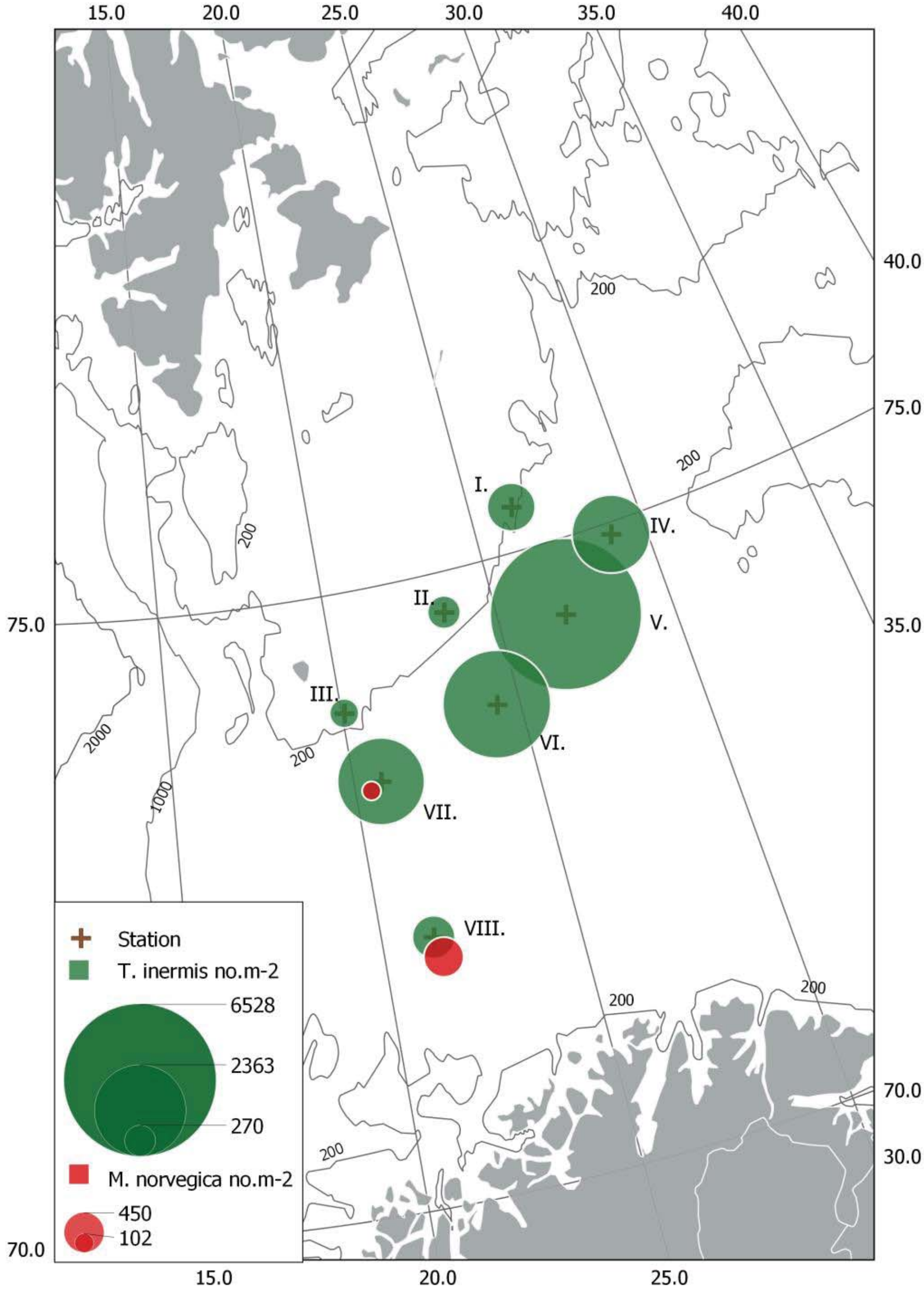


Figure 12. Abundances (no.m^{-2}) of egg and larvae found at each station in May-June 2015. Abundances at each station are shown by scaled circles for *T. inermis* (green) and *M. norvegica* (red). Station numbers are given beside the abundances.

Development of larvae

The three stations located at the edge of the Bear Island Bank show a south-to-north trend in the development of *T. inermis* larvae (Figure 12). Only eggs and nauplii were found at III, the southernmost station on the Bear Island Bank, while Calyptopes 1 (C1) was the most common stage at station II, and C2 was the most numerous stage at station I (Figure 13). In the Hopen Trench, at the stations IV, V and VI (Figure 12), the majority of the larvae were in calyptopes stages, and with appearances of early furcilia. The samples from the two southernmost stations VII and VIII mostly had later developmental stages of *T. inermis* larvae, the majority being F1 and F2, while no *T. inermis* calyptopis were present at the southernmost station (St. VIII, Figure 12). Larvae of *M. norvegica* were generally in an earlier phase of development at station VIII than *T. inermis,* as eggs were present and calyptopes was the most numerous stages (Figure 14). The larval stages of *T. longicaudata* and *T. raschii* were too few to give a clear indication of the species development at each station (Table A6 and A7, Appendix I). Length, standard deviation and length intervals for egg and larval stages for the analysed individuals are given in (Table A9, Appendix I). The lengths of *T. inermis* eggs and larvae show a continuous development from egg to F6. In late calyptopis and furcilia stages the lengths were overlapping between the different stages. The same was the case for *M. norvegica*, albeit no observations of nauplius were made (Table A8, Appendix I).

Table 5: Abundance (no.m^{-2}) of egg and larvae at each station

Station	*T. inermis*	*T. longicaudata*	*M. norvegica*	*T. raschii*
I	660	26	0	0
II	306	3	0	0
III	270	40	0	0
IV	1792	128	0	0
V	6528	0	0	0
VI	3328	0	0	0
VII	2363	175	102	1
VIII	524	116	450	1

Species identification by barcoding

Barcoding of the COI gene was successful for 12 out of the 15 samples subjected to the analysis. The phylogenetic tree shows that the specimen 2, 3, 5, 6, 7, 8, 9, 10, 12, 13 are similar to *T. inermis*, while sequence 14 and 15 are *T. raschii* and *M. norvegica,* respectively (Figure 15). This means that the identification based on morphometric characteristics was correct for nine out of twelve analysed samples. Of these, eight samples were correctly identified as *T. inermis* F1, and one as *M. norvegica* metanauplius. Three samples of F1 were incorrectly identified: two samples of *T. inermis* as *T. raschii* and *T. longicaudata,* respectively, while one specimen of *T. raschii* was wrongly identified as *T. inermis.*

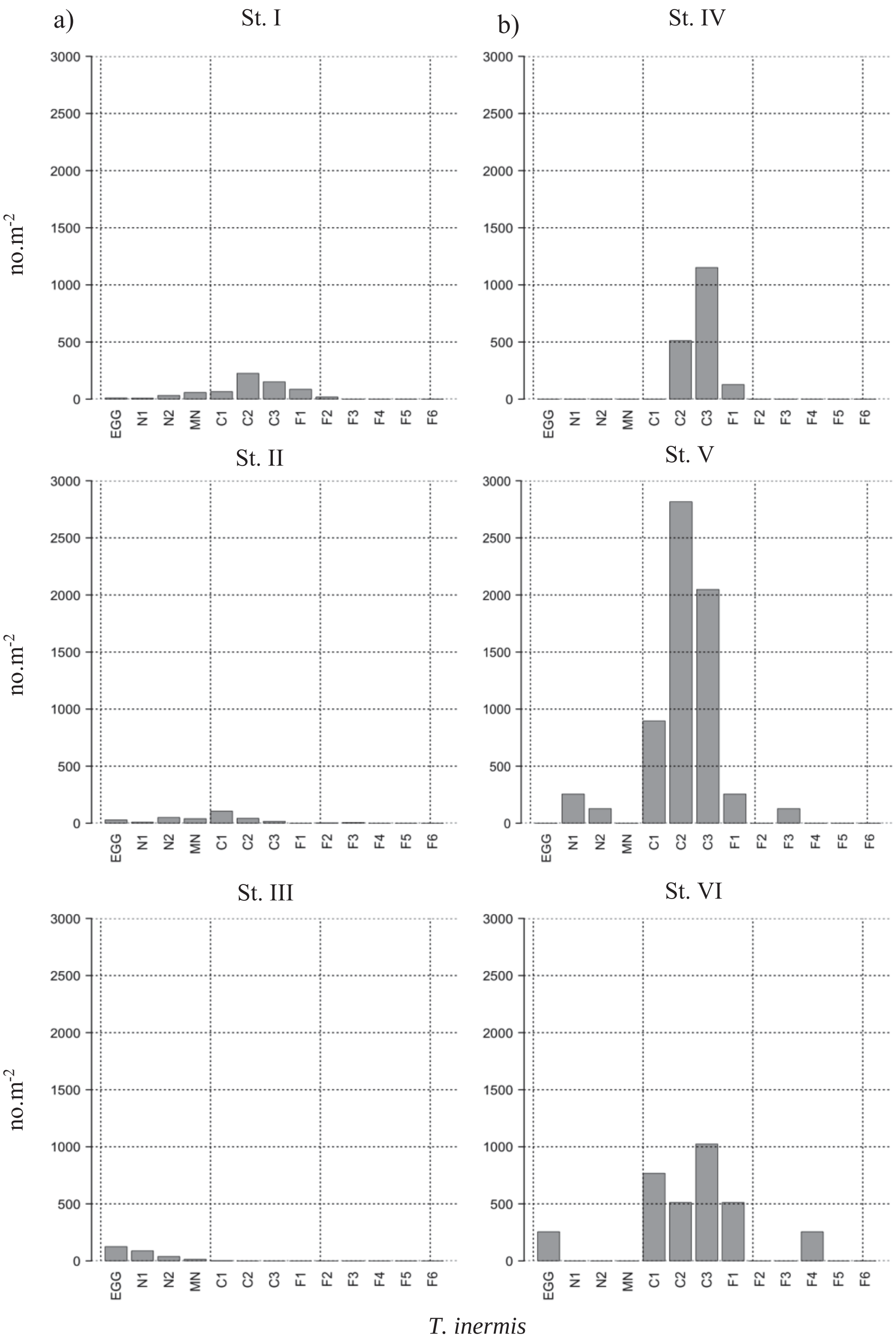
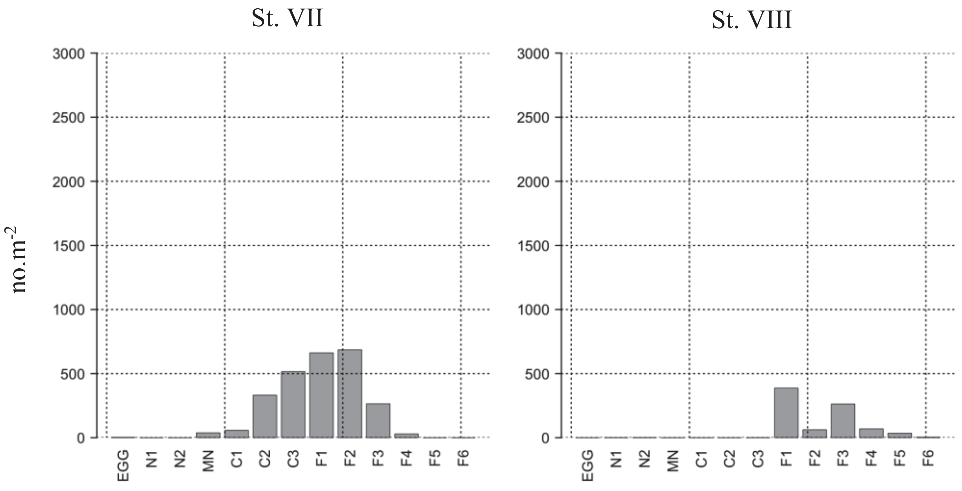
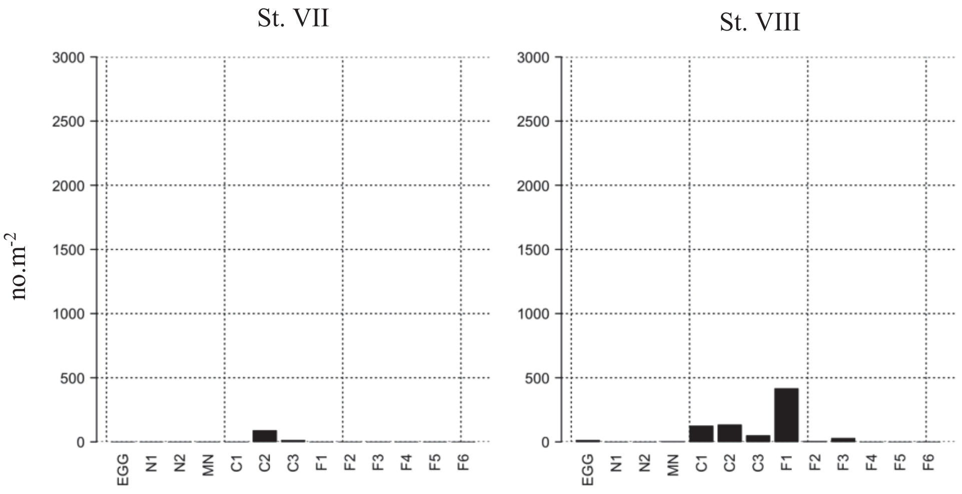


Figure 13: Distribution of *T. inermis* larval stages per station (no.m^{-2}) in a) Mixed/Arctic water and b) Atlantic water.



T. inermis



M. norvegica

Figure 14: Distribution of *T. inermis* (above) and *M. norvegica* (below) eggs and larval stages at the stations VII and VIII (no.m^{-2}).

