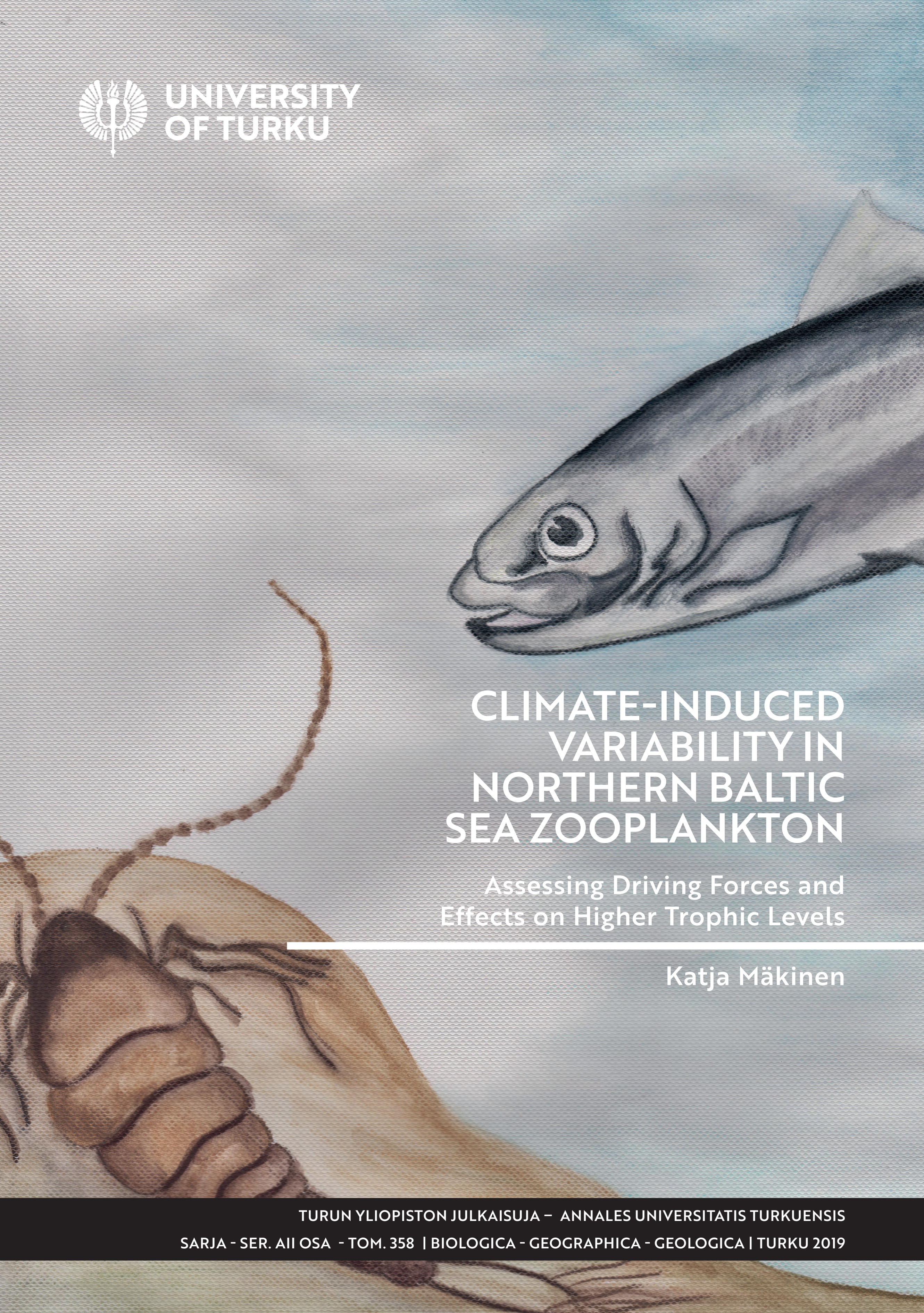

UNIVERSITY OF TURKU

CLIMATE-INDUCED VARIABILITY IN NORTHERN BALTIC SEA ZOOPLANKTON

Assessing Driving Forces and Effects on Higher Trophic Levels

Katja Mäkinen

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Tiivistelmä

Pohjois-Atlantin ilmastollisissa tekijöissä tapahtuneen vaihtelun seurauksena Itämeren ympäristöolosuhteissa on viime vuosikymmeninä tapahtunut muutoksia, joiden ansiosta on mahdollista takautuvasti tutkia lajien sopeutumista käynnissä oleviin ympäristömuutoksiin.

Väitöskirjassani tutkin Pohjois-Itämerellä vallitsevien eläinplanktonlajien ja yhteisön rakenteen pitkäaikaismuutoksia suhteessa meriveden suolapitoisuuden ja lämpötilan vaihteluun. Tarkastelemalla Saaristomerellä kutevaa silakkaa (*Clupea harengus membras*) ja makean veden *Limnocalanus macrurus*-hankajalkaista esimerkkitapauksina, tutkin myös miten ympäristöolosuhteissa ja ravintoverkon pohjalla tapahtuneet muutokset ovat vaikuttaneet ravintoverkon ylemmillä tasoilla.

Tutkimuksissani havaitsin, että eläinplanktonyhteisön koostumus on muuttunut yhtäaikaisesti meriveden makeutumisen ja lämpenemisen kanssa. Saaristomerellä nämä vedenlaadun muutokset ovat pääsääntöisesti olleet suotuisia pienikokoisille murtovesilajeille ja epäsuotuisia merilajeille. Runsausmuutosten lisäksi myös vuodenaikaisuudessa on tapahtunut vaihtelua, joista ilmeisin on kasviplankton- ja murtovesilajien aikaistunut esiintyminen. Tutkimukseni osoitti myös, että runsaat rasvavarastot omaava *L. macrurus* esiintyy Selkämerellä erittäin runsaana alkukesällä, jolloin silakan energiantarve on myös suuri. Loppukesällä, lajin siirtyminen syvemmälle oli yhteydessä aikuisten rasvavarastojen pienenemiseen ja lajirunsauden laskuun mahdollisesti ravinnonpuutteen aiheuttaman nälkiintymisen vuoksi. Tulokseni viittaavat myös siihen, että ilmastonmuutoksen aiheuttamat ympäristövaikutukset Selkämerellä ovat toisaalta mahdollistaneet silakkakannan positiivisen kehittymisen ja parantaneet silakan laatua ravintona, mutta toisaalta pienentäneet sen energiavarastoja lisäämällä kalojen talviaikaista energiankulutusta ja vähentämällä käytettävissä olevan ravinnon määrää.

Väitöskirjani tutkimukset osoittavat, että viime vuosikymmenien vedenlaadun muutokset ovat aiheuttaneen monenlaisia muutoksia Pohjois-Itämeren ravintoverkossa, jotka Saaristomeren eläinplanktonyhteisössä näkyvät erityisesti merilajien vähentymisenä ja murtovesilajien vuodenaikaisuuden muutoksina. Selkämerellä, näillä muutoksilla näyttää olleen sekä suoria että epäsuoria vaikutuksia ravintoverkon energiavirtoihin, jotka seuranta-aineistossa näkyvät sekä silakkapopulaation rasvapitoisuuden että ruumiinkoon pienentymisenä. Väitöskirjatutkimukseni tulokset antavat uutta tietoa Saaristomeren ja Selkämeren alueilla viime vuosikymmeninä tapahtuneista ympäristömuutoksista ja painottavat pitkäaikaisen ympäristöseurannan merkitystä ilmastonmuutoksen aiheuttamien muutosten ymmärtämiseksi.

Avainsanat: eläinplankton, silakka, Itämeri, ravintoverkko, ilmastonmuutos

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Katja Mäkinen: Climate-induced Variability in Northern Baltic Sea Zooplankton - Assessing Driving Forces and Effects on Higher Trophic Levels
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Abstract

During the recent decades, alterations in the northern Atlantic climate conditions have resulted in major modifications in the environmental conditions of the Baltic Sea that allows for a unique opportunity to assess species responses to climate-induced changes in the ecosystem.

In this thesis, I examined long-term changes in the northern Baltic zooplankton community in comparison to changes in seawater salinity and temperature. In addition, I estimated how the bottom-up changes in the Bothnian Sea have manifested themselves at higher trophic levels by using the Baltic herring (*Clupea harengus membras*) and its preferred prey species, a freshwater copepod *Limnocalanus macrurus*, as case examples.

I found that in the northern Baltic Sea major modifications in the salinity and temperature have resulted in concomitant changes in zooplankton species dynamics and community structure. In the Archipelago Sea, the freshening and warming of water have been favorable to most small-bodied brackish-water taxa and unfavorable to marine taxa. Moreover, the hydrography changes have also resulted in earlier peaks in the timing of phytoplankton and brackish-water taxa. In the Bothnian Sea, the results showed that *L. macrurus* has both large lipid reserves and occurs in high abundance during spring-early summer, when the energy requirements of herring are high. Later during summer, the descent of adult *L. macrurus* to deeper water levels coincided with a decrease in its abundance and lipid store size, indicating that at least part of the population suffered from starvation. The results also implied that while the warming and freshening of water have indirectly improved herring condition and thereby enabled the positive development of the herring stock, the changes have also increased the energy consumption of fish and caused a decline in the availability of prey resulting in a reduction of its lipid reserves.

In conclusion, during the past decades, the climate-induced changes in seawater salinity and temperature seem to have resulted in various changes in the northern Baltic ecosystem, which in the zooplankton data are manifested as a decrease of marine species and shifts in brackish-water species phenology. In the Bothnian Sea, the changes in the physical environment seem to have caused both indirect and direct effects on the energy cycles, which in the monitoring data appear as a decline in the lipid content as well as a decline in herring body size. The results of my thesis provide new information on the food web dynamics that can be used for further research and highlight the importance of long-term environmental monitoring to foresee climate-induced changes in the ecosystem and to provide an accurate picture of the trophodynamics.

Keywords: zooplankton, herring, Baltic Sea, food web, climate change

List of original publications

This thesis is based on the following publications and manuscript, which are referred to in the text by their Roman numerals:

I. **Mäkinen, K.,** Vuorinen, I., Hänninen, J. (2017). Climate-induced hydrography change favors small-bodied zooplankton in a coastal ecosystem. *Hydrobiologia*, *792*, 83–96.