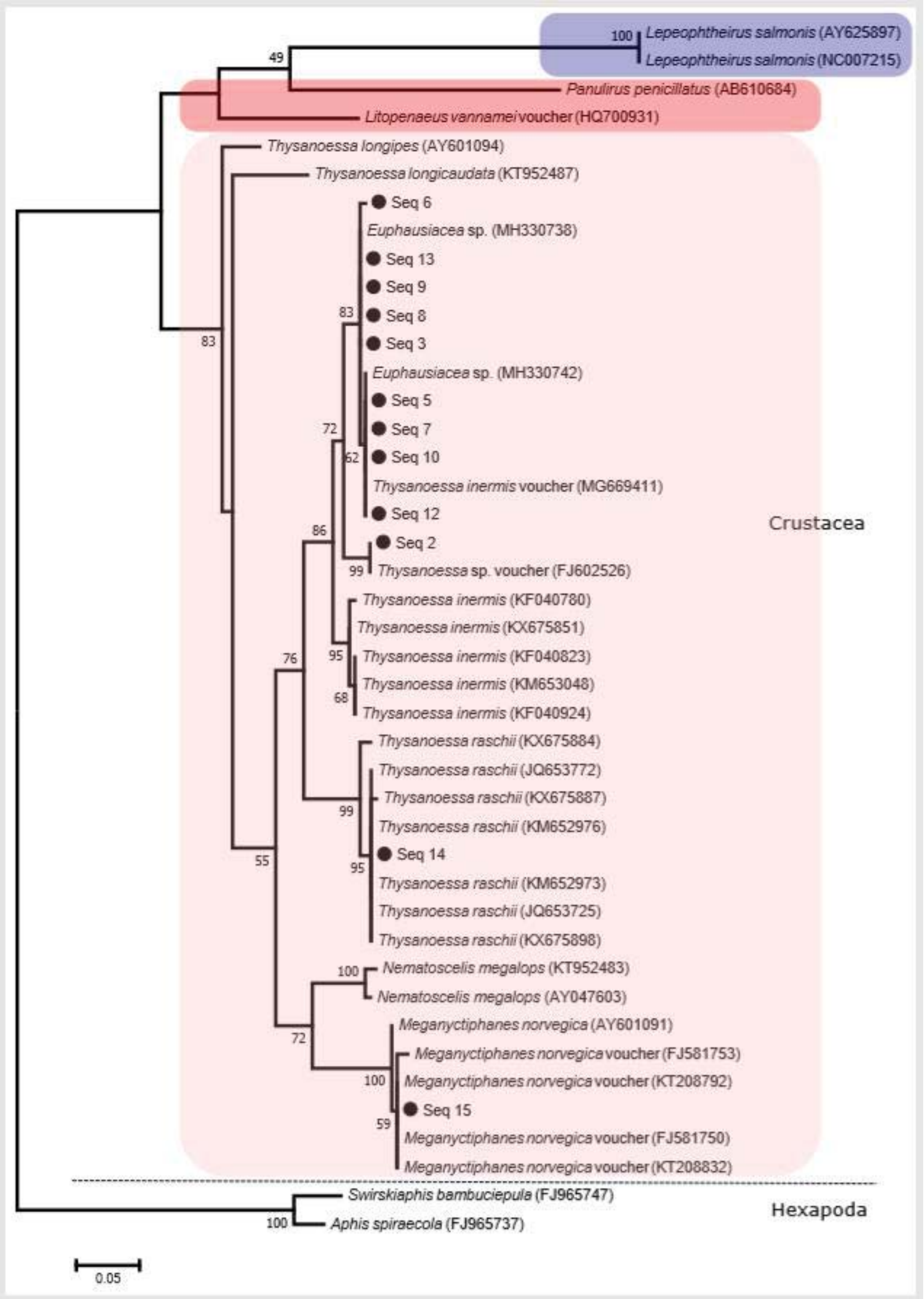


Figure 15: Phylogenetic tree. After sequence alignment using MUSCLE (Edgar, 2004), the phylogenetic tree was constructed using MEGA 7 (Kumar *et al.*, 2016) using the krill sequences obtained in the present study (black dots), together with available sequences downloaded from GenBank (accession numbers provided within parenthesis) via the maximum likelihood method based on the Jukes–Cantor model and 500 bootstraps. Blue color represents sequences from Class *Maxillopoda*, while red color represents sequences from Class *Malacostraca* (dark for Order *Decapoda* and light for Order *Euphausiacea*). Bootstraps below 50 are not shown.

Discussion

The sampling and monitoring of euphausiids is challenging (Eriksen et al., 2016), owing both to the natural variability of euphausiid distribution as well as methodological issues. Eriksen et al. (2016) suggests that there is a high degree of patchiness in the distribution of euphausiids, meaning that some stations will contribute disproportionately to the average abundances found per station in the 1984-1992 and 2007-2015 datasets. This effect is indicated by the high standard deviations of the average abundance found in my results. Due to this patchiness, the MOCNESS, covering around 2000 m^3 per haul, has a limited probability of target the infrequent aggregations of euphausiids (Eriksen et al., 2016), and thereby underestimating the abundance. The exact degree of under sampling is not known, although a rough comparison of euphausiid biomass sampled with the MOCNESS and winter bottom trawl indicated a serious underestimation by the MOCNESS (Eriksen et al., 2016). This was probably owing to the larger filtering capacity of the bottom trawl (20 000 m^3) (Eriksen et al., 2016) that would give a higher chance of target euphausiid swarms. Moreover, it is well established that the MOCNESS leads to an underestimation of large individuals that are able to visually avoid the net (Wiebe et al., 1982; Skjoldal et al., 2013). This especially concerns the larger species *M. norvegica,* which has a much higher avoidance factor than the three *Thysanoessa* species (Wiebe et al., 2013). A 2- to 11- fold underestimation of *M. norvegica* by MOCNESS has been suggested (Wiebe et al., 2013) in contrast to around two-fold underestimation for the larger individuals of *T. inermis* (Eriksen et al., 2016; Dalpadado and Skjoldal, 1991; 1996). Therefore, the results in this thesis should be regarded as minimum values, especially the abundances of *M. norvegica*. Despite the drawbacks, these data sets offer insight into the relative fluctuations of euphausiid abundance and population structure over longer time periods – an important study area considering the environmental changes that are unfolding in the Barents Sea ecosystem.

Abundance

When comparing all sampling stations over the two study periods, my results show significantly higher average abundance during the years 2007-2015 compared to the years 1984-1992, having risen by around 60% (Q1). Moreover, when only considering the stations sampled in the area with approximately equal sampling frequency (Figure 7), the same increase between the study periods can be seen, indicating that the rise in abundance is not resulting from any difference in the positioning of sampling stations between the study periods.

It has been established that euphausiid behavior change over the course of a year (Zhukova et al., 2009), staying close to the bottom in winter while being distributed in the pelagic layer during spring and autumn (Drobysheva, 1994; Mauchline, 1980; Orlova et al., 2008). Hence, due to the varying sampling seasons in the first study period (Table 2), the datasets of 1984-1992 and 2007-2015 are not strictly comparable. But as the seasonal vertical distribution of euphausiids are largely undiscovered (Eriksen et al., 2016; Orlova et al., 2008), it is hard to infer exactly how this have affected my data. One possibility is that the MOCNESS would have missed winter aggregations close to the bottom, as it samples around 20 above the seabed. Another possibility is that the lack of light during the Arctic winter limits the avoidance effect (Wiebe et al., 2013) and hereby results in higher catches. When excluding all data not sampled in autumn (August, September, October (Table 2)), from the study period 1984-1992, the average abundance per station was much lower, hence rising 236% to the second study period. This could indicate that the winter and spring catches in general are higher than in autumn. However, it is hard to conclude on this, as excluding all but autumn months results in a very small datasets which would further limit the chances of targeting one of the aggregations as discussed above. Further studies should concentrate on establishing the concrete underestimation these factors give.

Despite the likely sampling errors, there seem to be strong evidence for euphausiid abundance being considerably higher in the years 2007-2015 compared to the years 1984-1992. Euphausiid abundance is known to be controlled by a number of complex factors and vary considerably between years (Dalpadado et al., 2012). Care should therefore be taken when interpreting the changes in two separate and relatively short time periods such as the data used in this study. However, several authors also report of increased abundance and biomass of Barents Sea euphausiids in the recent years associated with the warming temperatures (Eriksen et al., 2017; Zhukova et al., 2009; Orlova et al., 2013; Orlova et al., 2015), despite high capelin predation pressure (Eriksen and Dalpadado, 2011).

Capelin biomass is considered an important factor controlling euphausiid populations (Eriksen and Dalpadado, 2011). When capelin stocks are high (4-7 million tonnes), it can consume up to 30 million tonnes of euphausiids (Drobysheva and Yaragina, 1990; Dolgov et al., 2011), creating an inverse negative relationship between capelin stock size and euphausiid biomass (Dalpadado et al., 2014; Eriksen and Dalpadado, 2011). This relationship can be seen in the 1984-1992 data set. From 1984 to 1986, euphausiid abundance was low, responding to a large capelin biomass of 4-7 million tonnes (WGIBAR, 2017). During the years 1986-1989, the capelin stock collapsed, and the consequent increase in the populations of *T. inermis* and *T. longicaudata* came as a response to the ease in predation (Dalpadado and Skjoldal, 1996). From 1990 and onwards, capelin biomass again recovered to around 4 million tonnes (WGIBAR, 2017; Dalpadado and Skjoldal, 1996) resulting in a marked decrease in euphausiid biomass. In contrast, capelin biomass was continuously high during the years 2007-2014, again constituting close to 4 million tonnes (WGIBAR, 2017), but no response in euphausiid abundance similar to the years 1984-1992 could be detected during this period. Euphausiid abundance during the years 2007-2015 was at a much higher level than what has previously been found in periods of similar capelin stock size (Eriksen and Dalpadado, 2011; WGIBAR, 2017). Indicating an alteration of the euphausiid - capelin relationship (Eriksen and Dalpadado, 2011) and less interannual fluctuations in the euphausiid populations (Orlova et al., 2013).

My results show that there is a strong, significant correlation between euphausiid abundance and Kola temperature in the recent years (Q1), a relationship demonstrated in other studies as well (Eriksen and Dalpadado, 2011). Rising sea temperatures and a longer open water season will probably result in increased primary production (Ellingsen et al., 2008; Dalpadado et al., 2014) that could benefit euphausiid populations, as the most dominant species are regarded as primarily herbivorous (Dalpadado et al., 2008b). Moreover, Orlova et al. (2013) claimed that if large abundances of euphausiids were to be maintained in years of high capelin predation, a strong inflow of euphausiids by Atlantic waters was necessary. It does seem that climate change affects hydrographic parameters in a way that years of high sea water temperature are connected to strong inflow of Atlantic water into the Barents Sea (Orlova et al., 2010), and that the volume of inflowing Atlantic waters have increased in the Barents Sea in recent years (Årthun et al., 2012; Spielhagen et al., 2011), affecting the influx of zooplankton (Slagstad, Ellingsen and Wassman, 2011). It seems that rising temperatures, the consequent rise in primary production as well as increased advection are contributing to the higher abundances of euphausiids registered in this study.

Distribution

The increase of Atlantic water into the Barents Sea are changing the areas formerly occupied by Arctic and Mixed waters (Dalpadado et al., 2012; Årthun et al., 2012) pushing the biogeographical boundaries northwards (Frainer et al., 2018; Orlova et al., 2011). This study found the largest abundances of euphausiids to be distributed south of 75°N in both study periods (Q2), and consequently the registered increase in abundance was mainly located in the southern Barents Sea. The 75°N latitude roughly delimits the traditional border for Arctic and Atlantic water masses, thereby the main distribution of the Barents Sea euphausiids (Dalpadado and Skjoldal, 1991). The limited rise north of 75°N found in this study could suggest that the Atlantification of the Barents Sea is still limited to the northern parts. However, in 2006, the euphausiid abundance in the northwestern areas of the Barents Sea were reported to be three times higher than the long-term mean (1952-2009) before it decreased in the consequent years, probably as a result of capelin predation (Orlova et al., 2010). In contrast, the abundances in the southern areas were found to increase in the same time period (Orlova et al., 2011). Dalpadado et al. (2014) also found the predation pressure from capelin to be especially high in the northern parts of the Barents Sea during 1998-2010. Orlova et al., 2015 predict that as capelin continues to expand further into the Barents Sea (Hop and Gjøsæter, 2013) the euphausiid-capelin relationship could be much more pronounced in Arctic water regions, while in the western regions if this relationship is buffered by the strong inflow of euphausiids with Atlantic water.

Despite un-significant increases of total euphausiid abundance north of 75°N, there is evidence of wider distributional ranges of *T. inermis*, *T. longicaudata* and *M. norvegica* in the second study period. *T. inermis* was the most widely distributed species in the study area and dominated the species composition north of 75°N. No significant increase in abundance could be seen in the restricted area north of 75°N. However, relatively large aggregations of *T. inermis* outside the comparable restricted area could be detected in 2007-2015, seeming to be more commonly distributed in the northern part of the Barents Sea in the second study period compared to the first. This is supported by findings of large abundances of euphausiids northeast of Svalbard (Eriksen et al., 2016) and of extended distributional ranges of *T. inermis* and *T. longicaudata* (Orlova et al., 2011). My data also indicate that *M. norvegica*, a boreal, North-Atlantic species, had a more northerly and easterly distribution in the years 2007-2015 than what was found in 1984-1992 (Q2). There were significantly higher abundances of *M. norvegica* north of 75°N in the second period. During the years 1984-1992, the northernmost observation of *M. norvegica* was at 75°N which was in agreement with Mauchline and Fisher (1969), who also found that *M. norvegica* generally had a distribution as far north as 75-76°N. In contrast, during 2007-2015, *M. norvegica* was common in samples as far north as 77-78°N. It is also quite probable that the observation of *M. norvegica* at 80°N also is relevant for this study, but as no samples from 1984-1992 were available at this latitude, this is not possible to conclude on. An expansion of *M. norvegica* has been reported by a number of other authors (WGIBAR, 2017; Orlova, et al., 2011; Bucholz, Werner and Bucholz, 2012) connecting the observations to the larger inflow of Atlantic waters (Zhukova et al., 2009). Results from this study indicates that the more Atlantic environment allows *M. norvegica* to sustain itself more widespread into the Barents Sea compared to what formerly observed, and that a shift in biogeographic boundaries likely is occurring.

Species composition

The expansion of *M. norvegica* is also reflected in the species composition of the Barents Sea euphausiids, changing markedly from the years 1984-1992 to 2007-2015 (Q2). In the second study period, *M. norvegica* constituted between 5-30% of the species composition, as opposed to the years 1984-1992 where the species constituted a few percent of the total abundance. Numbers of *T. raschii* on the other hand decreased significantly. Zhukova et al. (2009) in studying long time series of winter data, found a clear relationship between the proportion of *M. norvegica* in the species composition and warm years, while *T. raschii* was more prominent in colder years. In colder years such as the 80s, *M. norvegica* disappeared completely, while in the warmer 50s, the species constituted around 10-30% of the species composition (Zhukova et al., 2009). My results show that during 2007-2015 there was considerable variation in *M. norvegica* abundance but that overall *M. norvegica* seemed to constitute an important part of the euphausiid assembly in the southwestern parts of the Barents Sea.

Ecosystem effect

Due to the importance of euphausiids in the Barents Sea ecosystem (Dolgov et al., 2011), population changes are likely to affect higher trophic levels (Dalpadado et al., 2012). Larger biomass of euphausiids and more stable populations will likely benefit planktivorous fish such as Capelin, Herring *(Clupea harengus*), and Polar cod (*Boregadus saida*) (Ellingsen et al., 2008). Dalpadado and Mowbray (2013) reported of capelin increasing predation on euphausiids in recent years, and biomass of capelin seem to rise (Fall et al., 2018). However, with the northward expansion of cod and other planktivorous, boreal fish such as Blue Whiting (*Icromesistius poutassou*), and Mackrell (Scomber scombrus) (Anonymous, 2010), predation on euphausiids may increase and affect the stability of euphausiid populations in the future. For example, predation from cod may explain low numbers of *M. norvegica* even in years of high temperature and high Atlantic inflow (Zhukova et al., 2009).

Moreover, Zhukova et al. (2009) proposes that in warmer and colder periods, the euphausiids of different zoogeographical characteristics will replace each other, redistributing the species composition and making the total abundance of euphausiids a robust figure. And Dalpadado et al. (2012) report of a generally stable mesozooplankton biomass despite decreases in Arctic species. However, Slagstad, Ellingsen and Wassmann (2011) argues that the increase in Atlantic zooplankton does not necessarily compensate for the reduction in the Arctic species, as the inflow from the west does may not contribute to maintain these populations. *T. raschii* is the most important euphausiid species in the eastern parts of the Barents Sea, and there are reports of this species disappearing from the stomachs of capelin in these areas (Orlova et al., 2013). The change in species composition of euphausiids could affect higher trophic levels if the predators shift their diet to the more abundance species. *M. norvegica* for example, is an omnivorous species (Dalpadado et al., 2008b), and it may make a less energy-efficient prey than the *Thysanoessa* species who are primarily herbivorous (Dalpadado et al, 2008b).

Species composition of larvae

Due to the changing population structures in the Barents Sea, it is increasingly important to monitor larvae, a key to understand the response of euphausiid populations in a climate change scenario (Teglhus et al., 2015). Despite their importance, few studies have concentrated on detailed studies of this subject in the Barents Sea (Loftnes, 1993). For the investigations in this thesis, only eight stations have been available for analysis, which will limit the reliability of my results. However, my data still offer insight into the general situation of euphausiid larvae in the southwestern Barents Sea, May 2015. The results from this thesis largely confirmed the findings of Loftnes (1993) concerning species composition, distribution and development of larvae. The species composition of May 2015 was similar to what was found in May 1989 and June 1988 (Q3) (Loftnes, 1993). *T. inermis* egg and larvae dominated the larval assembly constituting around 90% of the species composition, while the larvae of *T. longicaudata*, *T. raschii* and *M. norvegica* were found in low numbers. The species composition of the larvae does not entirely reflect the species composition of adult euphausiids as stated above, suggesting that it is mostly *T. inermis* who spawn in the southwestern Barents Sea.

Distribution of larvae

The largest abundances of euphausiid egg and larvae were found at stations located in the Hopen Trench, at depths of around 400 m (Q3) (Figure 12). The same situation were reported by Loftnes (1993) in May 1989 and June 1988, which found the greatest abundances of larvae at stations south and east of Bear Island. Moreover, this is in agreement with Timofeev (1993) who suggested that the main spawning ground of Barents Sea euphausiids would be limited to this area. Shelf edges have previously been found to be important spawning regions for *T. inermis* and *M. norvegica* around Iceland and in the Norwegian Sea (Silva et al., 2016; Dalpadado, 2006), and it is possible that the area off the Svalbard bank could serve a similar purpose. Moreover, Silva et al. (2016) found that bathymetry, chlorophyll-a concentration and water temperature significantly explained the distribution and abundance of larvae around Iceland. They also found the highest abundances of euphausiid egg and larvae in areas of Atlantic waters and in the frontal zones where cold and warm water met.

Arctic water dominates the Svalbard Bank, and are separated from the warm Atlantic water in the Hopen Trench by strong gradients of temperature and salinity (Sakshaug and Sagstad, 1992), as well as varying volumes of Mixed water (Loftnes, 1993). There were clear abundance differences between the three stations situated in the Bear Island Trough and Hopen trench (IV, V, VI) and the adjoining stations located south of Bear Island and at the Svalbard bank (I, II, III), much smaller abundances being found at the stations at the latter area (Figure 12). No data on physical properties have been available for the stations in this thesis, but by comparing the positions of the stations with previous investigations on water masses, it seems likely that these stations are influenced either by Arctic or Mixed waters (Loftes, 1993:20; Sakshaug and Sagstad, 1992). Loftnes (1993) also found the lowest abundances at stations influenced by Arctic or Mixed water, which suggests that the reproduction of euphausiids may be retarded in colder waters, underlining the importance of Atlantic waters for euphausiid spawning (Silva et al., 2016; Einarsson, 1945).

Development of larvae

My results show that there is a distinction in the onset of spawning and the development of larvae relating to water mass (Q4). Station III, situated south of the Bear Island, was most probably influenced by Arctic of Mixed water masses. Most of the mature adults of both *T. inermis* and *T. longicaudata* were found at this station (Figure 4, Table A4, Appendix I), which could indicate that spawning was ongoing (Dalpadado and Skjoldal, 1991). Moreover, most of the larvae present at station III were in early developmental stages such as egg, nauplii 1 and 2 (Figure 13, Table A5, Table A7, Appendix I) which is also believed to indicate ongoing spawning activity (Makaraov, 1979). Due to the successive development of larvae, the most prominent larval stage at a station may be used as an indication of the timing since the peak spawning activity (Loftnes, 1993). At the two other stations at the Svalbard Bank, II and I (Figure 4), the main larval stage was C2 and C3 respectively, which therefore could indicate somewhat earlier spawning than at station III. Moreover, most of the adults found at station I, and half of the adults found at station II had no identifiable sexual characters (Table A4, Appendix I), which could indicate that spawning activity had ended here. At stations in the Hopen Trench (IV, V and VI (Figure 4), the larvae were also mostly centred around C2 and C3. Curiously, no adults were found at these stations, probably suggesting that spawning had ended. At the southern stations VII and VIII (Figure 14), the development of *T. inermis* larvae was more advanced, centred around furcilia stages.

Melle (1991) argue that euphausiids spawn when conditions are favorable, and temperature as well as chlorophyll-a concentration has been established to play an important part in the onset of the spawning and the development of larvae (Loftnes, 1993; Siegel, 2000; Silva et al., 2016). This could mean that the spawning and development of *T. inermis* larvae started at the southernmost station were temperatures and the chlorophyll-a concentration were higher, and that spawning proceeded northwards as the conditions were suitable. It could also mean that the development of the larvae was quicker in warmer water (Teglhus et al., 2015). The average chlorophyll satellite images (Figure A1, Appendix I) show that the spring bloom started in April, with high concentrations in the coastal areas off northern Norway which could support that the spawning started at the southernmost station. In May 1989 Loftnes (1993) found that the development of *T. inermis* egg and larvae largely responded to the different water masses, being the furthest developed in Coastal waters, and indicated that this could be because of the spring bloom often develops early here. However, without detailed information on water temperature and chlorophyll-a concentration at each station, the interpretation of the reason for the rate of development remains speculative.

Warmer seawater temperatures could allow for earlier onset of the spring bloom (Renaut, Devred and Bambin, 2018) higher phytoplankton production (Ellingsen et al., 2008) and may lead to higher survival of euphausiid larvae. Siegel (2000) argue that earlier onset of spawning gives faster developed and leaves the larvae more prepared for winter. Future changes in the timing and intensity of the phytoplankton bloom might therefore affect euphausiid reproduction and their recruitment success (Teglhus, et al., 2015).

M. norvegica

I found egg and larvae of *M. norvegica* in small numbers at station VII, while two mature males, eggs, calyptopes and early furcilia were found at the southernmost station (VIII). Silva et al. (2016) and Dalpadado (2006) found that *T. inermis* was mostly spawning in areas where the bloom was in the initial development, while *M. norvegica* spawned in area where the bloom was ending, which could explain this species late development compared to *T. inermis*. Loftnes (1993) found abundances of *M. norvegica* larvae (20-640 no.m^{-2}) comparable to what was found in this study (Table 5) in May 1989. The larvae were found at 12 out of 63 stations scattered around the whole study area, but never with more than one or two larval stages found per station. In June 1988, only a few observations of *M. norvegica* larvae were made.

Dalpadado and Skoldal (1991) did not find *M. norvegica* in a reproductive state in their investigations in the Barents Sea, and it is generally established that M. norvegica does not reproduce in the Barents Sea except from very warm years (Mauchline and Fisher, 1969). Given the high temperatures of the recent years it is however increasingly possible that *M. norvegica* would be able to spawn in the Barents Sea (Mauchline and Fisher, 1969; Einarsson, 1945), especially seeing that earlier limits of spawning seem to be shifting in Kongsfjorden, Svalbard (Bucholz, Werner and Bucholz, 2012). The presence of mature males, eggs and early stages of *M, norvegica* at the same station could indicate that spawning was ongoing (Timofeev, 1993; Teglhus et al., 2015). However, as *M. norvegica* were only found the southernmost stations, and as these were placed in the trajectory of inflowing water from the spawning grounds in the Norwegian sea, it is difficult to conclude on anything. Furthermore, even though spawning was occurring there might still be thermal constraints limiting the possibility for *M. norvegica* of fulfilling a complete life cycle of 2-3 years (Siegel, 2000).

Morphological identification of euphausiid larva

Further research is needed to verify whether *M. norvegica* might spawn in the Barents Sea. If *M. norvegica* starts spawning, this could also affect the euphausiid population dynamics and serve as an indication of ongoing Atlantification of the Barents Sea. An obstacle in improving this situation is their difficult identification. The larval stages of the Atlantic and boreal euphausiids have been thoroughly described (Einarsson, 1945; Lebour, 1924; 1926; Mauchline, 1971; MacDonald, 1928; Sars, 1989), however, within the genus *Thysanoessa* only subtle morphological characters separate the species, while some of the larval stages are impossible to distinguish by morphological characters alone (Einarsson, 1945).

DNA barcoding (the use of short DNA sequences for identifying species) can be an accurate and effective tool for species identification at the larval stages and can be used to assess the morphological identification. Barcoding verification showed that 75% of my identifications were correct, but that the identification of furcilia 1 to species level remain difficult. However, due to the documented dominance of *T. inermis* in the south-western Barents Sea (Loftnes, 1993, Dalpadado and Skjoldal, 1991;1996), it is highly probable that the main bulk of *Thysanoessa* Furcilia I larvae belong to *T. inermis*, as have been found both by Loftnes (1993) and in this study. Unfortunately, only specimens of furcilia 1 and metanauplii were available for barcoding analysis, due to the lack of alcohol preserved samples in the correct time period of larval development. Therefore, the degree of error in my identification is uncertain for the other larval stages. The most uncertain stages are the possible misidentification between eggs of *M. norvegica* and *T. inermis*, nauplii 1 and 2 of *T. inermis*, *T. raschii* and *M. norvegica*, and the metanauplii and calyptopes stages of *T. raschii* and *T. inermis*. There is still limited use of barcoding for euphausiids in the Barents Sea (Bucklin et al., 2010; Vereshchaka, Kulagin and Lunina, 2018), and further studies should concentrate on detailed examinations of morphologic characters verified with barcoding for all larval stages and species.

Conclusion

Euphausiids play a key role in the Barents Sea ecosystem. From the years 1984-1992 to 2007-2015 euphausiid abundance have increased in the southwestern and central Barents Sea, despite high capelin predation (WGIBAR, 2017), most probably as a result of increasing temperatures, stronger inflow of euphausiids into the Barents Sea (Slagstad, Ellingsen and Wassman, 2011), as well as increased primary production (Ellingsen et al., 2008; Dalpadado et al., 2014). These factors also influence the species composition and distribution of euphausiids. The abundances of the boreal North-Atlantic species *M. norvegica* increased substantially from the first to the second study period, constituting around 5-30% of the euphausiid species composition, while numbers of the cold-water species *T. raschii* decreased. *M. norvegica* also had a wider distribution in during the years 2007-2015 compared to 1984-1992, being observed as far north as 80°N. The species composition and distribution of euphausiid larvae in the southwestern Barents Sea 2015, were very similar to what was found by Loftnes in May 1989, the species composition being dominated by *T. inermis* egg and larvae, and the densest concentrations being found south and east of Bear Island in Atlantic water. The spawning and development of *T. inermis* larvae seemed to be affected by water mass and temperature, being more developed in Coastal and Atlantic waters compared to Mixed and Arctic waters. No evidence of *M. norvegica* spawning in the Barents Sea could be found in this study. However, as there is clearly a potential of *M. norvegica* spawning and completing its life cycle in Barents Sea waters, future research should concentrate on detailed studies of euphausiid larvae in the Barnents Sea and monitor the response of euphausiid population dynamics to climate change. Overall, I conclude that the warming climate has affected the abundance, distribution and species composition of euphausiids, and that these are symptoms of a general Atlantification of the Barents Sea.

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Appendix I

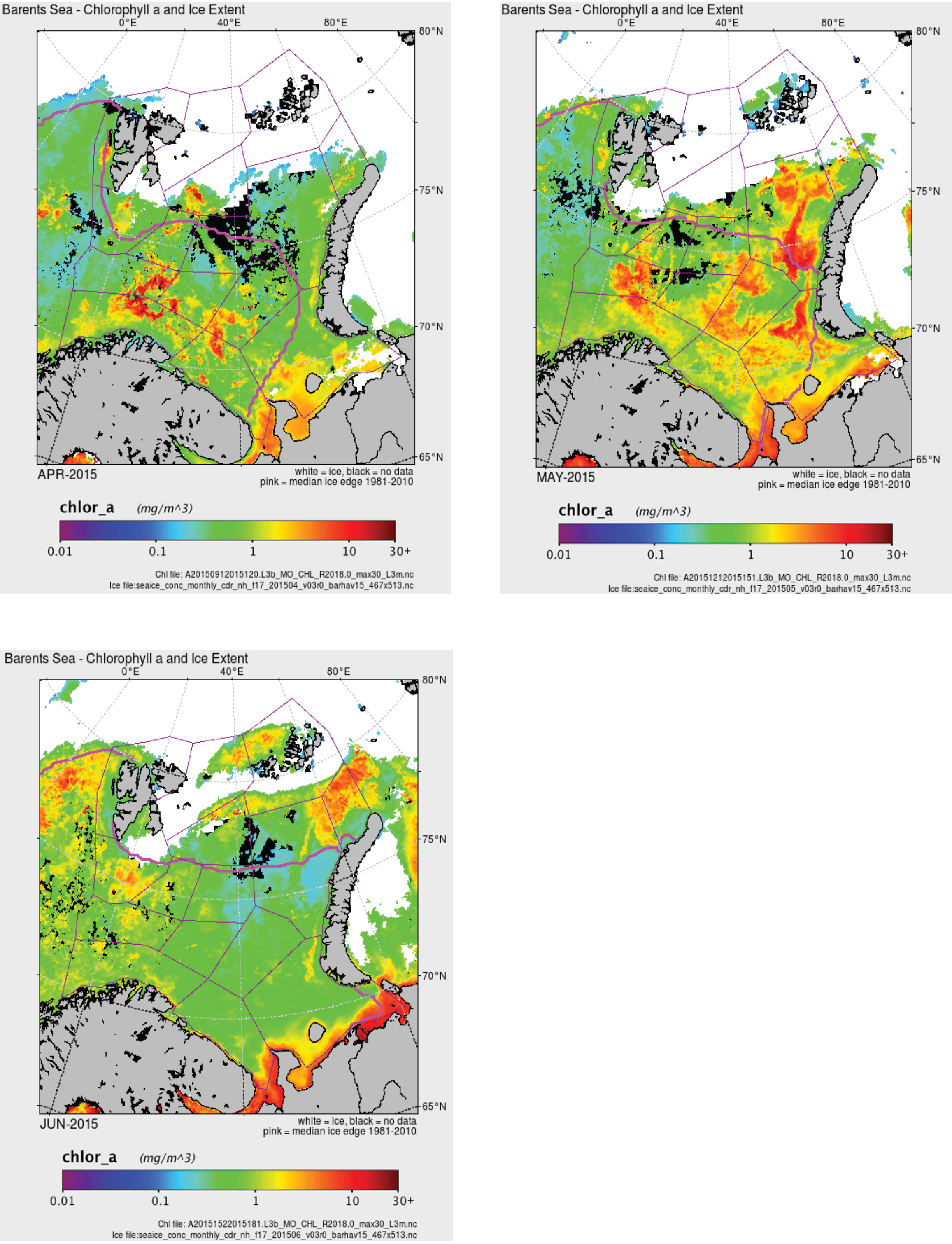


Figure A1: Chlorophyll a concentration averaged for April, May and June 2015.