II. **Mäkinen, K.**, Hänninen, J., Vuorinen, I. (2019). Variability in zooplankton phenology during major modifications in the northern Baltic Sea environment. *Submitted manuscript.*

III. **Mäkinen, K.**, Elfving, M., Hänninen, J., Laaksonen, L., Rajasilta, M., Vuorinen, I., Suomela, J.P. (2017). Fatty acid composition and lipid content in the copepod *Limnocalanus macrurus* during summer in the southern Bothnian Sea. *Helgoland Marine Research, 71*, 11.

IV. Rajasilta, M., Hänninen, J., Laaksonen, L., Laine, P., Suomela, J.P., Vuorinen, I. **Mäkinen, K.** (2018). Influence of environmental conditions, population density, and prey type on the lipid content in Baltic Herring (*Clupea harengus membras*) from the northern Baltic Sea. *Canadian Journal of Aquatic and Fisheries Science. In press.*

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Author contributions (in order of decreasing contribution) to the original publications:

	I	II	III	IV
Research design	KM, IV, JH	KM, IV, JH	MR, IV, JH, KM, JS	MR, KM
Practical/laboratory work	-	-	KM, MR, JH, ME	KM, MR
Lipid and fatty acid analyses	-	-	JS, LL	MR, JS, LL, PL
Data processing	KM	KM	KM, MR	KM, MR
Writing	KM, IV, JH	KM , JH, IV	KM, MR, JS, IV, JH	MR, KM, JS, IV, JH

KM = Katja Mäkinen, IV = Ilppo Vuorinen, JH = Jari Hänninen, MR = Marjut Rajasilta, JS = Jukka-Pekka Suomela, ME = Mikael Elfving, LL = Lea Laaksonen, PL = Päivi Laine

Abbreviations

ALA	Alpha-linolenic acid
ANOSIM	Analysis of similarities analysis
ANOVA	Analysis of variance
CB	Carbon biomass
COG	Center of gravity
CV	Coefficient of variation
DHA	Docosahexaenoic acid
DW	Dry weight
EFA	Essential fatty acid
EPA	Eicosapentaenoic acid
FA	Fatty acid
FAME	Fatty acid methyl esters
FATM	Fatty acid trophic marker method
GC-FID	Gas chromatography with flame ionization detection
GC-MS	Gas chromatography-mass spectrometry
GLMM	Generalized linear mixed model
ICES	International Counsil for the Exploration of the Sea
LIN	Linoleic acid
MBI	Major Baltic inflow
ODAS	Ocean data acquisition system
PCA	Principal component analysis
PUFA	Polyunsaturated fatty acids
SIMPER	Similarity percentage analysis
SSB	Spawning stock biomass
SVC	Singular value decomposition
TSB	Total stock biomass
WE	Wax esters

1. Introduction

Due to its short ecological history and low species diversity, the food web structure of the Baltic Sea is relatively simple, when compared to other sea areas. This, together with major modifications experienced in the abiotic conditions during the the recent decades, allows for a unique opportunity to assess species responses to climate-induced changes in the ecosystem. In order to project how the ecosystem will respond to future environmental changes, information about past changes, in particular on a regional scale, is important as the responses to climate change depend on local conditions and vary in space and time.

1.1 Climate-induced changes in the Baltic Sea ecosystem

During the recent decades, major shifts have occurred in the North Atlantic climate conditions with concomitant changes in the atmospheric circulation and amount of precipitation over northern Europe (e.g., Hänninen *et al.*, 2000; Swanson *et al.*, 2009). In the Baltic Sea, these alterations in climate conditions have resulted in various changes in the ecosystem, which include for example an increase in mean water temperature (e.g., Mackenzie *et al.*, 2007; Suikkanen *et al.*, 2013), a decrease in the length of the ice season and changes in the timing of spring runoff (e.g., Doney *et al.*, 2012; Hagen & Feistel, 2005; HELCOM, 2013). In addition, an increase in precipitation and river runoff in the northern and eastern subbasins together with a decline in the occurrence of saline inflows from the North Sea, i.e., major Baltic inflows (MBIs), have resulted in a decrease in salinity since the 1980s (Hänninen *et al.*, 2011; Möllmann *et al.*, 2005; Schinke *et al.*, 1998; Suikkanen *et al.*, 2013; Vuorinen *et al.*, 1998). By the end of this century, the climate change is expected to alter the physical environment of the Baltic Sea further. Depending on the climate model, the northern Baltic Sea is projected to experience a 2–4°C warming of seawater, a 50–80% decrease in ice cover, and possibly a ca. 30% increase in precipitation, causing a further decrease in salinity (Andersson *et al.*, 2015; BACC, 2008, 2015; HELCOM, 2013).

The above described changes in the environmental conditions can impact an organism's physiology directly or the effect can come indirectly through, e.g., food availability. Due to its short geological history and brackish-water, the species diversity in the Baltic Sea is relatively low, and the biota consists of a mixture of both limnic, brackish-water and marine species of which most live at the edge of their physiological limits (BACC, 2008, 2015). As a result, as reviewed by Doney *et al.* (2012) and Parmesan *et al.* (2006), even small changes in the physical conditions of the Baltic Sea may force organisms to either acclimatize, adapt, change the timing of annually reoccurring events (i.e, phenology), migrate to new habitable areas or become locally extinct if adaptation is not an option. In the Baltic Sea, the changes in hydrography have already manifested as shifts in species distribution and abundance (BACC, 2008, 2015; Hays *et al.*, 2005). So far, the biological changes in the Baltic Sea have for the most part occurred gradually, but abrupt biological regime shifts during 1989/1990 and 2000/2001 have also been documented in some subbasins (Dippner *et al.*, 2001; Hagen & Feistel, 2005; Möllmann *et al.*, 2009).

On the contrary to trends in species occurrence, climate-induced changes in species lipid content and their effect on the transfer of energy in food web in the Baltic Sea have received less attention. However, as shown by several studies, understanding which resources support productivity and how they affect the energy flow and transfer of matter in the food web is important, as lipids and their special components fatty acids (FA) act for example as energy reserves, membrane components, hormones, antioxidants and buoyancy aids, and therefore, play an important role during reproduction, ontogeny, diapause and other major life-cycle events (e.g., Dalsgaard *et al.*, 2003; Kattner *et al.*, 2007; Lee *et al.*, 2006). Concerning lipids, the FA that heterotrophic organisms cannot synthesize in adequate amounts in their body, and thus, must obtain them from their food, are especially important, as their structural and metabolic functions are related to the growth, survival and reproduction of heterotrophic organisms (Brett & Müller-Navarra, 1997; Lee *et al.*, 2006). These FAs, referred hereafter as essential fatty acids (EFA), include mainly polyunsaturated fatty acids (PUFA), i.e., FA with more than one double bond, and include alpha-linolenic acid [ALA, 18:3(n-3)]; linoleic acid [LIN, 18:2(n-6)]; the physiologically critical n-3 PUFA, i.e., eicosapentaenoic acid [EPA, 20:5(n-3)] and docosahexaenoic acid [DHA, 22:6(n-3)]. In aquatic ecosystems, plankton have an important role in the transfer of EFA in the food web as they are the primary source of energy and the ultimate producer and provider of the n-3 PUFA in the food web (Gladyshev *et al.*, 2013; Hixson *et al.*, 2016).

1.2 Zooplankton in the northern Baltic Sea

Zooplankton are defined as a diverse group of small (0.2 μm–200 mm) drifting organisms that, together with phytoplankton, form the base of the grazing chain (e.g., Telesh *et al.* 2009). Zooplankton transfer energy and matter among primary producers and those at upper trophic levels, and therefore, shifts in their abundance or species composition can influence not only productivity but also the circulation of nutrients and organic matter (Hays *et al.*, 2005; Ikauniece, 2001; Kiørboe, 1997; Richardson, 2008). In addition, due to their life-cycle characteristics and high abundance, zooplankton have been found to be good indicators of ecosystem change and health, and therefore, they are considered useful in assessing climate-induced changes in the ecosystem (Richardson, 2008; Ojaveer *et al.*, 1998).

In the Baltic Sea, mesozooplankton (0.2–20 mm) are the dominant zooplankton group in terms of biomass (Telesh *et al.*, 2009). The group consists of large rotifers (Rotifera), water fleas (Cladocera), copepods (Copepoda), and to a lesser extent, meroplanktonic larvae (Polychaeta, Mollusca, Cirripedia, Bryozoa, and Echinodermata) and some benthic invertebrates (e.g., Harpacticoida) from both marine, brackish-water and limnic origins (Telesh *et al.*, 2009). Based on the monitoring data used in Chapters **I**–**II** and literature (O'Brien *et al.* 2011; Telesh *et al.* 2009), in the study areas, the dominant large rotifers include the brackish-water species *Synchaeta baltica* (Ehrenberg, 1834) and *S. monopus* (Plate, 1889). Cladoceran species include brackish-water species *Bosmina* (*Eubosmina*) *longispina maritima* (Leydig, 1860) and *Pleopsis polyphemoides* (Leuckart, 1859), marine species *Podon intermedius* (Liljeborg, 1853) and *Evadne nordmanni* (Lovén, 1836). On the contrary, the most abundant calanoid copepods include eurytherm and euryhaline taxa *Acartia* spp. [combined of *A. bifilosa* (Giesbrecht, 1881), *A. tonsa* (Dana, 1849) and *A. longiremis* (Lilljeborg, 1853)] and *Eurytemora affinis* (Poppe, 1880). The rotifers, cladocerans and small copepods occur abundantly in the surface water with the exception of egg-bearing *E. affinis* females, which during daytime dwell deeper in the water column to avoid predation (Telesh *et al.* 2009; Viitasalo *et al.*, 1994; Vuorinen, 1982). Of marine copepods, *Pseudocalanus elongatus* (Boeck, 1865), *Temora longicornis* (Müller, 1785) and *Centropages hamatus* (Lilljeborg, 1853) are the most abundant. These large-sized copepods occur mainly below the thermocline due to their affinity for saline and cold water (Telesh *et al.*, 2009). Conversely, *Limnocalanus macrurus* (Sars, 1863), a large-sized glacial-relict copepod, is generally found in deep lakes and brackish-water areas in the northern hemisphere due to its affinity to cool temperatures and low salinity (Hirche *et al.*, 2003; Lindqvist, 1959, 1961; Vanderploeg *et al.*, 1998). In the Baltic Sea, *L. macrurus* is mainly found in low-salinity areas such as the Gulf of Bothnia or the Gulf of Riga (O'Brien *et al.* 2011), but some individuals can also be found below the thermocline in other areas as well (Sandström & Sörlin, 1981).