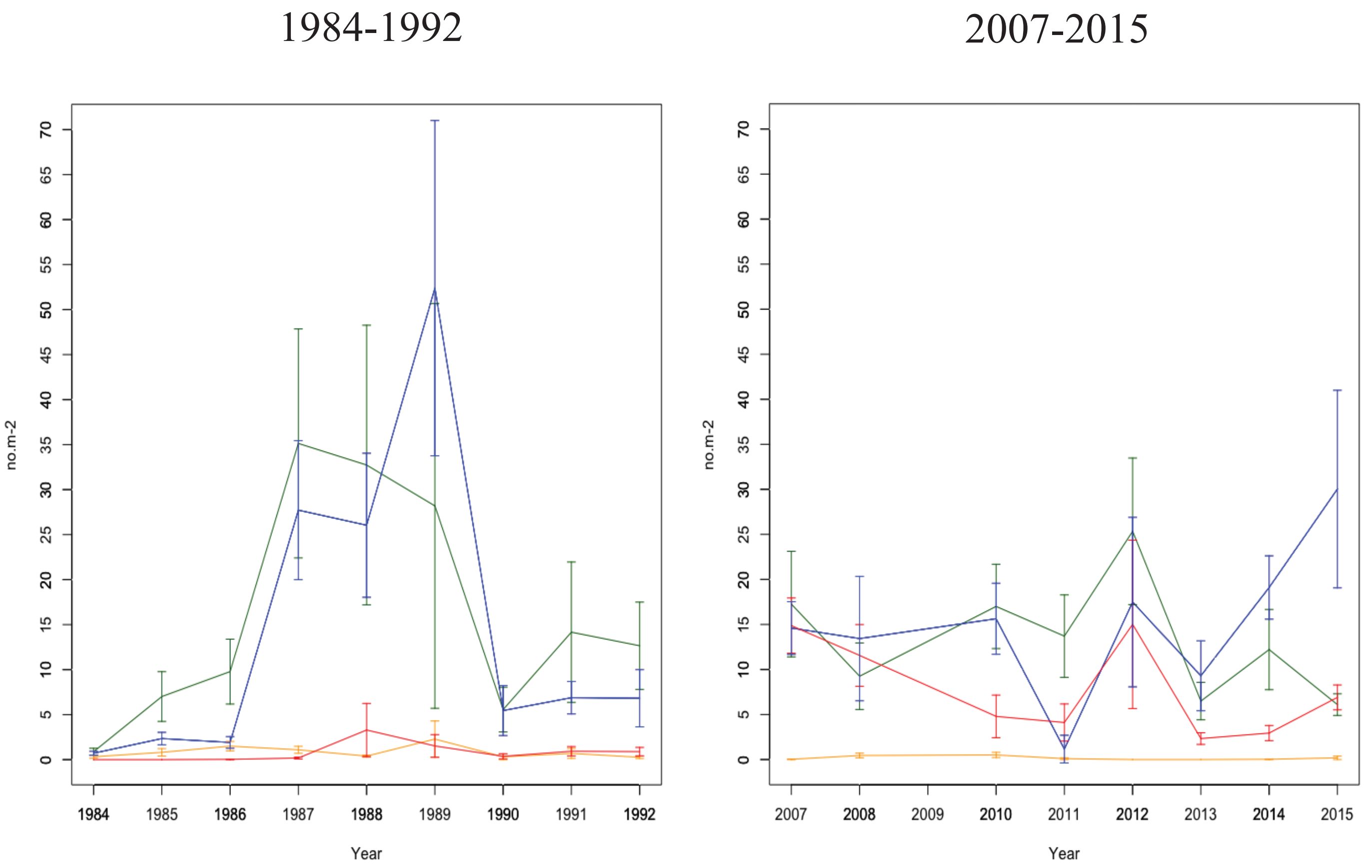


Figure A2: Abundances (no.m^{-2}) of euphausiids in the two study periods 1984-1992 and 2007-2015. Standard error of mean (SEM) is given for each of the species *T. inermis* (green), *T. longicaudata* (blue), *M. norvegica* (red) and *T. raschii* (orange).

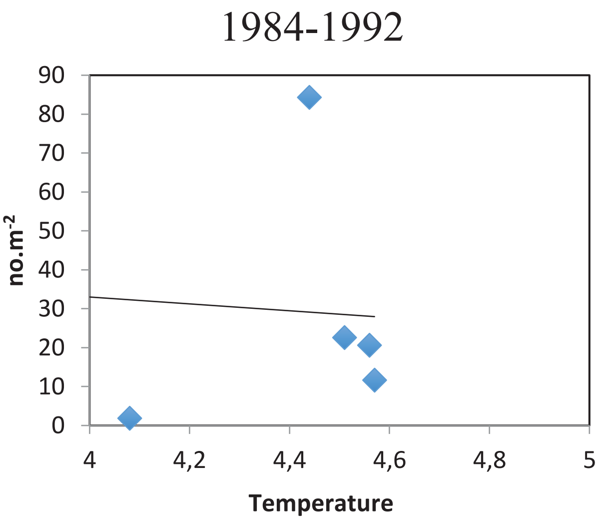


Figure A3: Correlation of Kola temperature and total abundance in the years 1984-1992.

Table A1: Euphausiid abundance (no.m^{-2}) in average, standard deviation and interval per year in the two study periods 1984-1992. All stations and sampling months are included.

Year	N. St.	*T. inermis*			*M. norvegica*			*T. longicaudata*			*T. raschii*			Unid.		
		AV	SD	CV	AV	SD	CV	AV	SD	CV	AV	SD	CV	AV	SD	CV
1984	27	0,88	1,98	2,26	0,00	0,00	0,00	0,71	1,12	1,59	0,32	0,88	2,78	NA	NA	NA
1985	26	7,01	14,09	2,01	0,00	0,00	0,00	2,34	3,53	1,51	0,81	2,12	2,62	NA	NA	NA
1986	6	9,78	8,83	0,90	0,03	0,08	2,45	1,91	1,58	0,83	1,50	1,27	0,85	NA	NA	NA
1987	17	35,13	52,45	1,49	0,18	0,46	2,56	27,72	31,83	1,15	1,09	1,55	1,42	NA	NA	NA
1988	16	32,73	62,13	1,90	3,29	11,81	3,59	26,04	32,01	1,23	0,39	0,47	1,20	NA	NA	NA
1989	5	28,19	50,28	1,78	1,52	1,92	1,26	52,38	41,65	0,80	2,28	4,50	1,98	NA	NA	NA
1990	6	5,56	13,23	2,38	0,37	0,69	1,85	5,45	6,80	1,25	0,31	0,77	2,45	NA	NA	NA
1991	9	14,16	6,09	0,43	0,93	1,55	1,67	6,88	14,22	2,07	0,69	1,66	2,40	NA	NA	NA
1992	23	12,65	14,02	1,11	0,89	2,14	2,41	6,82	14,57	2,14	0,26	0,61	2,35	NA	NA	NA
Tot.	135	14,68	34,00	2,32	0,72	4,27	5,91	11,23	22,52	2,01	0,65	1,57	2,41	NA	NA	NA
2007	28	17,26	31,00	1,80	14,87	24,64	1,66	14,60	15,487	1,06	0,03	0,18	5,29	1,15	4,00	3,48
2008	24	9,25	18,09	1,95	11,56	16,80	1,45	13,43	33,819	2,52	0,45	1,26	2,77	7,61	18,46	2,43
2010	28	17,00	24,77	1,46	4,79	12,51	2,61	15,63	20,856	1,33	0,51	1,51	2,95	9,71	20,88	2,15
2011	16	13,70	18,32	1,34	4,11	8,26	2,01	1,16	6,145	5,29	0,10	0,38	4,00	17,44	22,98	1,32
2012	14	25,34	30,44	1,20	15,01	34,98	2,33	17,48	35,213	2,01	0,00	0,00	0,00	20,04	58,09	2,90
2013	31	6,49	11,57	1,78	2,33	3,61	1,55	9,30	21,606	2,32	0,00	0,00	0,00	7,79	14,99	1,92
2014	49	12,21	31,17	2,55	2,94	5,89	2,00	19,10	24,608	1,29	0,04	0,12	3,52	3,94	6,95	1,77
2015	47	6,10	8,23	1,35	6,90	9,46	1,37	30,02	75,185	2,50	0,19	1,28	6,86	10,92	23,03	2,11
Tot.	237	11,99	23,26	1,94	6,66	13,79	2,07	17,31	40,011	2,31	0,16	0,88	5,49	8,41	21,71	2,58

Table A2: Restricted area: Euphausiid abundance (no.m^{-2}) in average and standard deviation north (N75) and south (S75) of 75°N in the years 1984-1992. “Unid.” gives unidentified euphausiids and “Tot.” represents the total euphausiid abundance.

	T. inermis		*M. norvegica*		*T.longicaudata*		*T. raschii*		Unid.		Tot.	
N75	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
1984	0,52	1,04	0,00	0,00	0,55	0,99	0,20	0,44	NA	NA	2,74	2,00
1985	6,69	15,17	0,00	0,00	1,85	2,48	0,37	0,80	NA	NA	40,60	15,72
1986	NA	Na	0,00	Na	Na	Na	NA	Na	NA	NA	0,00	Na
1987	22,69	25,19	0,00	0,00	33,02	40,71	1,06	1,62	NA	NA	150,47	66,89
1988	NA	NA	0,00	NA	Na	NA	NA	NA	NA	NA	0,00	NA
1989	8,03	0,00	0,00	0,00	16,61	0,00	1,11	0,00	NA	NA	25,75	0,00
1990	1,84	2,53	0,00	0,00	1,24	1,92	0,00	0,00	NA	NA	8,06	2,45
1991	1,40	1,63	0,09	0,19	1,65	2,34	0,00	0,00	NA	NA	8,72	3,95
1992	5,04	5,70	0,77	2,18	4,02	4,53	0,13	0,35	NA	NA	25,86	9,86
S75	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
1984	3,02	4,35	0,50	1,01	3,05	3,35	0,15	0,30	NA	NA	11,37	7,47
1985	14,82	14,59	0,00	0,00	6,72	5,98	3,57	4,64	NA	NA	44,33	20,44
1986	6,71	5,20	0,04	0,09	2,07	1,72	1,34	1,35	NA	NA	16,70	5,74
1987	20,74	32,17	0,22	0,54	19,70	23,46	1,05	1,67	NA	NA	75,54	49,14
1988	49,15	66,87	4,71	13,55	32,99	33,64	0,60	0,73	NA	NA	155,05	106,37
1989	33,23	56,58	1,91	3,09	61,33	42,19	2,57	5,15	NA	NA	160,76	82,35
1990	13,00	0,08	1,12	0,85	13,88	2,63	0,94	1,33	NA	NA	30,35	4,72
1991	23,82	28,81	1,20	1,98	9,45	5,81	1,25	2,16	NA	NA	66,68	36,74
1992	31,07	31,73	1,78	2,82	15,60	23,25	0,31	0,59	NA	NA	81,07	47,38

Table A3: Restricted area: Euphausiid abundance (no.m^{-2}) in average and standard deviation north (N75) and south (S75) of 75°N in the years 2007-2015. “Unid.” gives unidentified euphausiids and “Tot.” represents the total euphausiid abundance.

	T. inermis		*M. norvegica*		*T.longicaudata*		*T. raschii*		Unid.		Tot.	
N75	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
2007	0,54	1,42	3,73	6,22	2,30	4,29	0,00	0,00	0,08	0,22	18,57	6,46
2008	2,41	4,56	2,84	6,71	2,58	5,21	0,52	1,47	6,84	19,33	33,14	25,64
2009	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2010	12,95	31,56	0,28	0,85	1,15	2,47	0,52	1,55	0,00	0,00	51,33	33,88
2011	6,76	14,27	0,28	0,47	1,65	2,99	0,00	0,00	5,35	8,09	31,78	20,02
2012	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2013	0,48	18,92	0,00	3,57	0,00	0,00	0,00	0,00	5,23	10,72	28,19	24,72
2014	26,20	30,33	0,75	1,26	1,40	2,51	0,05	0,15	4,40	6,59	67,06	30,26
2015	3,89	3,85	0,77	1,18	2,54	3,79	0,00	0,00	7,19	9,94	23,20	13,94
S75	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD	AV	SD
2007	30,35	41,27	12,15	10,74	26,05	16,07	0,00	0,00	3,11	6,79	183,47	54,46
2008	12,97	18,48	20,94	20,76	15,07	19,60	0,00	0,00	9,93	23,31	139,24	42,25
2009	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2010	13,19	20,78	3,96	3,94	19,44	14,72	0,00	0,00	19,21	20,04	125,55	34,25
2011	32,70	21,06	8,96	12,69	5,40	8,92	0,38	0,76	41,12	31,79	182,87	63,57
2012	40,02	34,29	22,01	46,60	14,73	19,93	0,00	0,00	39,45	80,19	285,62	115,19
2013	22,51	15,56	4,18	4,43	16,43	16,06	0,00	0,00	13,41	18,72	126,93	38,79
2014	13,19	42,80	3,19	5,45	32,55	30,65	0,03	0,12	4,59	7,19	183,30	56,19
2015	8,95	10,85	6,53	10,07	52,93	107,06	0,44	1,96	17,98	32,88	326,26	119,55

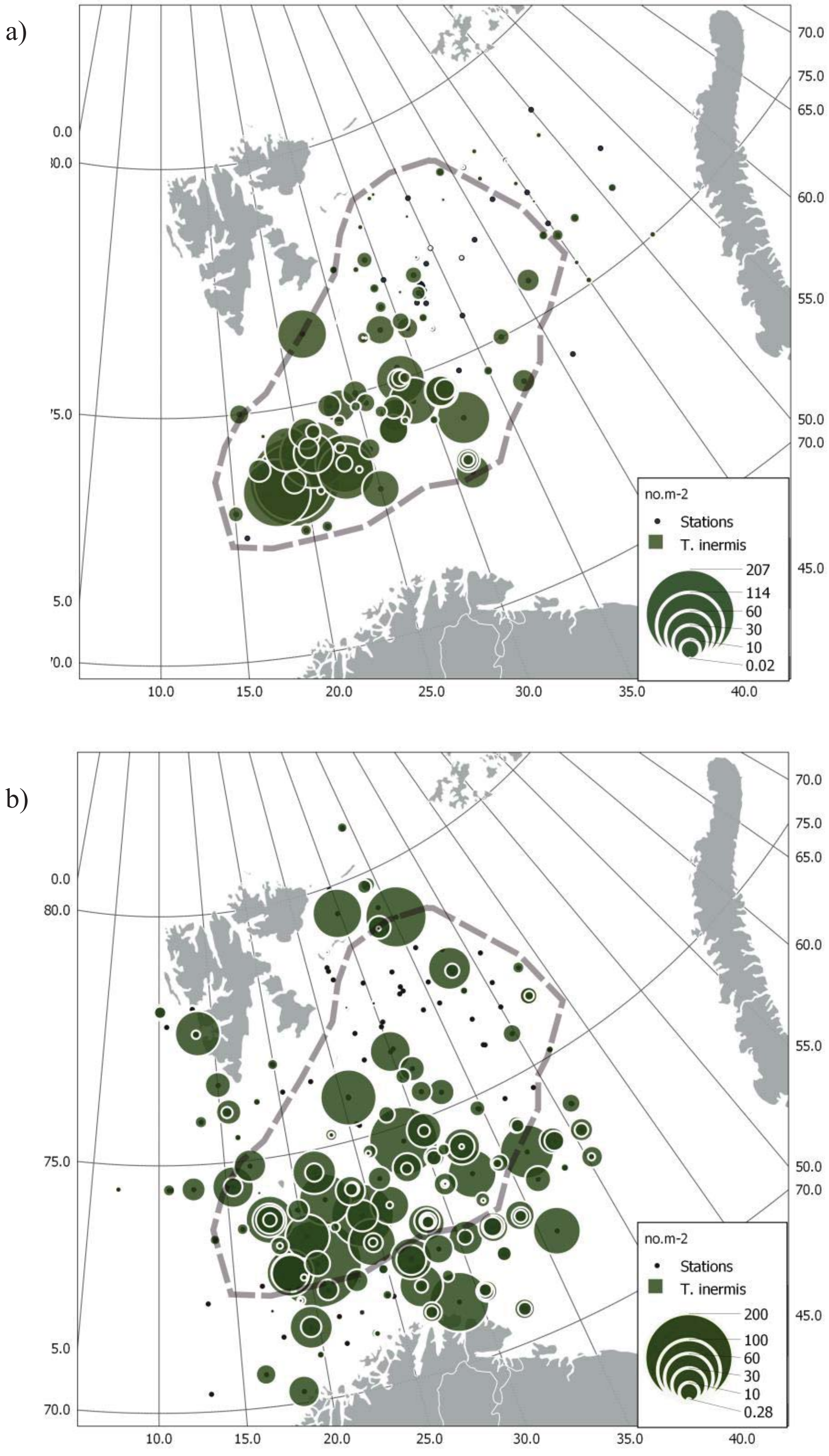


Figure A4: Distribution of *T. inermis* in the study area in a) 1984-1992 and b) 2007-2015. The restricted area is given by grey line.

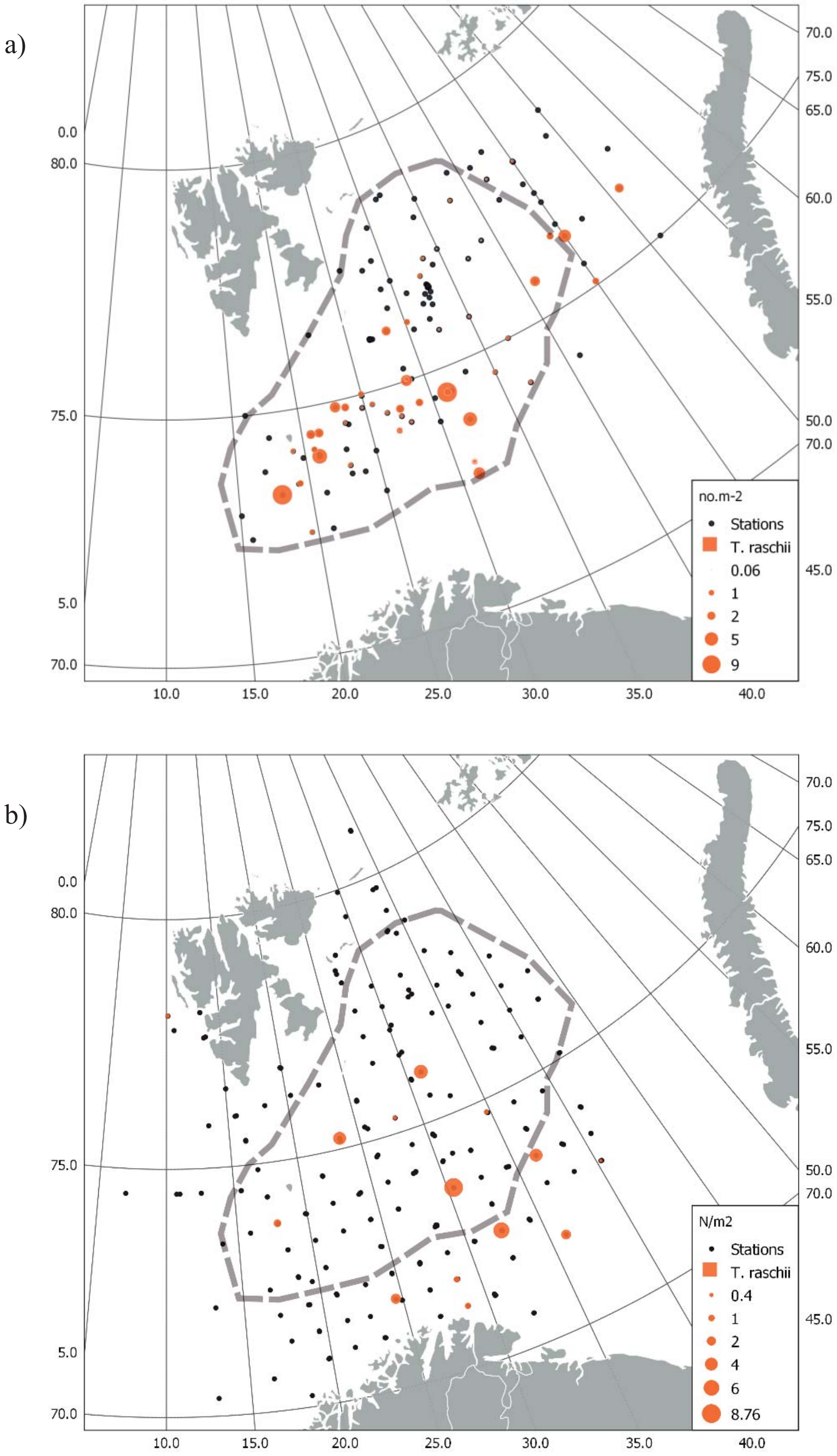


Figure A5: Distribution of *T. raschii* in the study area in a) 1984-1992 and b) 2007-2015. The restricted area is given by grey line.

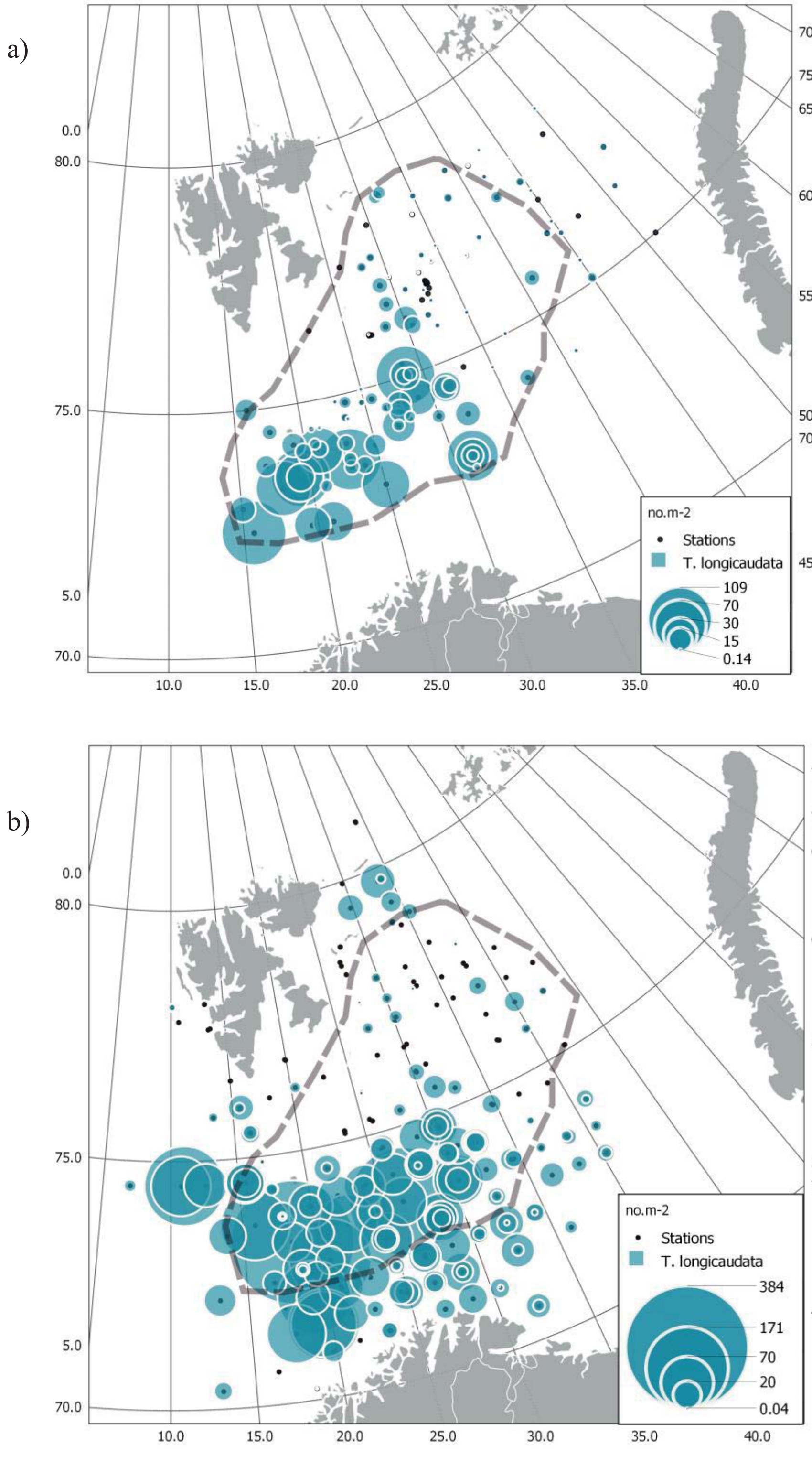


Figure A6: Distribution of *T. longicaudata* in the study area in a) 1984-1992 and b) 2007-2015. The restricted area is given by grey line.

Table A4: Maturity-stages of adult euphausiids: Male, Female and unidentified (U) May-June 2015.

	T. inermis									*T. longicaudata*								
	Male				Female				U.	Male				Female				U.
	1	2	3	4	1	2	3	4		1	2	3	4	1	2	3	4	
I	0	0	0	0	0	4	0	0	52	0	8	18	16	0	6	6	0	50
II	0	0	4	0	0	0	0	0	8	0	4	4	0	0	0	0	0	12
III	0	4	20	12	0	4	0	20	16	0	6	56	18	4	0	0	66	26
VII	0	0	0	0	0	0	0	0	0	0	0	9	2	4	2	0	2	13
VIII	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	2	0

Table A5: Abundances (no.m^{-2}) of egg and larvae May-June 2015 for *T. inermis*.

	EGG	N1	N2	MN	C1	C2	C3	F1	F2	F3	F4	F5	F6
I	10	9	32	58	66	225	151	86	19	0	0	0	0
II	29	9	50	40	106	43	16	0	3	6	0	0	0
III	125	88	39	14	3	0	0	0	0	0	0	0	0
IV	0	0	0	0	0	512	1152	128	0	0	0	0	0
V	0	256	128	0	896	2816	2048	256	0	128	0	0	0
VI	256	0	0	0	768	512	1024	512	0	0	256	0	0
VII	3	0	0	28	58	332	515	661	685	265	29	0	0
VIII	0	1	1	0	0	0	0	387	62	263	69	34	4

Table A6: Abundances (no.m^{-2}) of egg and larvae May-June 2015 for *T. raschii*.

	EGG	N1	N2	MN	C1	C2	C3	F1	F2	F3	F4	F5	F6
VII	0	0	0	0	0	0	0	0	1	0	0	0	0
VIII	0	0	0	0	0	0	0	0	1	0	0	0	0

Table A7: Abundances (no.m^{-2}) of egg and larvae May-June 2015 for *T longicaudata*.

	EGG	N1	N2	MN	C1	C2	C3	F1	F2	F3	F4	F5	F6
I	10	0	5	0	0	0	10	1	0	0	0	0	0
II	0	0	0	0	3	0	0	0	0	0	0	0	0
III	32	3	5	0	0	0	0	0	0	0	0	0	0
IV	0	0	0	0	0	0	32	0	0	0	0	0	0
VII	0	0	0	0	0	0	0	175	0	0	0	0	0
VIII	0	0	0	0	0	0	1	58	0	0	28	30	0

Table A8: Abundances (no.m^{-2}) of egg and larvae May-June 2015 for *M. norvegica*.

	EGG	N1	N2	MN	C1	C2	C3	F1	F2	F3	F4	F5	F6
VII	0	0	0	0	0	89	12	0	0	0	0	0	0
VIII	12	0	0	3	124	133	49	416	4	28	0	0	0

Table A9: Lengths, standard deviations and length intervals of egg and larvae, May-June 2015

	T. inermis				***T. longicaudata***				***M. norvegica***				***T. raschii***			
Stage	**Av.**	**SD**	**N**	**Interval**	**Av.**	**SD**	**N**	**Interval**	**Av.**	**SD**	**N**	**Interval**	**Av.**	**SD**	**N**	**Interval**
EGG	*0,69*	*0,32*	*29*	*0,61-0,78*	0,38	0,14	7	0,31-0,43	*0,70*	*0,33*	*13*	*0,63-0,78*	0,68		1	
N1	0,53	0,26	26	0,44-0,58	0,27		1									
N2	0,56	0,27	28	0,53-0,64	0,43	0,009	2	0,43-0,44								
MN	0,63	0,06	27	0,53-0,85					0,65	0,06	3	0,52-0,87				
C1	1,20	0,45	55	0,72-1,43	1,07		1		1,18	0,29	21	0,76-1,83				
C2	1,88	0,84	87	1,15-2,35					1,69	0,50	31	1,46-2,32				
C3	2,63	1,16	83	1,87-2,9	2,49	0,19	2	2,36-2,63	2,30	0,44	12	1,76-2,8				
F1	*3,24*	*1,07*	*40*	*2,31-3,79*	*3,20*	*0,53*	*9*	*2,73-3,46*	3,56	0,45	5	3,04-4,92				
F2	3,48	1,26	50	2,38-4,02					4,87		1		3,53	0,27	2	2,36-3,71
F3	3,88	1,22	35	3,33-4,52					4,42		1					
F4	4,37	0,68	8	3,89-4,69	4,92		1									
F5	4,82	0,31	4	4,5-5,19	5,13	0,4	2	4,99-5,28								
F6	5,69		1													

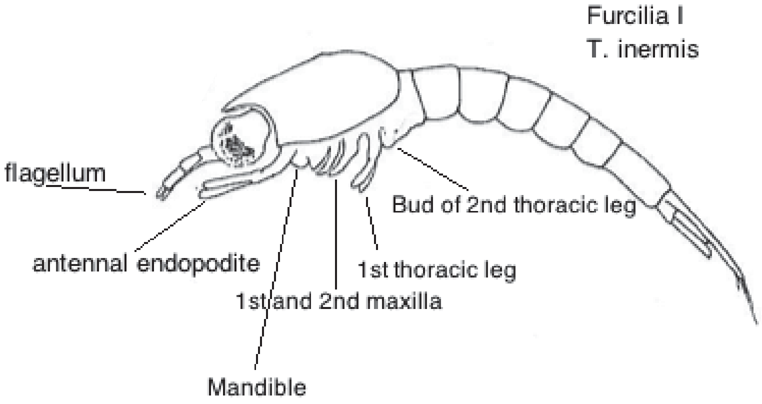
Appendix II

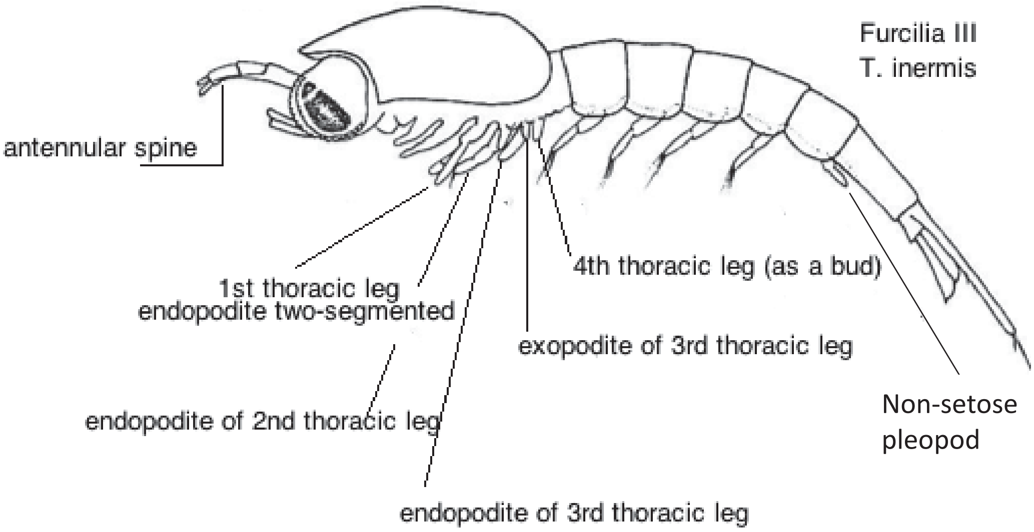
Euphausiids larvae of the Barents Sea.