1.2.1 Environmental and biological factors controlling zooplankton dynamics

Zooplankton dynamics are controlled by several physical and biological factors, which can be classified into either bottom-up and top-down effects. Bottom-up effects are defined as abiotic factors such as salinity and temperature and (or) biotic factors such as food availability and quality. In the Baltic Sea, salinity has for a long time been seen as the most important environmental factor that controls the biodiversity, and the wide-scale distribution and growth of species, as many of them live at the edge of their physiological limits (Remane & Schlieper, 1958; Segerstråle, 1969). There is also strong evidence that the structure of zooplankton communities in the Baltic Sea is to a large extent regulated by hydrography and stratification of the water (e.g., Dippner *et al.*, 2001; Hansson *et al.*, 2010; Ranta & Vuorinen, 1990; Viitasalo *et al.*, 1990, 1995; Vuorinen & Ranta, 1987; Vuorinen *et al.*, 1998). The physical gradients determine both the horizontal and vertical distribution of zooplankton and therefore even small changes in salinity can cause changes in zooplankton species composition (Ackefors, 1969; Schulz & Hirche, 2007). In addition to salinity, the temperature of water is an important controlling mechanism. The Baltic Sea is situated in a temperate climate zone, therefore, it experiences seasonal temperature changes that may be strong depending on the annual ice cover. According to Doney *et al.* (2012), changes in ambient temperature can directly influence zooplankton, for example, by affecting their physiological performance (e.g., accelerating basal metabolic rates and respiratory demands), leading to changes in behavior (e.g., feeding, predator avoidance, and digestion) and (or) demography (i.e, by initiating hatching of eggs, shortening development time and supporting growth and reproduction).

In addition to affecting zooplankton directly, hydrography changes can influence them indirectly, for instance, by altering the availability and quality of prey organisms (Doney *et al.* 2012). In general, high primary production and (or) changes in phytoplankton species composition, caused by increasing nutrient emission levels and the changes in the physical environment, are predicted to enhance zooplankton production (Hays *et al.*, 2005). However, as some phytoplankton species are of better food quality than others, phytoplankton community changes can impact the food quality of herbivorous zooplankton, and thereby yield changes in the net energy available for growth and reproduction (De Bernadi & Giussani, 1990; Diekmann *et al.* 2012; Suikkanen *et al.* 2013). In addition, shifts in planktonic species occurrence may result in mismatches between species food requirement and food availability affecting the survival of grazers and predators (Cushing, 1990).

In addition to bottom-up factors, top-down effects such as predation pressure caused by planktivores, can have a major impact on zooplankton abundance, composition and distribution (Möllmann *et al.*, 2008; Rudstam *et al.*, 1992, 1994). In the Baltic Sea, the dominant planktivorous fish include the Baltic herring (*Clupea harengus membras*) and sprat (*Spratus sprattus*), but other species, such as smelt (*Osmerus eperlanus*) and three-spined stickleback (*Gasterosteus aculeatus*), and fish larvae also feed on zooplankton (Ojaveer *et al.* 1981; Rudstam *et al.* 1992, 1994). On the contrary the most common invertebrate predators of zooplankton in the northern Baltic Sea are mysid shrimps (Mysidacea, Crustacea) and medusae (Scyphozoa, Cnidaria) (Hosia *et al.* 2012; Viherluoto *et al.* 2000). Of the planktivorous predators in the Baltic Sea, the Baltic herring, sprat and mysids have been shown to have the strongest influence on zooplankton (Flinkman *et al.*, 1998; Rudstam *et al.*, 1992; Viherluoto *et al.*, 2000). For example, by selectively feeding on larger zooplankton, adult fish are able to modify the species composition and size structure of the community, but the importance of predation varies with season (Flinkman *et al.*, 1992, 1998; Rudstam *et al.*, 1992, 1994). Despite their potentially high impact, estimation of the effect of predation on zooplankton is considered difficult mainly because of the wide range of predators and the lack of data on macrozooplankton and seasonal food consumption patterns (Arrhenius & Hansson, 1993; Rudstam *et al.*, 1994). Due to the lack of data and the fact that in the northern Baltic Sea the effect of abiotic controlling factors on zooplankton are stronger to that in the southern Baltic Sea (Hänninen, 1999), in this thesis I focus only on the bottom-up effects in the ecosystem excluding the top-down effects.

1.3 Herring in the northern Baltic Sea

The Baltic herring is a subspecies of the Atlantic herring (*Clupea harengus harengus L.*). Despite herring being a marine species, it is well-adapted to low salinity as it occurs even in the northernmost areas of the Baltic Sea, where the surface salinity is below 3 PSU (Parmanne *et al.*, 1994). In the Baltic Sea, herring is an important commercial pelagic fish with an annual commercial catch and landings of over 100 000 tons in the Gulf of Bothnia alone (ICES, 2017). In addition, the Baltic herring is a key species in the ecosystem that connects the lower and upper trophic levels in the food web. During its early life stages, herring preys mainly on cladocerans, and later, during its adult life stages, begins to selectively prey on large-sized adult copepods, mysids and amphipods (Flinkman *et al.*, 1992, 1998). In addition to being one of the main grazers on zooplankton, the Baltic herring is also a major forage fish for cod (*Gadus morhua*), salmon (*Salmo salar*) and grey seal (*Halichoerus grypus*) and other top predators of the ecosystem (e.g., Rudstam *et al.,* 1994; Ojaveer *et al.,* 1981). Moreover, herring act as a major food competitor to sprat and other planktivorous species (Rudstam *et al.*, 1994).

In the northern Baltic Sea, the herring lives in the open water, being neither close to the bottom or the shore, but every year migrates to shallow coastal waters to reproduce (Kääriä *et al.* 2001; Ojaveer *et al.* 1981; Parmanne *et al.* 1990). One of the main spawning areas of herring in the northern Baltic Sea is located in the inner part of the Archipelago Sea (Parmanne *et al.*, 1990; Rajasilta, 1992). In this area, the herring show an annual migration pattern and homing behavior over a relatively large spawning area: first spawning usually starts at the end of April and continues to the middle of July or even August (Kääriä *et al.*, 2001; Parmanne, 1990; Rajasilta *et al.*, 1993). According to tagging studies, during the spawning period, the Archipelago Sea is inhabited by large schools of herring that are either arriving to their spawning area or returning back to their designated feeding and overwintering areas, which are situated in the outer archipelago, the Bothnian Sea or in the Central Baltic Sea (Kääriä *et al.*, 2001; Parmanne, 1990; Rajasilta, 1992).

During the past few decades, the northern Baltic herring stock has shown large changes in growth rate, condition and recruitment, which have been linked to temporal changes in hydro-climate conditions, zooplankton species composition and cod predation (Axenrot & Hansson, 2003; Casini *et al.*, 2011; Flinkman *et al.*, 1998; Möllmann *et al.*, 2003; Rudstam *et al.*, 1994). In the Central Baltic Sea, the herring spawning stock biomass (SSB) decreased continuously between the 1980s and 2001, but after that revived and has been above the maximum sustainability yield since 2006 (ICES, 2017). On the contrary, in the Gulf of Bothnia, the changes in growth have been more subtle, and the SSB has continuously increased since 1981 (ICES, 2017). The opposite trends in the subbasins are hypothesized to result from hydrography changes having varying effects on the zooplankton community (Lindegren *et al.*, 2011; Rajasilta *et al.*, 2014).

2. Aims of the thesis

The broad aim of this thesis was to identify what species- and community-related changes have occurred in the northern Baltic Sea zooplankton in response to climate-induced changes in the hydrography, and how the changes in the bottom of the grazing chain have manifested themselves at higher trophic levels. To do this, I set out to demonstrate a step-by-step functional analysis of the northern Baltic Sea pelagic ecosystem from bottom-up environmental factors (i.e., temperature and salinity) via phyto- and zooplankton to top predators, i.e., vertebrate planktivores. My first aim was to examine and identify long-term temporal patterns in the abundance and biomass of dominant zooplankton species and groups and to assess how they are connected to hydrographical changes, i.e., changes in mean surface salinity and temperature (**I**). Second, my objective was to analyse long-term seasonal changes in the zooplankton functional groups and also to assess how they are connected to the changes in hydrography and phytoplankton biomass and phenology (**II**). Moreover, I wanted to study how the climate-induced changes in the hydrography have manifested themselves in the northern Baltic pelagic food web. To do this, I used the Baltic herring and its favored prey species, *L. macrurus,* as case study examples (**III–IV**). First, I set out to study the quantity and quality of *L. macrurus* lipids in relation to its summertime occurrence and feeding ecology (**III**). The lipids of *L. macrurus* were of special interest, because the parallel trend of its abundance with that of the herring stock suggests there is a causative link between the two species (Lindegren *et al.* 2011; Rajasilta *et al.* 2014). Second, my aim was to analyse long-term changes in the Baltic herring lipid reserves in comparison to abiotic and biotic changes in the ecosystem and to identify major driving factors (**IV**).

3. Materials and Methods

In order to attain the objectives of this thesis, multi-decadal environmental monitoring data, collected in the Archipelago and Bothnian Sea areas, were utilized in Chapters **I–II** and **IV**. In addition, faunal and environmental data were collected through field samplings in Chapter **III**. Various univariate and multivariate techniques, suitable for time-series and observational data, were used to identify trends and relationships among the variables. In the following sections, I provide an overview of the used methods, a more detailed description can be found in the original Chapters **I–IV**.

3.1 Study area

Field studies for this thesis were undertaken in the Archipelago Sea and southern Bothnian Sea situated in the northern Baltic Sea (Fig. 1). According to a review by Leppäranta & Myrberg (2009), the Archipelago Sea, which comprises of the archipelago in the Southwest Finland, is characterized by great topographic complexity as it consists of tens of thousands of small islands and has a shallow mean water depth of 23 m. Conversely, the Bothnian Sea is characterized as a approximately 70 000 km^2-wide pelagic area with an average water depth of 66 m. As a result of the isolating effect of the coastal Archipelago Sea and direct river runoff from the mainland, both areas are characterized by low salinity, which varies between zero in river mouths and over 6 in the outer areas of the archipelago. Due to the low salinity, salinity stratification, i.e., the primary halocline, is either weak or non-existent, and stratification is mainly controlled by temperature variations (Leppäranta & Myrberg, 2009). As a part of the temperate climate zone, both areas undergo drastic seasonal variation in their environmental conditions. Every spring (April–June), temperature stratification, i.e., thermocline, forms to approximately 10–20-m depth and breaks down in autumn (September–November) as the surface water cools and the effect of autumn/winter storms increases. In addition, every winter (November–March), the sea often at least partly freezes over, but the timing of the freezing as well as the length of the ice period vary annually (Leppäranta & Myrberg, 2009).