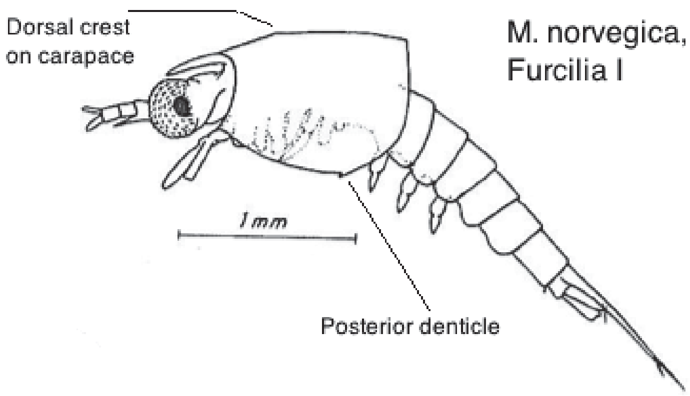
Comparison of the species *Thysanoessa inermis, T. longicaudata, T. raschii* and *Meganyctiphanes norvegica*

Illustrations used here are compiled from the work of Einarsson (1945), Mauchline (1971), Labour (1926; 1924), and MacDonarld (1928). Some of the illustrations used are modifications from the abovementioned authors, reworked by the Marine Species Identification Portal (http://species-identification.org/index.php). Descriptions of lengths are taken from Loftnes (1993).

Anatomical terms



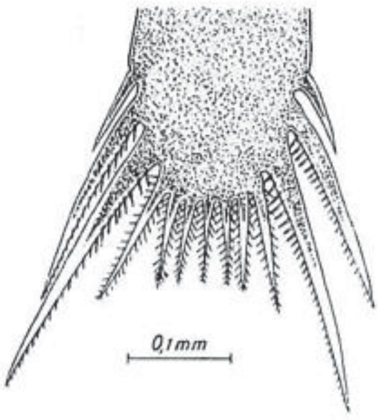




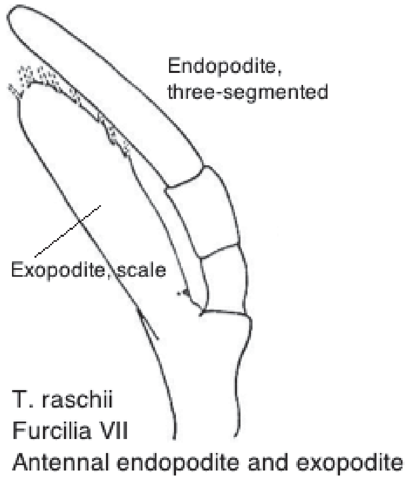
Pleopods
Earlier stages of furcilia can be differentiated by the development of pleopods and whether they have developed setose or not. For example, specimens without developed pleopods are denoted as: 0´, four setose pleopods and one non-setose pleopod will be denoted as: 4´´1´.

Terminal spines of the telson
In later stages of Furcilia, the number of terminal spines on the telson can be used as a way of differentiating the species.

Antennal exopodite and endopodite
The development of the antennal endopodite and exopodite can also be used to differentiate the later stages of furcilia.

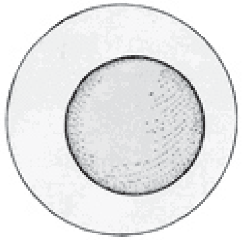
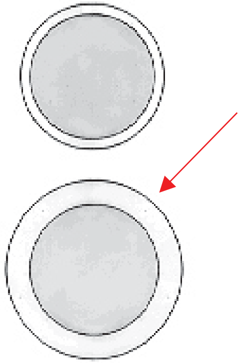


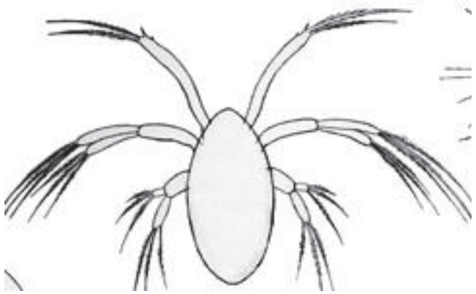
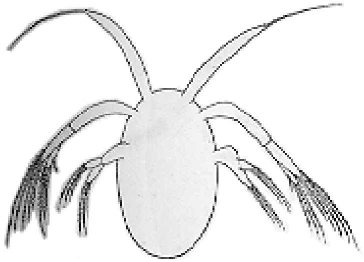
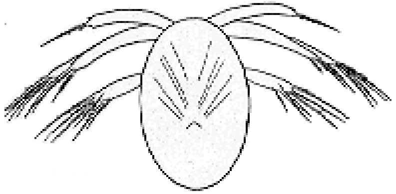
Telson with seven terminal spines (denoted: 7t).

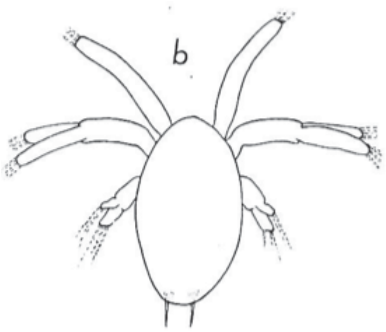
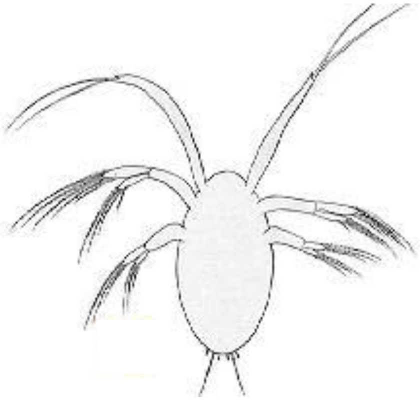
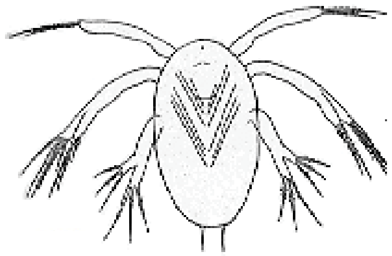


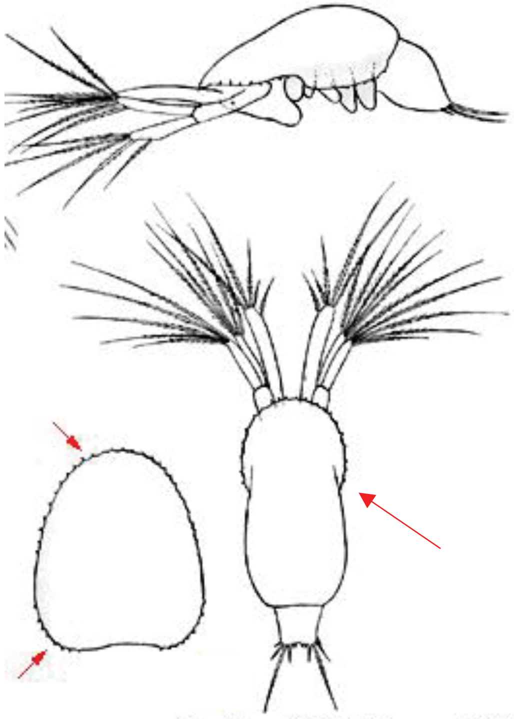
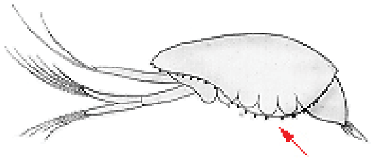
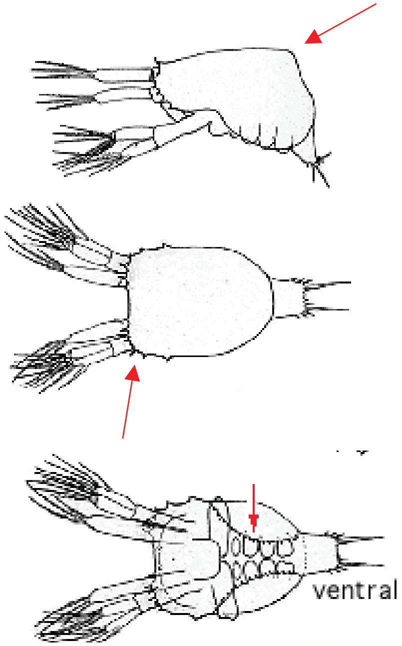
The endopodite
here has developed the form of the flagellum and the exopodite have developed the shape of the scale.

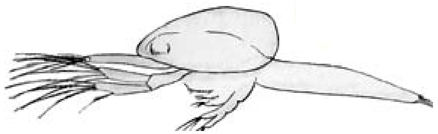
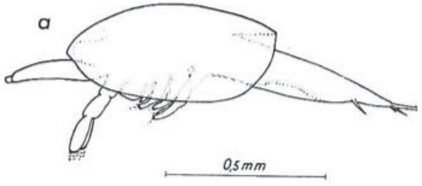
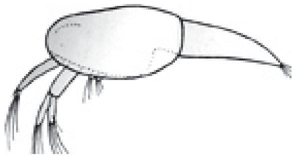
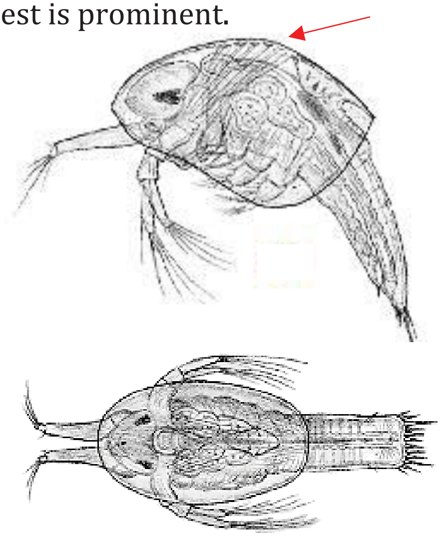
Egg – Calyptopis III

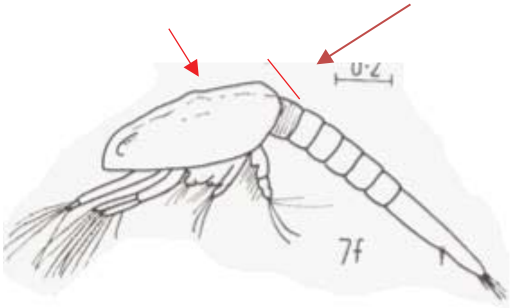
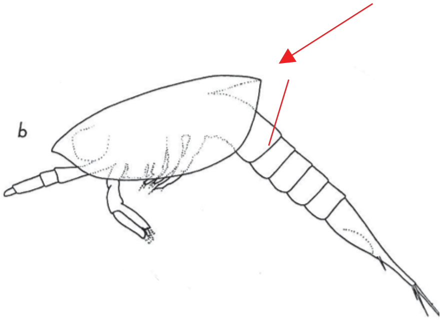
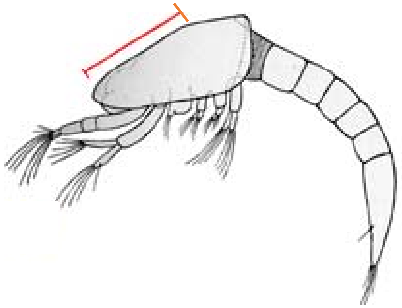
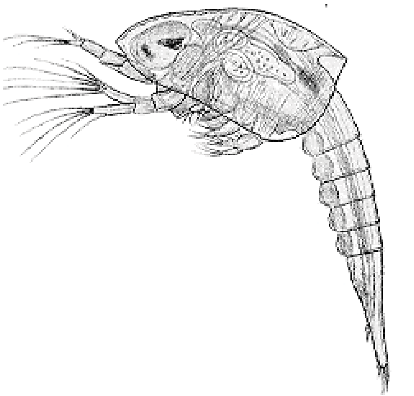
	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Egg	0.53-0.73 Majority of the eggs around 0.6 mm (Einarsson 1945*).* Closely similar to that of *M. norvegica* except that, in the live state, it is colourless (Mauchline 1971). The eggs of *T. inermis* are easily distinguished from those of *T. raschii* by larger space between egg and capsule, but in this they do not differ from the eggs of *M. Norvegica* (Einarsson 1945). 	0.29-0.31 No eggs have been encountered (Einarsson 1945)	0.40-0.60 Smaller size and pervilline space than those of *T. inermis* and *M. norvegica* (Mauchline 1971). 	0.67-0.75 Indistinguishable from *T. Inermis.* In fresh state they might have a pinkish colour, while *T. Inermis* is colourless (Einarsson 1945). Large perviline space mostly distinguishes them from *T. Raschii* (Mauchline 1971). 

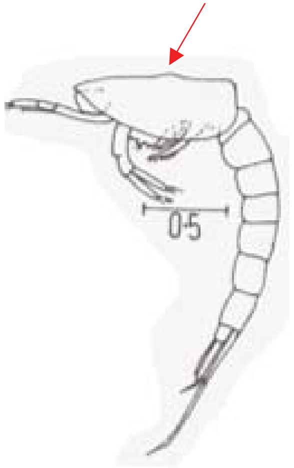
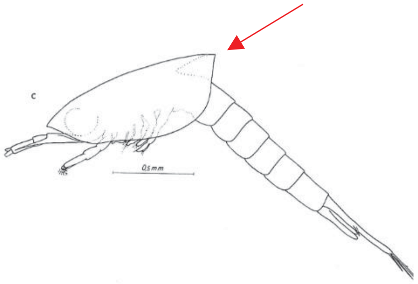
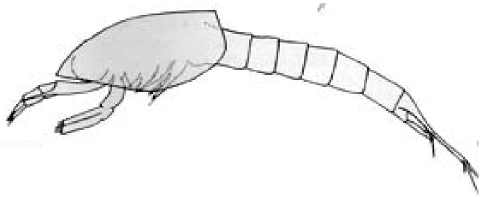
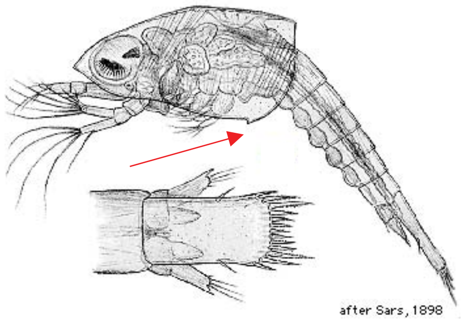
	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Nauplii I	0.48-0.56 Has no spines on posterior end (Einarsson 1945, Mauchline 1971). Loftnes (1993) claim that Nauplii I could develop spines in the transition to Nauplii II. 	0.34-0.47 No record of this stage (Einarsson 1945)	0.45-0.47 Closely resembles the stages of *T. Inermis*, and it is not possbile to see any difference (Einarsson 1945) 	0.48 (Single measurement) Very difficult to distinguish from those of *Thysanoessa* species, (although they are slightly heavier in build) (Einarsson 1945). Einarsson (1945) refrained from distinguishing them. Has no conspicuous spines at posterior end (Mauchline 1971) 

	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Nauplii II	0.51-0.60 Has three spines on posterior end, two pairs being small and inconspicuous (Einarsson 1945). 	0.40-0.42 No record (Einarsson 1945) Can be distinguished by its smaller size compared to the other *Thysanoessa* species	0.47-0.49 Closely resembles the stages of *T. Inermis*, and is not possible to see any difference (Einarsson 1945) 	0.48 (Single measurement) Very difficult to distinguish from those of *Thysanoessa* species, (although they are slightly heavier in build) Einarsson 1945). Einarsson (1945) refrained from distinguishing them. 

	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Meta-nauplii	0.58-0.65 Carapace is regularly toothed along anterior margin (Mauchline 1971). after Lebour, 1926a; Einarsson, 1945	0.41-0.53 No record of this stage (Mauchline 1971), Einarsson (1945)	0.56 (single measurement) This larvae closely resembles the corresponding stages of *T. inermis* and is impossible to distinguish (Mauchline 1971) 	0.50-0.52 The regular anterior dentition on the carapace and the gibbous prominence of the carapace make this larva recognizable from those of other species (Einarsson 1971) 

	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Calyptopis I	1.00-1.45 These larvae are slenderly built. They may be distinguished from those of *T .longicaudata* by the general shape of the carapace (Mauchline 1971) The first stage is difficult to distinguish from *T. longicaudata* (Einarsson 1945). (I did not find the carapace of T. inermis C1 to be as swollen posteriorily as is depicted by Mauchline (1971), - more similar to *T. raschii)* 	1.00-1.50 The calyptopis stages of *T. lonicaudata are* distinguishable from those of *T. Inermis and T. Raschii* by the more pointed posterior margin of the carapace (Einarsson 1945). The abdomen is unsegmented, cylindrical but showing constrictions in the middle part (Einarsson 1945). 	0.70-1.05 Cannot be distinguished from *T. inermis* (Einarsson 1945) 	1.03 (average measurement) The body is almost spherical. The carapace is hood-like and rounded anteriorly: it goes far down on the sides, and dorsally there is a distinctive crest. The abdomen is unsegmented and the telson carries six terminal spines (Einarsson 1945). Easily distinguished from *Thysanoeassa* (spp.). Carapace is almost transparent and the dorsal crest is prominent. 

	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Calyptopis II	1.60-2.20 Can be distinguished from *T. longicaudata* by the shape of the carapace. In *T. longicaudata* the carapace is pointed posteriorly, the posterior tip reaching behind the posterior margin of the lateral parts. This is not the case in *T. inermis,* where the dorsal part of the posterior margin is shorter than the lateral parts (Einarsson 1945) 	1.80-2.00 See description for *T. Inermis.* Has developed six abdominal segments (Einarsson 1945). 	1.20-2.00 Cannot be distinguished from *T. inermis* (Einarsson 1945) 	1.59 (average measurement) Is easily distinguishable from the more slender *Thysanoessa* larvae (Einarsson 1945) The antennula has three segments in this stage, the abdomen has six segments and the telson carries seven terminal spines. The uropods can be seen under the skin, but they are not free (Einarsson 1945) 

	T. inermis	*T. longicaudata*	*T. raschii*	*M. norvegica*
Calyptopis III	2.40-2.70 The eyes are not wholly covered by the carapace as is the rule in *T. Longicaudata.* A small crest may be seen on the carapace a little behind the middle (Einarsson 1945). 	2.5 (average measurement) The carapace is pointed posteriorly and normally covers the eyes. No dorsal crest on the carapace. The antennular spine has developed and the 2nd thoracic limb is present as a bud (Einarsson 1945). 	1.70-2.60 Cannot be distinguished from *T. inermis* (Einarsson 1945) 	2.4 (average measurement) The antennule now has an antennular spine and the abdomen has seven segments. The uropods are free (Einarsson 1945). Posterior denticle is clearly visible. 

Furcilia I - XI

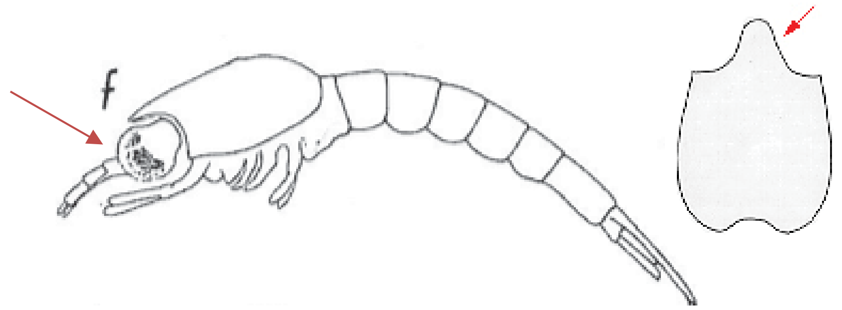
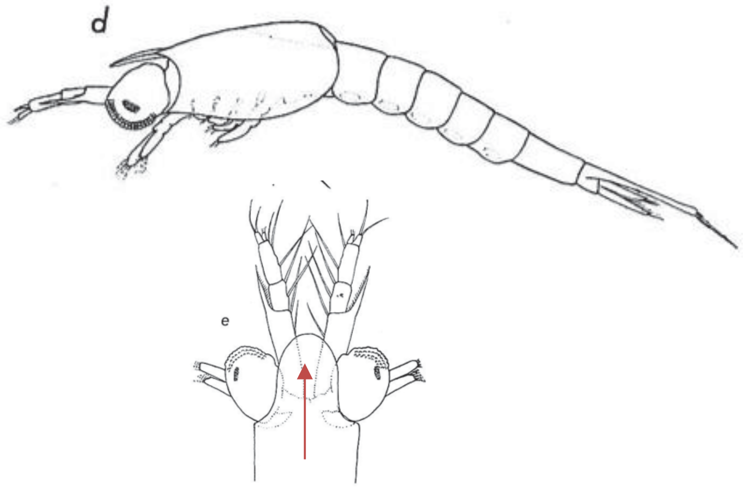
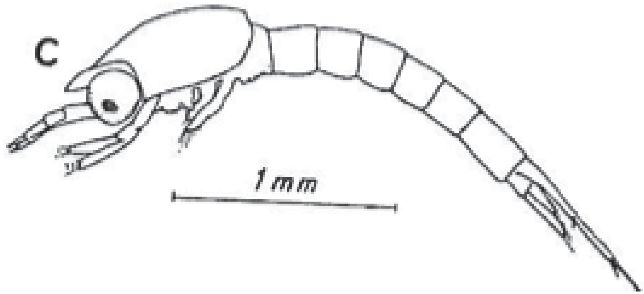
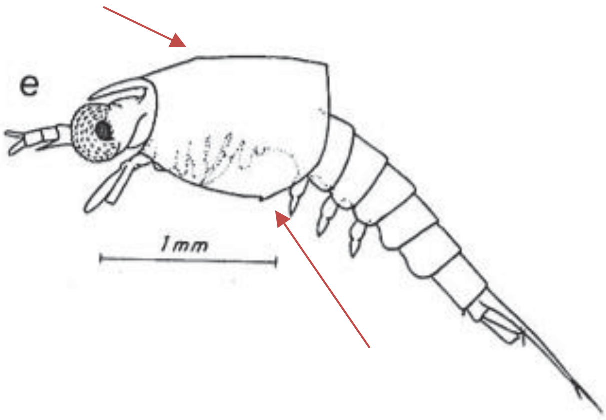
Notes:
The comparisons are mainly based on Einarsson (1945), with supplements from Mauchline (1971). In cases where Einarsson (1945) and Mauchline (1971) disagree, Mauchline's opinion is given in red.

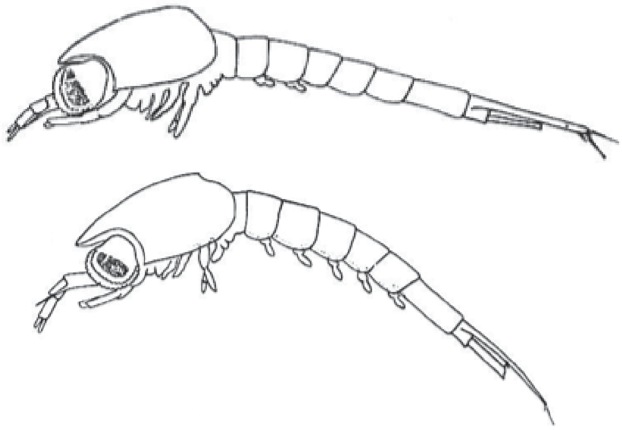
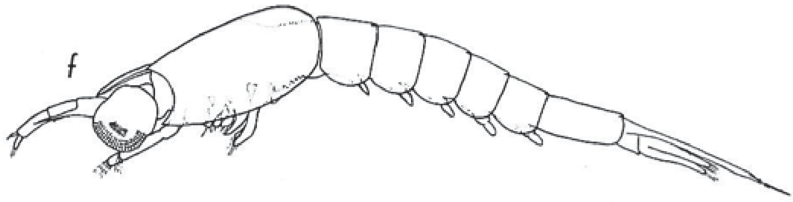
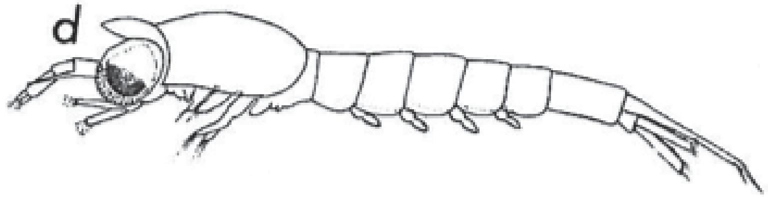
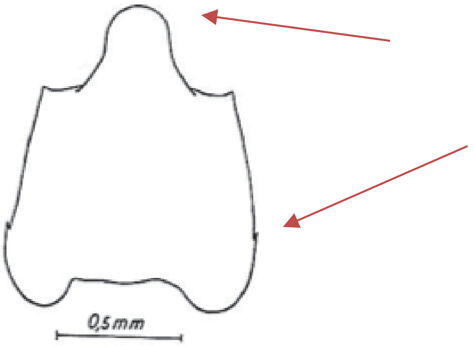
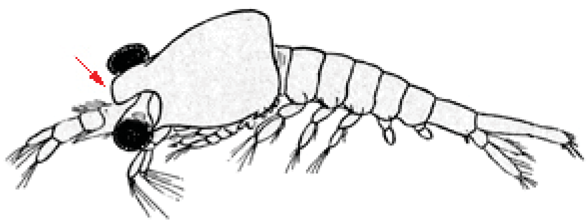
Lengths:
Lengths are based on the findings of Loftnes (1993) in the south-western Barents Sea, and should be measured from the tip of the rostrum to the end of the telson (terminal spines not included).

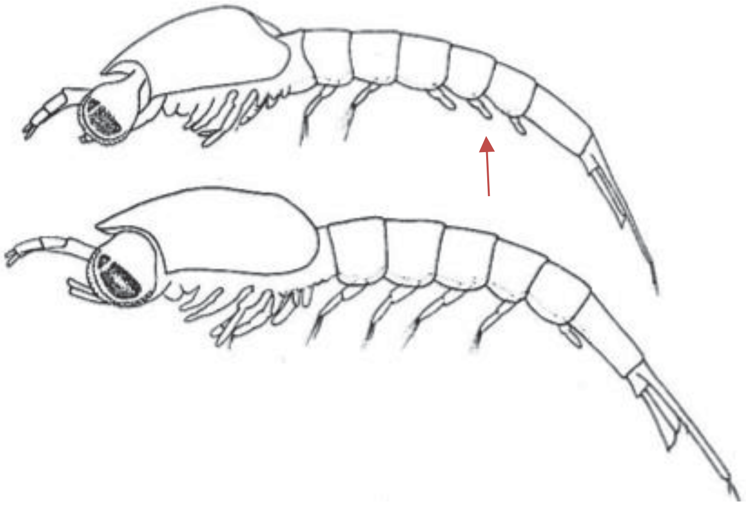
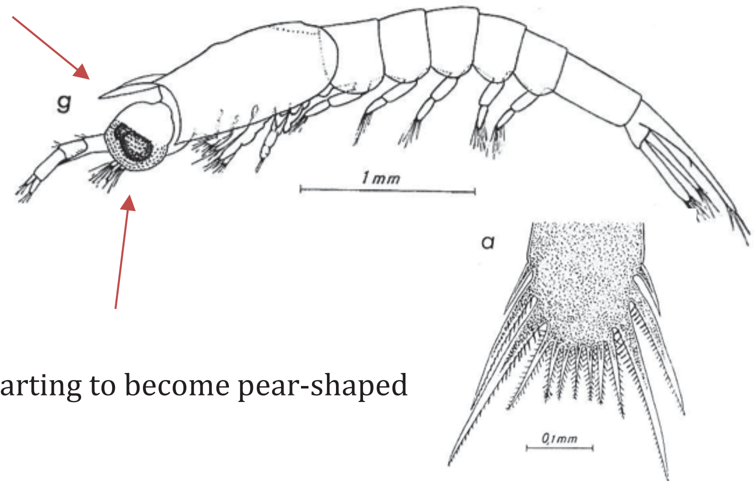
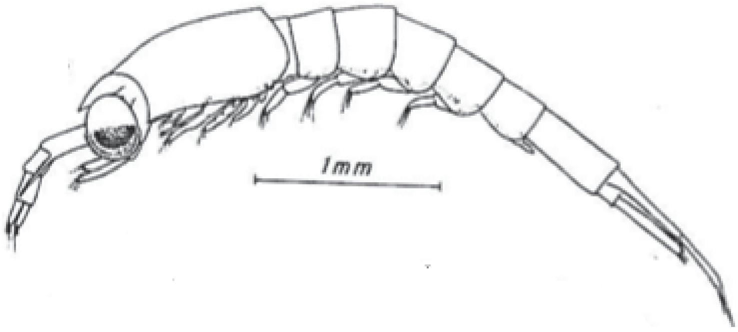
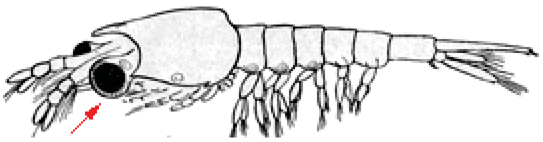
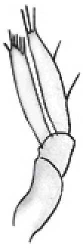
	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
T.inermis	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.9	8.0	
T.longicaudata	3.2	3.7	4.0	4.5	4.9	5.5	5.8	6.0			
T.raschii	3.0	3.5	4.0	4.5	4.5-5.0	4.5-5.5	5.0-6.0	5.0-6.5	5.5-7.0	6.0-7.5	6.5-9.0
M. norvegica	3.0	4.0	5.0	6.0	7.0	7.5	8.0	8.5			

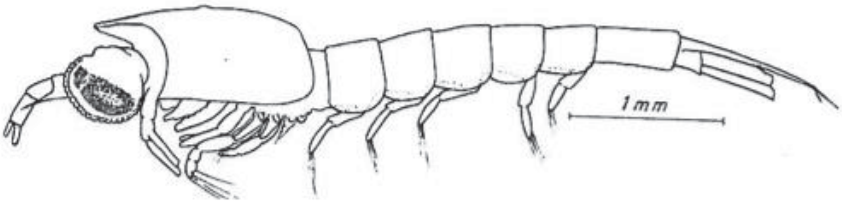
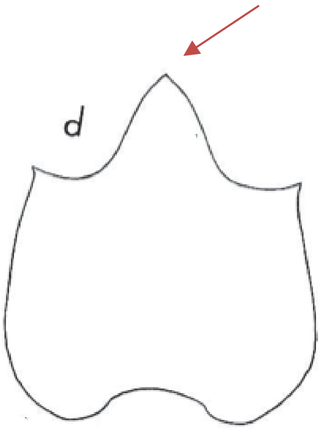
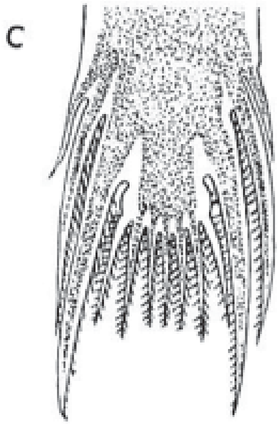
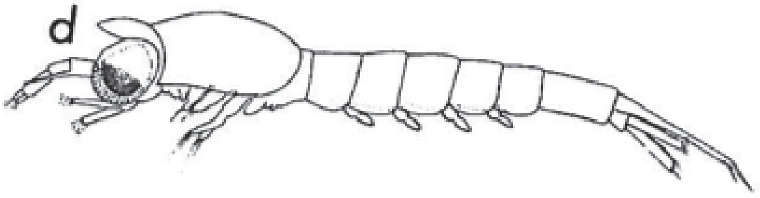
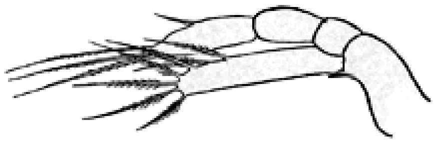
A general key, based on Einarsson (1945)