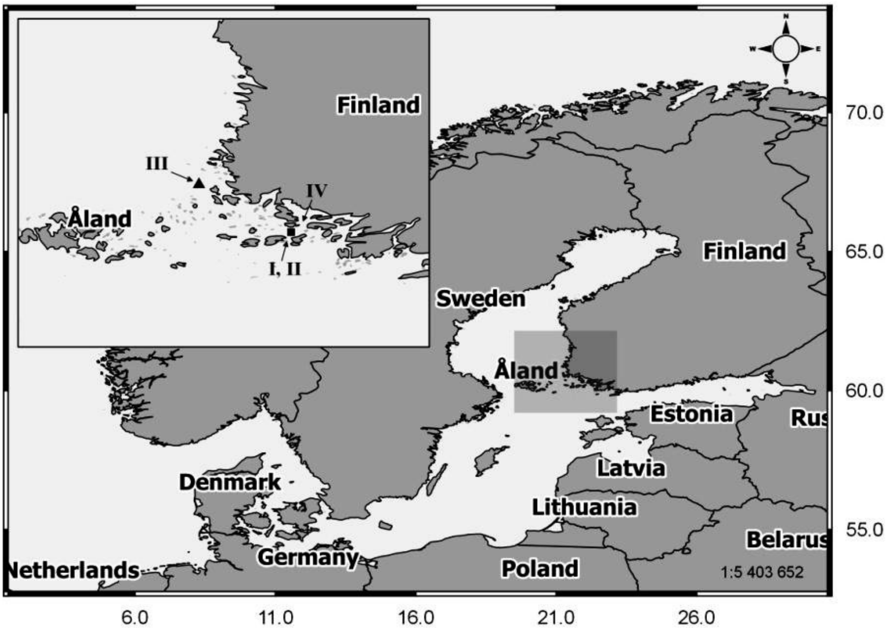

Figure 1. Map of the study areas in the Archipelago Sea and southern Bothnian Sea. The monitoring station in the Archipelago Sea is marked with a black square. The sampling points in the southern Bothnian Sea is marked with a black triangle. Roman numerals (I–IV) refer to the chapters of this thesis.

3.2 Monitoring data

The environmental and biological monitoring data that I used in Chapters **I**–**II** and partly in **IV** were collected from a 50-m deep Ocean Data Acquisition System (ODAS) monitoring station, located amidst a relatively open sea area in the middle region of the Archipelago Sea (60° 15'19.89" N, 21° 57'10.8" E) (Fig. 1). The used zooplankton data consist of monthly samples collected for 41 years (1967–1984 and 1991–2013) (Table 1). No zooplankton data were collected during 1985–1990 due to a change in data provider. The zooplankton samples were collected by a single vertical haul from a 25-m depth to the sea surface with a 150-µm plankton net (1967–1985: Hensen net, mouth opening Ø 70 cm; 1991–2013: conical net, mouth opening Ø 35 cm) and analysed according to standard methods, recommended by the Baltic Marine Environment Protection Commission's (HELCOM) Cooperative Monitoring in the Baltic Marine Environment (COMBINE) Programme (HELCOM, 2017, 1988).

The mesozooplankton species considered in Chapters **I**–**II** were chosen based on their ecological importance and dominance in the zooplankton community and their occurrence in previous studies (Ranta & Vuorinen, 1990; Viitasalo *et al.*, 1990, 1995; Vuorinen & Ranta, 1987; Vuorinen *et al.*, 1998). The species names used in this thesis follow traditionally used nomenclature. In Chapter **I**, the zooplankton abundances (ind./m^3) were converted to biomasses (wet weight, mg/m^3) by multiplying the species abundance with species- or taxon-specific body wet weight values. As a result, I examined the dynamics of all taxa, i.e., *B. longispina maritima, E. nordmanni, P. intermedius, P. polyphemoides, S. baltica, Acartia* spp., *E. affinis, C. hamatus, T. longicornis, P. elongatus*, and *L. macrurus*, and developmental stages (i.e., adults and copepodites I–V) that wet weight values were available in the literature (Flinkman *et al.*, 1998; Hernroth, 1985). In addition, I pooled the species into functional groups, i.e., total zooplankton biomass (incl. all study species), Cladocera (incl. *B. longispina maritima, E. nordmanni, P. intermedius, P. polyphemoides*), Copepoda (incl. *Acartia* spp., *E. affinis, C. hamatus, T. longicornis, P. elongatus*, and *L. macrurus*), large-size copepods (*C. hamatus, T. longicornis, P. elongatus*, and *L. macrurus*), small-sized copepods (incl. *Acartia* spp. and *E. affinis*), brackish-water taxa (incl. *Acartia* spp., *E. affinis, B. longispina, P. polyphemoides* and *S. baltica*) and marine taxa (*C. hamatus, T. longicornis, P. elongatus, P. intermedius* and *E. nordmanni*). The taxa and groups were examined during May–September (**I**) because it comprises the main production period, and because the same months have been used in previous studies (Ranta & Vuorinen, 1990; Viitasalo *et al.*, 1990, 1995; Vuorinen & Ranta, 1987; Vuorinen *et al.*, 1998. To study and illustrate species variability, annual anomalies were calculated from the biomass data by following the procedure described by Mackas & Beaugrand (2010) and O'Brien *et al.* (2013). Based on the findings of Chapter **I**, in Chapter **II**, I analysed the changes further by studying the timing of life-cycle events of selected groups i.e., Cladocera, Copepoda, small copepods, brackish-water taxa and marine taxa during January–December.

Water quality data (0–20 m), consisting of discrete temperature (°C) and salinity (PSU) measurements at a 0-m, 5-m, 10-m and 20-m depth were collected with a water sampler (1967–1984 Ruttner, 1991–2013 Limnos) in ca. 10-day sampling intervals from the ODAS station during 1967–2013 (**I**–**II**) (Fig. 1; Table 1). Data on chlorophyll-α concentration (chl-α; μg/L), analysed from pooled water samples collected between 0-m and 10-m depth at the ODAS station, was used as a proxy for phytoplankton biomass and eutrophication (**II**), because no coherent long-term time series of phytoplankton species abundance or biomass were available from the monitored area. The chl-α data, spanning 30 years (1983–2013), were obtained from an open database (Water Quality of Surface Waters) provided by the Finnish Environment Institute SYKE and the Centres for Economic Development, Transport and the Environment (Table 1). Prior to statistical analyses, the chl-α and hydrographical data were averaged into monthly arithmetic means in order to homogenize time intervals among the variables. In order to study and illustrate the variables' seasonal and interannual variability, annual anomalies were calculated for temperature (**I–II**), salinity (**I–II**) and chl-α (**II**) in a similar manner as described above.

In Chapter **II**, four timing indices widely used in plankton phenology literature were calculated from the zooplankton abundance data to quantify the seasonal timing of population development. Based on the results of Atkinson *et al.* (2015) and Thackeray *et al.* (2012), I chose to use a suite of timings to ensure that the choice of an index was not influencing my conclusions. The first index, called a "Threshold" index, is defined as "the timing of the initial increase of abundance above a defined value" (Mackas *et al.*, 2012), which for the mesozooplankton data was set as half of the long-term mean value. In addition, the "Threshold" index was calculated for chl-α data with the exception that the date when chl-α concentrations first become 5% greater than the local annual median was set as the threshold (Siegel *et al.*, 2002). The second and third indices for mesozooplankton were based on 25th and 50th percentiles of cumulative seasonal abundance, described in detail by Mackas *et al.*, (2012). The fourth index was a "centre of gravity" of the seasonal population maxima (COG), described by both Edwards & Richardson (2004) and Mackas *et al.*, (2012). The COG was calculated using the following equation, provided by Edward & Richardson (2004):

$$COG = \frac{\sum_{m=1}^{12} = m x_m}{\sum_{m=1}^{12} = x_m} \tag{1}$$

where x_m is the species abundance in a month m (m in January = 1,..., in December = 12). The COG was calculated throughout the entire year, because visual inspection of the average seasonal cycle of each taxon (i.e., the average value of each month calculated over the entire sampling period) showed that all studied taxa were unimodal, i.e., had one growing season or a non-defined seasonal cycle. As the mouth openings of the sampling nets differed during 1967–1984 and 1991–2013, the indices were calculated separately for both periods in order to overcome any biases caused by the potential variability in sampling efficiency.

Monitoring data on the Baltic herring lipid content was used in Chapter **IV** (Table 1). The monitoring data on herring muscle lipid content was measured from samples of 100–200 spawning fish, collected annually in the Archipelago Sea from a commercial trap net catch during 1987–2006 and 2013–2014. As the lipid content in the herring muscle has been shown to fluctuate seasonally, among the fishing grounds, with fish size and with the maturation stage of gonads (Aro *et al.*, 2000; Rajasilta, 1992; Røjbek *et al.*, 2014; Szlinder-Richert *et al.*, 2010), in Chapter **IV** the sampling of fish was executed in the same time and place to reduce spatial and temporal variation. In addition, the sampling was focused on females with the same maturity status (i.e., ripe or spawning) and the effect of length was controlled in the statistical analyses. Moreover, only spring-spawning (May–June) herring were used as previous studies have shown that the early-spawning fish collect their lipid reserves during the previous summer and autumn, whereas those spawning later are able to supplement their energy reserves during the spawning season due to an increase of zooplankton production (Rajasilta, 1992; Rajasilta *et al.*, 2001). In addition to the muscle lipid content, the mesentric fat content of female and male herring overwintering in the northern Archipelago Sea were examined from a sample collected in January 2017 from a commercial trawler catch operating in the same area as in 1988 (Rajasilta, 1992).