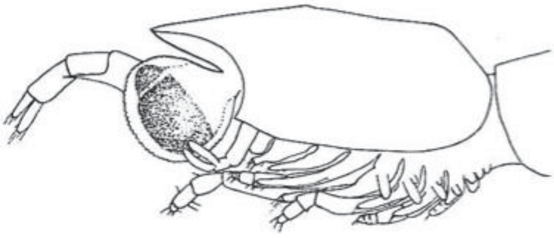
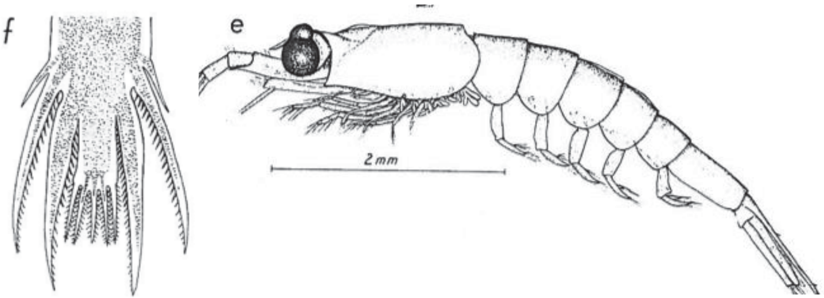
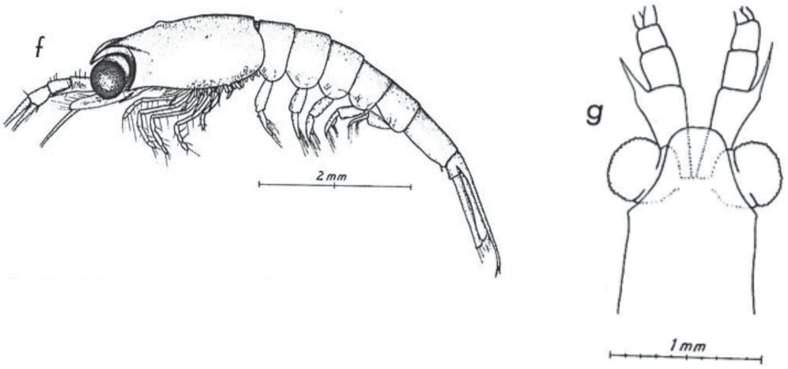
1. With lateral denticles on the carapace
    a. Eyes not divided, circular or sub-circular
        i. Larvae of heavy build, dorsal crest...*M. norvegica*
        ii. Slenderly built larvae...*T. raschii*
2. No lateral denticles on the carapace
    a. Eyes divided
        i. Rostrum broad, leaf-like. Dominants 0→5´→5´´.
        Legs of later stages slender, the second only sligthly elongate and
        thickened...*T.longicaudata*
        ii. Rostrum narrower, often truncate.
        No dominants. Legs of later stages strong,
        the second conspicuously long and
        thickened:..*T. Inermis*

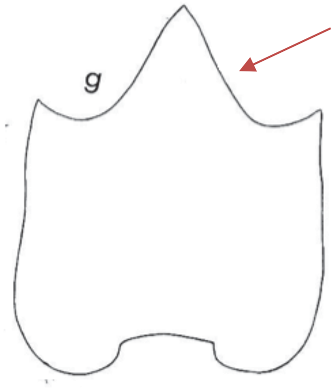
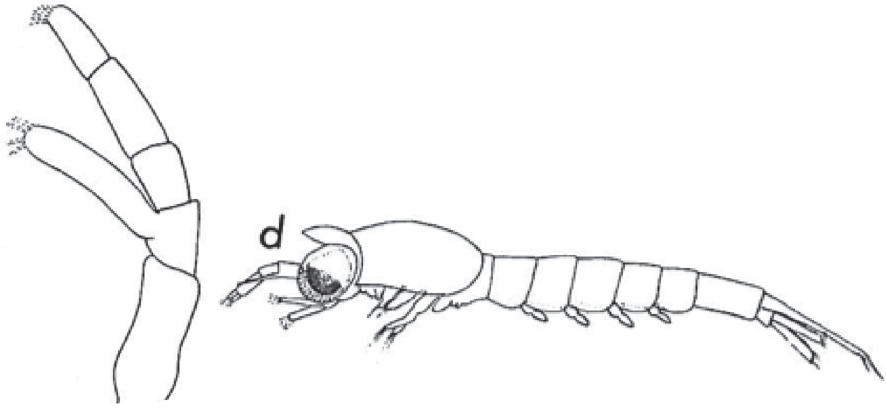
Species	mm	Details	Furcilia I
T. inermis	*3.0*	**Pleopods**: 0´ **Eyes:** Segmentation of upper and lower eye **Limbs:** 3rd limb as a small proturberance	 All Thysanoessa Furcilia I are very simililar and hard to discern
T. longicaudata	3.2	**Pleopods:** 0´ but visible cell accumulations for pleopods **Carapace:** Rounded, leaf-like rostrum, broader than other species **Limbs:** 2nd limb as a single jointed bud	
T. raschii	3.0	**Pleopods:** 0´ **Eyes:** No segmentation **Limbs:** 2nd limb: as a bud	 Posterior denticle not yet visible
M. norvegica	3.0	**Pleopods:** 2’/**3’**/4’ **Carapace:** Dorsal crest on carapace Posterior denticle **Limbs:** 3rd t. limb as a bud	

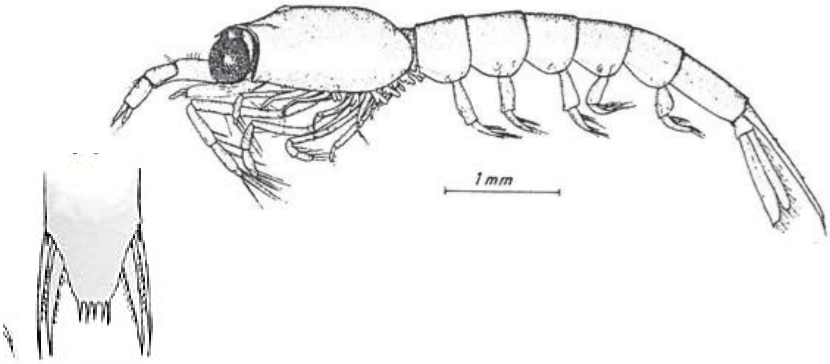
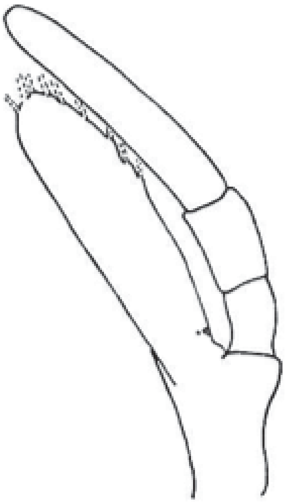
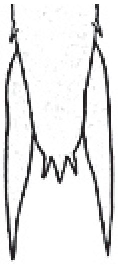
Species	mm	Details	Furcilia II
T. inermis	*3.5*	**Pleopods:** 1’-5’ **Eyes:** Fully pigmented eyes, higher than they are broad, with at narrower upper portion **Limbs:** 3rd as a bud	
T. longicaudata	3.7	**Pleopods:** 5’ **Carapace:** Rounded, leaf-like rostrum, broader than other species **Photophores:** 4	
T. raschii	3.5	**Pelopods:** 3’-5’ **Eyes:** Some pigmentation **Carapace:** Small but distinct posterior denticle **Limbs:** Buds in 3rd and 4th, while the 5th has a small proturbance	 
M. norvegica	4.0	**Pleopods:** 2”2’/2”3’/**3”2’**/4”1’ **Carapace:** Dorsal crest and posterior denticle **Limbs:** 4th, 5th and 6th as bud and small protrurbances	**Photophores:** have appeared on those abdominal segments having setose pleopods 

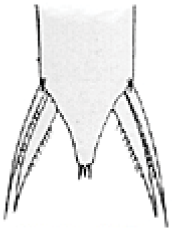
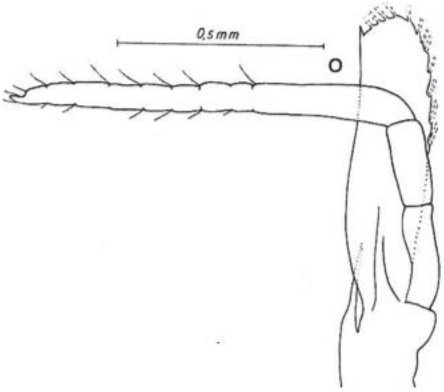
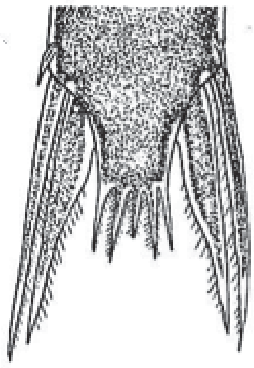
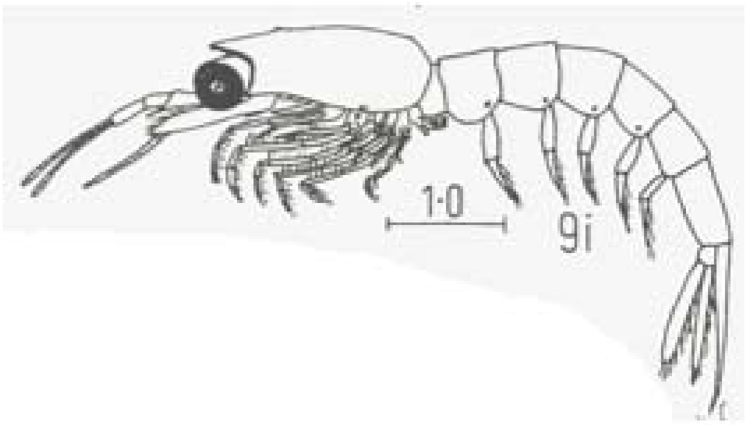
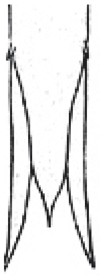
Species	mm	Details	Furcilia III
T. inermis	*4*	**Pleopods:** 1”4’/2”3’ 3”2’/4”1’/5” **Eyes:** Fully pigmented. Higher than they are broad, with at narrower upper portion **Limbs:** 4th limb as a bud **Photop.**: 2	
T. longicaudata	4.0	**Pleopods:** 5” **Carapace:** Rostrum has become clearly pointed, triangular in shape with the sides slightly convex **Photoph.:** 4	 Eyes starting to become pear-shaped
T. raschii	4	**Pleopods:** 4”1’/5” **Eyes:** more developed, no division between upper and lower eye **Photop.:** Might have 1 (2)	 **Carapace:** Small but distinct denticle
M. norvegica	5	**Pleopods:** 5” **Carapace:** Dorsal crest and denticle on posterior margin **Photop.:** 4	**Limbs:** 5th limb as a bud 6th and 7th limb as small proturbances – not free  

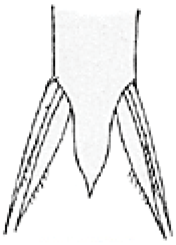
Species	mm	Details	Furcilia IV
T. inermis	*4.5*	**Pleopods:** 5´´ **Carapace:** Rounded rostral plate antiorily. Truncate and more narrow than in T. longicaudata. **Photop.:** 2(3)	
T. longicaudata	4.5	**Pleopods**: 5´´ **Telson:** 7t, but with indication of only 5 successors under the skin **Carapace:** Cleary pointed frontal plate triangular in shape with the sides slightly convex	 
T. raschii	4.5	**Pleopods**: 5´´ **Carapace:** Rounded rostral plate and very distinct posterior denticle **Photop.:** 2(3)	 **Antennular spine:** reaches two-third up the third segment
M. norvegica	6	**Pleopods:** 5´´ **Telson:** 7t and 2 long lateral spines **Carapace:** Rounded rostrum	

Species	mm	Details	Furcilia V
T. inermis	*5*	**Telson:** 7t **Photop.:** 2 (3) **Eyes:** Division of upper and lower eye No denticle on carapace **Antennular spine**:reaches slightly beyond the second segment	 **Limbs:** 5th limb: Endopodite with traces of three segments, with one bristle at the terminal end. Exopodite non-setose 6th limb: Endopodite unsegmented, non-setose. Exopodite bud-like. 7th limb: As a bud 8th limb: As a bud
T. longicaudata	4.9	**Telson:** 5t **Carapace:** Low, but well defined crest **Photop.**:4	 **Antennular spine:** reaches slightly beyond the second segment
T. raschii	4.5-5	**Telson:** 7t **Carapace:** Very distinct denticle, more anterior position **Eyes**: Round eye **Photop.**:3 (4)	
M. norvegica	7	**Telson:** 5t with two long lateral spines **Carapace**: Dorsal crest **Antennular spine:** reaches half-way up the third segment	

Species	mm	Details	Furcilia VI
T. inermis	*5.5*	**Telson:** 7t (5), but with 5 successors under the skin **Eyes:** Upper and lower eye divided	
T. longicaudata	5.5	**Telson:** 3t **Carapace:** Pointed	 Sides of frontal plate straightens
T. raschii	4.5-5.5	**Telson**: 7t **Eyes:** Round eye **Carapace:** Posterior denticle **Antennal endopodite:** three segments	
M. norvegica	7.5	**Telson:** 3t and two long lateral spines	

Species	mm	Details	Furcilia VII
T. inermis	*6*	**Telson:** 5t (3) **Eyes:** Segmentation of upper and lower eye **Carapace:** No denticle	
T. longicaudata	5.8	**Telson:** 1t (0) - and 2 long lateral spines **Carapace:** The frontal plate has straight sides No denticle	
T. raschii	5-6	**Telson:** 7t (5)- but indications of 5 successors under the skin **Antenna:** The exopodite of the antenna has developed the scale form **Photop.**: 4	
M. norvegica	8	**Telson:** 1t - and 2 long lateral spines **Carapace:** Posterior denticle	

Species	mm	Details	Furcilia VIII
T. inermis	*6.5*	**Telson:** 3t	
T. longicaudata	6.0	**Telson:** One pair of long lateral spines	
T. raschii	5-6.5	**Telson:** 4-5t **Antenna:** The flagellum of the antenna reaches beyond the antennular peduncle and is distinctly jointed.	  
M. norvegica	8.5	**Telson:** 1t and two short lateral spines	 Juvenile (Lebour, 1925)

Species	mm	Details	Furcilia IX
T. inermis	*7.0*	**Telson:** Two long lateral spines **Eyes**: divided	
T. longicaudata	–		
T. raschii	5.5-7.0	**Telson:** 3 and two pairs of long lateral spines and one pair of short lateral spines **Eyes**: round	
M. norvegica	–		

Species	mm	Details	Furcilia X
T. inermis	*8.0*	**Telson:** Outer pair of long lateral spines is reduced	
T. longicaudata	-		
T. raschii	6.0-7.5	**Telson:** two pairs of long lateral spines with successors under the skin. One pair of short lateral spines without successors	
M. norvegica	-		

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