In order to assess factors influencing herring lipid content, data on salinity, temperature and herring stock size were obtained from open databases (**IV**). Annual measurements of surface water salinity, measured at the Finnish Environment Institute's monitoring station in the Bothnian Sea (SR5; 61°05' N, 19°35' E), were obtained from a HELCOM database provided by the International Council for the Exploration of the Sea (ICES, Dataset on Ocean Hydrography, Copenhagen, 2014). In addition, the effect of winter temperature on the lipid content was studied, because its effect is expected to be greater in early spawning fish than those spawning later in the season. As no temperature data with year-round monthly sampling is collected in the Bothnian Sea, winter temperature data (January–April), collected at 10-day intervals from a 20-m depth, was obtained from the ODAS monitoring station in the Archipelago Sea (Fig. 1). The total number of herring in the Bothnian Sea, describing the size of the herring stock, was used instead of the total stock biomass (TSB). The total number of herring in the Bothnian Sea was calculated from a stock assessment report (ICES, 2015) by dividing TSB with the mean weight of herring at different ages and then summing up the age-class numbers.

3.3 Field measurements

In order to study the occurrence and nutritional quality (i.e., lipid content and FA composition) of *L. macrurus* and its prey (III), field sampling was conducted during May–September, 2013–2014 at a 50-m deep sampling point located in the southern Bothnian Sea (60°42'14.6'' N 20°41' 3.04'' E) (Fig. 1; Table 1). Adult *L. macrurus* were collected for lipid analyses by vertical hauls from the bottom to the sea surface with a 150-µm standard plankton net (Ø 35 cm). In addition, the abundance (ind./m^3) and life-cycle estimates of *L. macrurus* were calculated from zooplankton samples collected by taking 3 vertical net tows at 0–50 m depth with the 150-µm plankton net. The vertical distribution of *L. macrurus* was estimated from samples collected from two water layers (0–25 m and 25–50 m) with a 150-µm closing plankton net (Ø 30 cm). Moreover, in order to study how the lipids of *L. macrurus* have been produced and to specify the overall plankton species composition in the study area, plankton samples were collected during the same study period by hauling a 50-µm standard net horizontally at variable depths (0–10 m). The ambient salinity and temperature conditions of *L. macrurus* was studied by taking vertical profiles of salinity (PSU) and temperature (°C) at each sampling date with a CTD–sonde.

In order to also examine the FA composition of herring, fish samples were obtained from the Bothnian Sea and the Archipelago Sea in the spring of 2013. In the Bothnian Sea, fish were obtained from commercial trawlers, which caught herring in the open sea, whereas in the Archipelago Sea, the fish were collected from a commercial trap net catch and caught spawning herring in the inner archipelago. Prior to the FA analyses, the fish were measured for total length, and their sex and maturity stage were determined. Then the fish were gutted and carefully filleted and skinned, and the fillets were wrapped individually in aluminium foil and stored at –80 °C. The stomachs of fish were also preserved in a 10% formalin solution for content analysis, which was done using a dissecting microscope. Only females (n = 5 at each date) were taken for the FA analysis, but the stomach contents were studied from mixed samples (n = 10–24).

Table 1. Summary of the data utilized in the Chapters (**I–IV**) of this thesis.

	I	**II**	**III**	**IV**
Monitoring data				
Zooplankton abundance (ind./m³) and biomass (mg/m³)	x	x		x
Salinity (PSU)	x	x		
Temperature (°C)	x	x		x
Herring muscle lipid content (% w.wt)				x
Field and laboratory measurements				
Salinity (PSU)			x	
Temperature (°C)			x	
Zoolankton abundance (ind./m³)			x	
Total body, prosome and oil sac length (µm) of *L.macrurus*			x	
L.macrurus lipid content (µg/L & wax ester % of dry weight)			x	
L.macrurus and plankton fatty acid composition (mol% and µg/ind.)			x	x
Herring fatty acid composition (mol%)				x
Herring mesenteric fat content (relative scale 0–4)				x
External data sources				
ELY Center open database (chlorophyll-a; µg/L)		x		
ICES HELCOM database (salinity; PSU)			x	x
ICES stock assessment report (total stock biomass; tons)				x

3.4 Determination of fatty acids and lipid content

The lipid content of adult *L.macurus* was estimated from total body, prosome and oil sac lengths (μm) measured with an inverted microscope and an ocular micrometer (**III**, Fig. 2). During measuring, the presence of spermatophores in females was recorded and used as an indicator of reproduction. Similarly to Dahlgren *et al.* (2012) and Vanderploeg *et al.* (1998), the oil sac length of adult *L. macrurus* was measured from oil sacs present in the prosome region and used as a indicator for lipid content. The oil sac length was measured from the anterior edge to the posterior edge of an oil sac, and the measured lengths were summed together if multiple oil sacs were present (Fig. 2). In order to compare the results with earlier studies (Dahlgren *et al.*, 2012; Vanderploeg *et al.*, 1998), I assumed that the oil sacs consisted mainly of wax esters (WE) and also converted the lengths to total WE content (μg/ind.) and concentration (WE % of dry weight). Based on the example provided by Dahlgren *et al.* (2012), the WE concentration was calculated by first converting the prosome length to carbon biomass (CB) using a length-CB regression ($R^2 = 0.41$) provided by Kankaala and Johansson (1986). Then, I converted the CB to dry weight (DW) by assuming that DW is 2.5 times the CB. The oil sac length was converted to total WE content (μg/ind.) according to the regression proposed by Vanderploeg *et al.* (1998): $y = \exp(3.07x)$, where y is WE (μg) and x is the oil sac length (μm).

The lipid content of herring muscle tissue (% wet weight) (**IV**) was determined from dried samples, which were homogenized, mixed with 0.5 g of anhydrous sodium sulphate and extracted with diethyl ether in a Soxhlet apparatus. The described procedure was used, because it ensures the efficient extraction of stored lipids, predominantly triglycerides (Castera, 1995). Similarly to Rajasilta (1992), the mesenteric fat content of the overwintering female and male herring was estimated visually using a relative scale (0 = no fat, 1 = fat distinguishable as a narrow thread along the gut, 2–4 = increasing fat deposits in the body cavity).

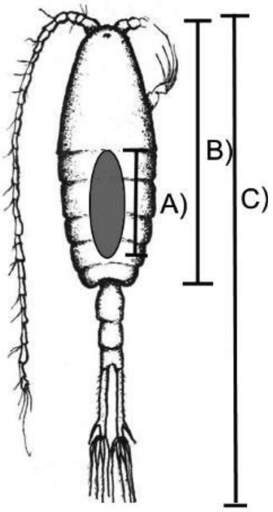

Figure 2. A schematic description of oil sac (A), prosome (B) and total body lengths (µm) (C) of an adult *Limnocalanus macrurus* as seen from a dorsal view. Original drawing by Marjut Rajasilta.

FAs were extracted from samples of adult *L. macrurus*, pooled plankton (**III**) and female herring muscle (**IV**) using a modified Folch method with a chloroform/methanol (2:1, v/v) mixture (Folch *et al.*, 1957). Fatty acid methyl esters (FAME) were prepared at 92°C by boron trifluoride-catalyzed transesterification from the lipid extracts after the solvent was evaporated under nitrogen (Ågren *et al.*, 1992; Morrison & Smith, 1964). The FAME (dissolved in hexane) were analyzed by gas hromatography with flame ionization detection (GC-FID) with the exception of *L. macrurus,* collected in May, which were further analysed using gas chromatography-mass spectrometry (GC-MS), because exceptional peak characteristics were observed in the chromatograms. Because of this, the exact quantity of FA could not be determined from the May samples of *L. macrurus*. For all samples, a percentage composition of FA (i.e., fatty acid weight percentage (%) of total fatty acids) was calculated on the basis of their gas chromatographic peak areas. The FAs were also expressed as concentration per adult (µg/ind.) when appropriate.

3.5 Statistical analyses

In order to identify long-term monotonic temporal trends and elucidate relationships between hydrographical and biological monitoring data, both linear regression (**I–II**), Seasonal Kendall Trend test (**I–II**) and Generalized Linear Mixed Models (GLMM) (**I** & **IV**) were used. Linear regressions were calculated with the function *lm* in the package *stats* 3.6.0 in the R statistical software version 3.20 (R Core Team, 2016). The robust Seasonal Kendall trend tests were calculated with the functions *kendallSeasonalTrendTest* and *SeasonalMannKendall,* in the R packages *EnvStats* 1.0.2 (Millard *et al.*, 2013) and *Kendall* 2.2 (Hipel *et al.* 1994), respectively. The GLMM's were generated using *GLIMMIX* procedure in SAS software for Windows, version 9.3 (SAS Institute Inc., 2013). The GLMM was used, because it incorporates normally distributed random effects and is capable of handling auto-correlated time-series data with first-order autoregressive structure $AR_{1,}$ and heterogeneous variances (Bolker *et al.*, 2009). In addition to long-term changes, I also studied the effect of selected high- and low-salinity and temperature periods (i.e., short-term periods) on the zooplankton anomalies with post hoc comparisons (*ESTIMATE*-statements in the GLMM) whenever a a significant relationship was found between the response and explanatory variables. In addition to the GLMM's, the relationship among respective changes in zooplankton biomass, phenology, herring lipid content and abiotic factors was studied with Pearson's product-moment correlation coefficient (**II–IV**). In Chapter **IV**, a Pearson's correlation test was also used to test the coefficient of variation (CV) of the lipid content against time (year) after checking the data for autocorrelation (no autocorrelation was observed). The correlation coefficients were calculated with the function *cor.test* in the R package *stats* and by using IBM SPSS Statistics version 22 (IBM Corp. Released, 2012). In order to study changes in the herring lipid and mesentric fat content, selected pairwise comparisons also were performed with a Student's t-test for normal variables and a Mann-Whitney U-test for non-normal variables using IBM SPSS. In Chapters **III–IV**, Analysis of Variance (ANOVA) was used to analyze differences among group means in samples and multivariate techniques were used to study the differences and similarities in FA compositions. In Chapter **III**, Principal Component Analysis (PCA) was used to visually study patterns in the *L. macrurus* FA data. In Chapter **IV**, an analysis of similarities (ANOSIM) together with Similarity Percentages analysis (SIMPER) (Clarke, 1993; Clarke & Gorley

2006; Clarke & Warwick 2001) were used to study similarities and differences between the FA compositions of the Baltic herring and *L. macrurus*. The PCA analysis were calculated with the function *prcomp* in the R package *Vegan* 2.4-2 (Oksanen *et al.*, 2017), because it uses the uses singular value decomposition technique (SVD) that allows computation of PCA, even in cases when there are as many or more variables than there are samples (Legendre & Legendre 2012). ANOVA was calculated with functions *aov* and *anova* in the R package *stats*. ANOSIM and SIMPER analyses were calculated with functions *ANOSIM* and *SIMPER* in the R package *Vegan* (Oksanen *et al.*, 2017). More detailed descriptions of the used statistical methods are given in the original Chapters **I–IV**.

4. Results and Discussion

In this thesis, I have studied bottom-up changes in the Archipelago and Bothnian Seas by examining and comparing the long-term dynamics of hydrography and zooplankton, and in turn, assessed how the changes on the bottom of the grazing chain have influenced the transfer of energy in the pelagic food web by using the Baltic herring and *L. macrurus* as case examples. In the following sections, I will discuss all these findings and relating study objectives in depth based on data gathered during the work for this thesis.

4.1 Zooplankton dynamics in a changing climate

During the recent decades, several studies have shown a chain of events from climate variation (e.g., North Atlantic Oscillation Index) via hydrography to zooplankton in the Baltic Sea (Dippner *et al.*, 2001; Hansson *et al.*, 2010; Hänninen *et al.*, 2000, 2003; Vuorinen *et al.*, 2003). The findings of Chapters **I–II** indicated that in the Archipelago Sea, major modifications have occurred in the zooplankton community composition that, for the most part, were connected to temporal changes in the physical environment.

During the study period, all of the studied groups and taxa showed considerable year-to-year fluctuation in their numerical dominance, but only marine taxa, large copepods, the marine copepod *C. hamatus* and the marine cladoceran *E. nordmanni* showed highly significant monotonic decreasing trends, which seemed to began at the turn of the 1990s (**I**, Fig. 3). In addition, the small copepod *Acartia* spp. showed a moderate decreasing trend, which seems to be mostly caused by the decreased occurrence of *A. longiremis,* a poorly known marine species (Diekmann *et al.,* 2012). On the contrary, total zooplankton biomass, Copepoda, Cladocera and small copepods, showed no abundance trends, most probably because the groups were dominanted by species capable of tolerating large environmental changes. In some cases, the rare occurrence of species seemed to prevent significant trends from being found, although the decrease in their occurrence was still evident. For instance, during 1967–1975, the occurrence of adult *T. longicornis* and *P. elongatus* in the data was fairly frequent and relatively abundant. However, since the 1990s, the species occurred sporadically or not at all (**I**, Fig. 3). Non-published monitoring data, collected monthly at the monitoring site since May 2015, suggest that the marine species low occurrence in the data was not caused by them migrating deeper in the water column, as they seem not occur below the thermocline (20–40-m depth) either. More research is however required to corroborate the validity of this observation. In addition to marine copepods, the occurrence of the large-bodied freshwater copepod *L. macrurus* was also sporadic showing no trend in biomass (**I**, Fig. 3). Based on the results of this thesis (**I** & **III**), it seems that, so far, the Archipelago Sea represents a marginal region for *L. macrurus*, as it is found much more abundantly in the Gulf of Bothnia, where the environmental conditions are arguably better suited for the species' physiological needs (**III**, Dahlgren *et al.*, 2012).

In addition to interannual variation, all studied zooplankton taxa showed pronounced variation in their annual seasonal cycle, of which, the cladocerans showed the strongest seasonality, and the marine taxa showed the largest variation in standard deviation (**II**, Fig. 4). In addition, each group showed great inter-annual variability in their timing of annual recurring events (i.e., four phenology indices averaged for each group), which varied often by well over one month between respective years. Marine taxa and Copepoda showed the most variation in timing, whereas Cladocera, small copepods and brackish-water taxa showed the least (**II**, Fig. 4). By and large, the results suggested that, since the end of the 1980s, the phenology of Copepoda, small copepods and brackish-water taxa has shifted towards spring by approximately one month, whereas no trends in phenology were observed for marine taxa and Cladocera (**II**).

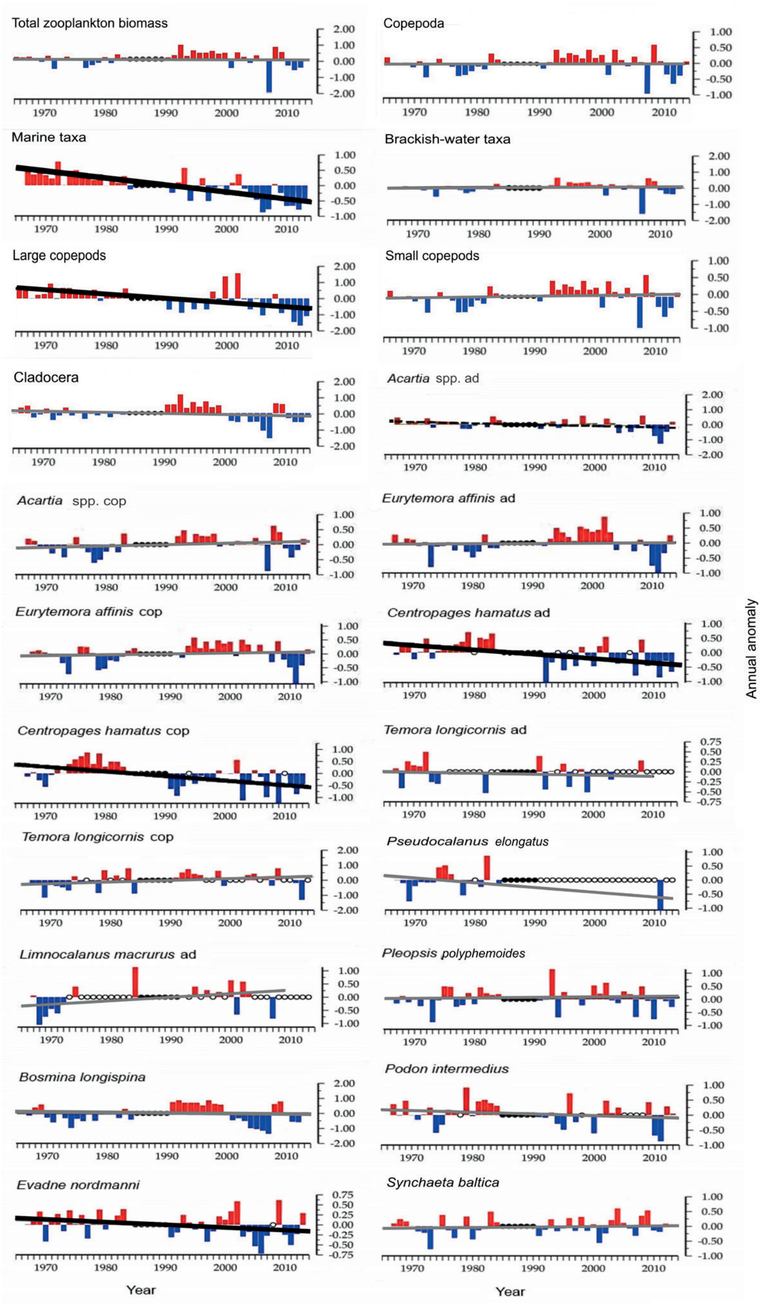

Figure 3. Annual positive (red) and negative (blue) biomass (wet weight mg/m^3) anomalies of mesozooplankton taxa during May–September, 1967–2013 in the northern Baltic Archipelago Sea. No data was collected between 1985–1990 (black points). Blank circles indicate that the number of individuals of the taxon in question was below the detection limit in the sample. The lines represent linear regressions of the annual anomalies versus year (solid black line = p≤0.01, dashed black line = p≤0.05, grey line = non-significant). Note the different scales between y-axes. Ad = adults; cop = copepodites.

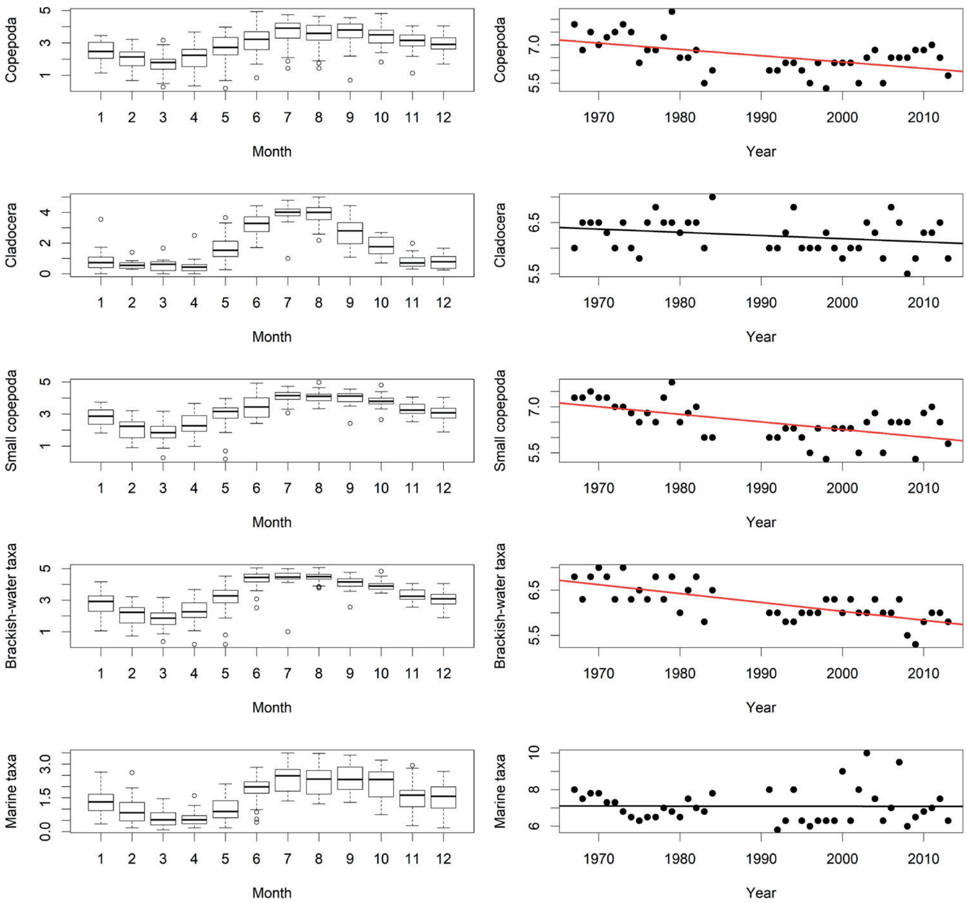

Figure 4. Left-hand box plots show mean seasonal variation of log10(x+1) zooplankton abundance (ind./m³) during January–December (1–12), 1967–2013. Right-hand graphs show interannual variation of zooplankton phenology (four phenology indices averaged for each group) during 1967–2013. Trend lines are fitted linear regression lines (red lines = p<0.05, black lines = p>.0.05). No data was collected between 1985–1990.

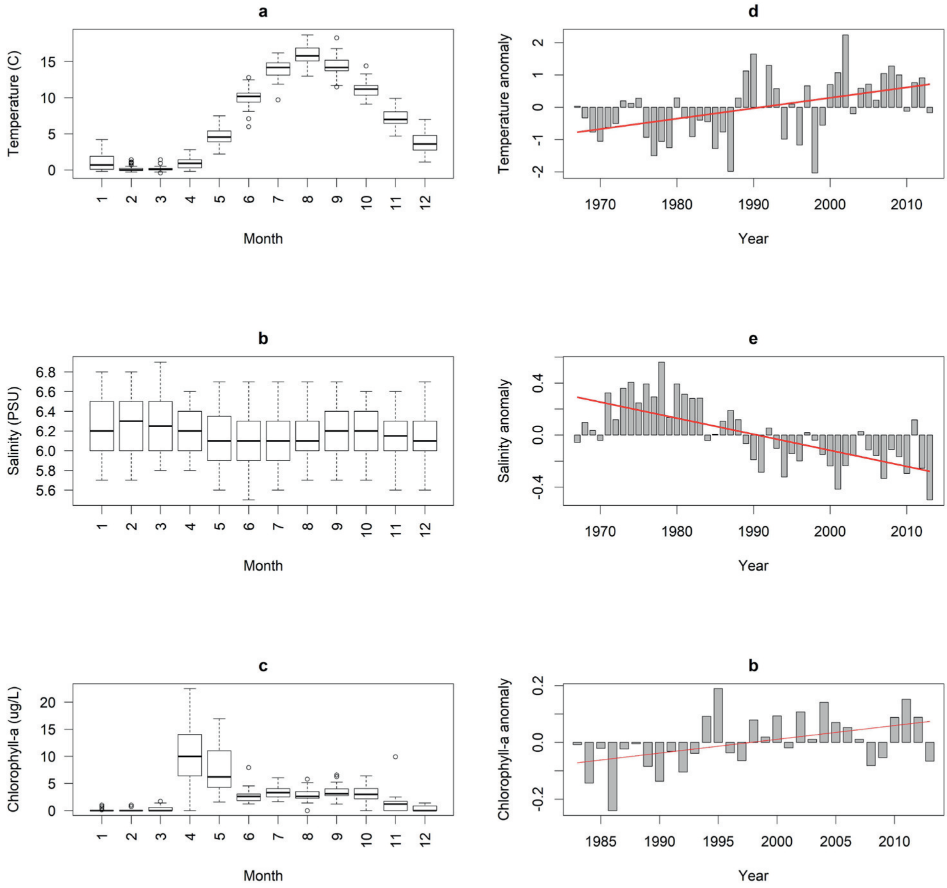

Figure 5. Left-hand box plot graphs show mean seasonal variation of mixed layer (0–20 m) **a)** temperature (°C), **b)** salinity during January-December, 1967–2013, and **c)** log10(x+1) chlorophyll-α (Chl-α) concentration at 0–10-m depth during January–December, 1983–2013. Right-hand graphs show **d)** temperature and **e)** salinity during April–September, 1967–2013, and **f)** chl-α anomalies during April–September, 1983–2013 (bars; positive/negative bars being, e.g., warmer/colder than average) with significant linear trend lines in red color ($p<0.05$).

In order to understand and determine the main driving mechanisms behind the zooplankton dynamics, I compared the zooplankton biomass (I) and phenology (II) with salinity, temperature (I–II), chl-α concentration and phenology (i.e., a proxy for food availability and eutrophication) (II). During the 47-year monitoring period, salinity and temperature underwent clear changes that, in the literature, have been linked to large-scale changes in the North Atlantic climate conditions (Dippner *et al.* 2001; Hänninen *et al.*, 2000; Viitasalo *et al.*, 1995). In the Archipelago Sea, the spring-summer water temperatures (0–20 m) have increased on average from 9.5°C to 10.3°C, whereas salinity has decreased from 6.3% to 5.9%

(**I**–**II**, Fig. 5). Similarly to other subbasins (Suikkanen *et al.*, 2013), the chl-α concentrations in the Archipelago Sea also showed an increase over the 30-year study period from 4.5 µg/L to 5.9 µg/L (**II**, Fig. 5). The parameters showed seasonal dynamics typical for the northern hemisphere. Annually, the Archipelago Sea experienced considerable summer warming, which begins during April, peaks during August and gradually declines afterward. The mean annual variation of salinity is small: salinity is the highest in February–March, after which the values decrease until June and gradually increase afterward. Similarly to temperature, the chl-α concentrations also show strong seasonality by peaking during April–May (**II**, Fig. 5).

In the Baltic Sea, salinity has been for a long time considered to be the most important abiotic factor controlling zooplankton dynamics (Segerstråle, 1969). In Chapter **I**, salinity showed a negative correlation with total zooplankton biomass as well as with Copepoda, marine taxa and large copepods. As expected, positive correlations were also observed with the euryhaline copepods *Acartia* spp. and *E. affinis.* Despite its importance in the Baltic Sea, the effect of salinity on zooplankton phenology has not been widely explored probably due to its low seasonal variation. In Chapter **II**, salinity was positively associated with the phenology of Copepoda, small copepods and brackish-water taxa. In the recent decades, the northern Baltic Sea has experienced an increase in net precipitation and a decrease in the severity of winters that has lead to an overall decrease in salinity (BACC, 2008, 2015). Therefore, the observed "earlier when fresher" response is likely an indirect indication of the species response to the earlier onset of spring.

Several studies have shown that the composition, abundance and phenology of plankton communities in marine environments are tightly linked to water temperature (e.g., Mackas *et al.*, 2012; Richardson, 2008). As expected, in Chapter **I**, the warming of water correlated positively with the occurrence of *Acartia* spp., *E. nordmanni*, *B. longispina maritima,* and the group brackish-water taxa. Yet, the relationships with the selected high- and low-temperature periods varied, *E. nordmanni* being the only one to show a significant response to short-term variability in temperature. The results in Chapter **II** also revealed that the groups of Copepoda, small copepods and brackish-water taxa had shifted their occurrence in accordance with the hypothesized "earlier when warmer" response. The shift in timing seems to have taken place around the end of the 1980s coinciding with the onset of the warming trend.

In the Baltic Sea, eutrophication is a major environmental problem due to high nutrient emissions and internal loading of phosphorus (Voss *et al.*, 2011). Previously in the Archipelago Sea, eutrophication, reflected by intensifying blooms, has been hypothesized to favor opportunistic species, such as ciliates and rotifers, utilizing the spring bloom (Vuorinen & Ranta, 1987). Viitasalo *et al.* (1990) also suggested that environmental factors, coupled with solar radiation, such as primary production, are likely to control zooplankton living above the thermocline. In Chapter **II**, the positive trend in chl-α concentration corroborated the well-known fact that the Archipelago Sea suffers from eutrophication but can also indicate that the recent warming has favored the growth of some phytoplankton species as discussed by Tuovinen *et al.* (2010) who examined eutrophication in the Archipelago Sea from sediment cores. In Chapter **II**, the data also indicated that during the 2000s, the spring phytoplankton peak appreared approximately 10 days earlier than during the 1980s. On the contrary to the expected positive relationship, the results indicated a moderate negative correlation between chl-α phenology and small copepods, i.e., the species phenology began later during years, when the phytoplankton peak occurred earlier. Due to the lower temporal resolution of the data, the ecological explanation for this correlation is unclear, and more intense research is needed to confirm and understand the relationship between the two variables.

4.1.1 Learning from the past in order to understand the future

In this thesis, I have analysed one of the longest running zooplankton monitoring series in the Baltic Sea. Previously, segments of the data have been examined in the light of hydrographical changes (Dippner *et al.* 2001; Ranta & Vuorinen, 1990; Viitasalo *et al.*, 1990, 1995; Vuorinen & Ranta, 1987; Vuorinen *et al.*, 1998), atmospheric conditions (Dippner *et al.* 2001; Viitasalo *et al.*, 1995) as well as chlorophyll-a content, nutrient levels and population densities of the Baltic herring (Viitasalo *et al.*, 1990). Based on these previous studies, zooplankton community composition during spring-summer is affected by climatic factors, affecting the salinity and temperature of sea water (Dippner *et al.* 2001). Out of the environmental variables, salinity is the most important one, as most species show either an increasing or a decreasing trend that correlate with the concurrent salinity changes either positively or negatively (Dippner *et al.* 2001; Ranta & Vuorinen, 1990; Viitasalo *et al.*, 1990, 1995; Vuorinen & Ranta, 1987; Vuorinen *et al.*, 1998). During the past decades, the effect of decreasing salinity has been especially clear for marine and large-bodied copepods living below the thermocline. Other factors coupled with solar radiation, such as temperature and to a lesser extent eutrophication, have been hypothesized to be more important for species occurring above the thermocline (Viitasalo *et al.* 1990). Prior to this thesis, Vuorinen *et al.*

(1998) had analyzed the longest segment of the monitoring data (i.e., 24 years) and showed an increase of cladocerans over marine copepods and connected it to a decrease in salinity. By and large, Chapters **I–II** showed similar results corroborating that since 1967, the warming and freshening of water have influenced the zooplankton community, of which the most clear change is the decrease of marine and large-bodied taxa. Since the beginning of the 1990s, the community has been comprised more of euryhaline and eurytherm taxa, which biomasses seem to fluctuate with short-term changes in salinity and temperature, either positively or negatively. The brackish-water taxa, Copepoda and small copepods also showed "earlier when warmer and fresher" responses that, together with the earlier onset of phytoplankton peak, indicate that the species have responded to an earlier onset of the summer season.

In Chapters **I–II**, the studied groups and taxa showed some deviant and mixed responses suggesting that the effect of ambient environmental conditions is not only species- and stage-specific, but varies temporally and may act as a paraller or to balance each other out, thereby complicating the ecological interpretation of the monitoring data. In addition, it remains uncertain to what degree the monthly sampling interval data was able to follow the dynamics of some species, such as cladocerans that are capable of rapid parthenogenetic reproduction. More research is needed to confirm the influence of the sampling frequency in order to reduce the uncertainty brought by this factor.

4.2 *Limnocalanus macrurus* - a model organism for the future Baltic Sea?

In the Bothnian Sea, the climate-induced freshening of water seem to have increased the abundance of the freshwater copepod *L. macrurus* with the result that the species has become a dominant member of the pelagic ecosystem (O'Brien *et al.*, 2011). During spring-summer *L. macrurus* is abundant when other zooplankton are scarce (Lindqvist, 1959). Presumably as a result of its large size (adult size 2–3 mm) and large lipid reserves (Dahlgren *et al.*, 2012), *L. macrurus* is a favored prey species for herring (Rajasilta *et al.*, 2014). In the Bothnian Sea, Rajasilta *et al.* (2014) studied the stomach contents of herring and showed that the condition of herring improved in spring after the fish started to feed on *L. macrurus*, suggesting that the copepod has a key role in improving herring condition during a period when the energy requirements of fish are high.

With the ongoing climate change, the freshening and warming of the Baltic Sea are projected to continue (BACC, 2008, 2015). Similar changes are projected also in other sea areas, which according to Reusch *et al.* (2018), makes the Baltic Sea a potential "time machine" for future conditions. Vuorinen *et al.* (2015) assessed climate-induced changes in the Baltic Sea biota and projected that the loss of marine fauna will, to some extent, be balanced by the increased abundance and distribution of freshwater fauna. In their study, the freshwater copepod *L. macrurus* was one of the species projected to widen its distribution into the Central Baltic Sea and replace the large-bodied marine copepod *P. acuspes* as a stable food for the Baltic herring. Yet, despite the apparent and potential future role of *L. macrurus* in the ecosystem of the Baltic Sea, only a few studies have recently examined its ecology in the Baltic Sea (Dahlgren *et al.*, 2010, 2012; Hiltunen *et al.*, 2014; Lindqvist, 1959, 1961), and thus, surprisingly little is known about the species seasonal occurrence, reproduction and nutritional quality in brackish-water ecosystems. The findings of Chapter **III** provide insight into the seasonal development of *L. macrurus* population in relation to summer warming and prey availability and bring further support to previous studies suggesting that the copepod occupies a central role in the ecosystem of the Bothnian Sea (Lindegren *et al.,* 2011; Rajasilta *et al.*, 2014).

4.2.1 Seasonal occurrence

In Chapter **III**, I surveyed the summertime and vertical occurrence of *L. macrurus* in the water column and found that it occurs in high abundances in the surface water during spring-early summer, when the energy requirements of herring are the greatest. During May–July, the abundance of adult *L. macrurus* ranged between 200 and 770 ind./m^3, which is higher than that in the Bothnian Bay during the same months (200–300 ind./m^3) (Dahlgren *et al.*, 2012). Despite the relatively high abundance, the occurrence of *L. macrurus* adults and its developmental stages showed large seasonal variation among the summer months. The sampling started during May, when the naupliar phase was mostly over, and the majority of the generation born earlier in spring had developed into copepodites and adults. By the beginning of July, practically all copepodites had developed into adults (**III**, Fig 5). Of the females, approximately 3–6% contained spermatophores suggesting that at least a part of the spring generation had reached sexual maturity and reproduced during July. In freshwater ecosystems, the main reproductive period of *L. macrurus* is during winter (November–May) (Roff & Carter, 1972; Vanderploeg *et al.*, 1998), whereas in the northern Baltic Sea, *L. macrurus* is found to reproduce throughout the year, although the highest intensity of reproduction seems to be during late autumn and winter (Kankaala, 1987; Lindqvist, 1959, 1961). Probably as a consequence of the apparent reproduction, the abundance of nauplii increased at the end of July (**III**, Fig. 6), but their abundance should be considered only indicative, because the used 150-μm sampling net catches quantitatively only the largest naupliar phases. Despite this caveat, the clear peak of nauplii at the end of July did not result in an increase of copepodites and adults during August–September as could be expected, but their abundance remained low possibly due to either predation or some other factor influencing their survival.

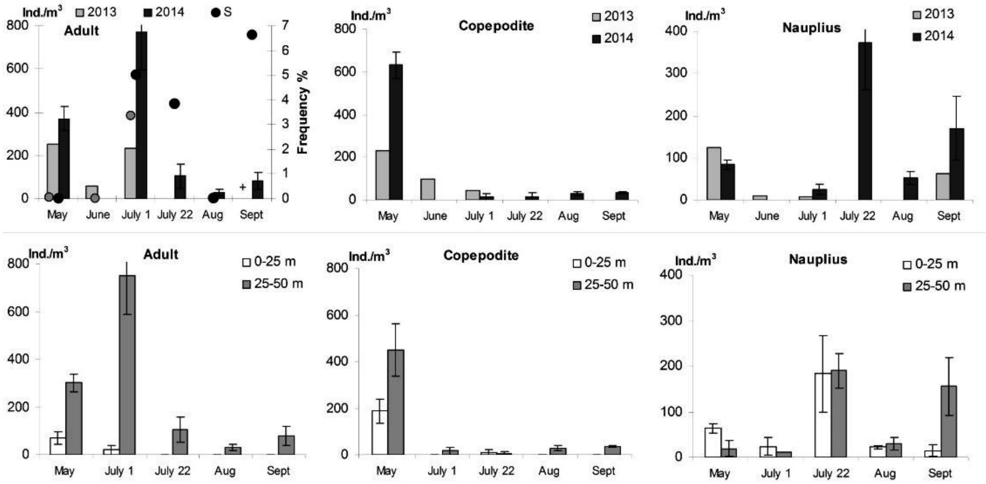

Figure 6. Abundance (mean ± SD ind./m^3) of *Limnocalanus macrurus* adults, copepodites and nauplii. Upper panels indicate abundance at 0–50-m depth during May–September, 2013 and 2014. Lower panels indicate the abundance at different water layers during May–September, 2014. S = the prevalence of spermatophores attached to the females during May–September, 2013 and 2014 (frequency; % of females examined); grey circle = 2013; black circle = 2014; (+) = <1 ind./m3. Note the different scales between y-axes.

Additional samples, collected the next year from two depth layers, gave more insight to the species seasonal cycle (**III**, Fig. 6). In May, adults and copepodites were rather dispersed in the whole water column. However, by the beginning of July, the majority of adults had moved well below the thermocline located approximately at a 10–20-m depth. The descent to deeper water levels occurred simultanously with the decline in adult abundance. For a cold-stenothermic species, moving down to colder water levels with summer warming is expected, but according to literature this behavior can also indicate predation pressure (Hansson *et al.*, 1990; Rudstam *et al.*, 1994; Webster *et al.*, 2015). While the results of Chapter **III** do not exclude the possibility that the decrease in the abundance of adults and copepodites was influenced by predation, which has been shown to exert strong control on zooplankton populations during late summer (Hansson *et al.*, 1990;

Rudstam *et al.*, 1992, 1994), the content and quality of lipids together with the species movement in the water column suggest that the dynamics could have been, to some extent, influenced by the availability and quality of food.

4.2.2 Nutritional quality

Like many high-latitude copepods, *L. macrurus* stores lipids in large oil sacs or droplets in the body that allow it to overcome long starvation periods and provide energy for reproduction during times of low food availability (Hirce *et al.*, 2003; Vanderploeg *et al.*, 1998). During June-September, adult *L. macrurus* contained lipid reserves that varied between 1.3–2.6 µg/ind. (**III**; Fig. 7). The observed lipid content was of similar magnitude to those reported in Lake Michigan (WE % DW) and Bothnian Bay during the same season (1.7–2.2 µg/ind.) (Dahlgren *et al.*, 2012; Vanderploeg *et al.*, 1998) and are larger than that of *P. acuspes* (0.9–1.8 µg/ind. during May–September), the preferred prey species of herring in the Central Baltic Sea (Peters *et al.*, 2006). In addition to the size, the lipids of *L. macrurus* contained high amounts of EFA, which are crucial for species survival, reproduction and growth.

According to Kattner *et al.* (2007), copepod lipid stores are not static but vary seasonally with food availability and diet. During the study years, the size and quality of the *L. macrurus* lipid reserves varied also seasonally and (or) among individuals (**III**, Fig. 7). In May, all adults contained either medium- or large-sized oil sacs, but from May onwards, the frequency of adults having no oil sacs increased with the result that by the end of the summer only 30–50% of the studied adults contained oil sacs. The decrease was also apparent in the total WE content (µg/ind.) and WE concentration (WE % DW) in 2014, when the study period was extented to September.

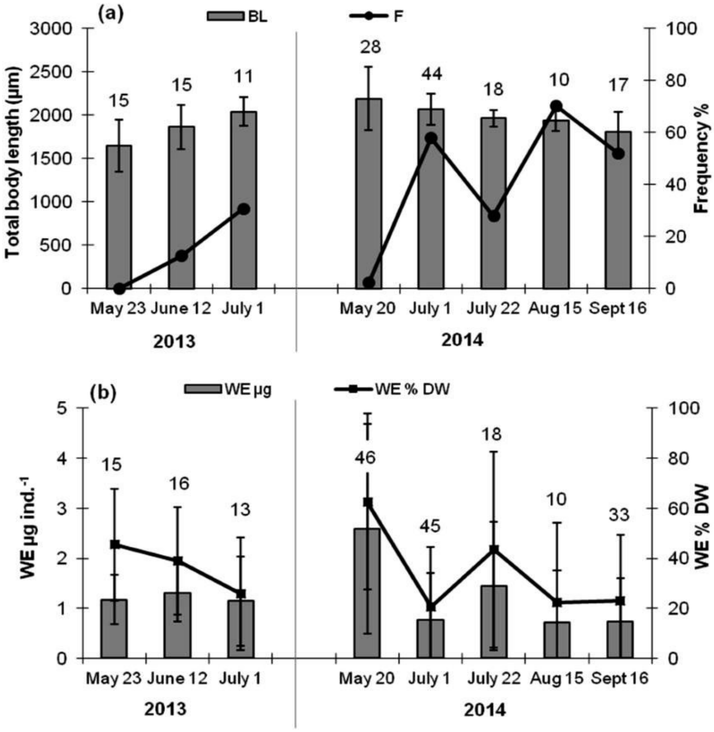

Figure 7. a) Total body length (BL; mean ± SD µm) of adult *Limnocalanus macrurus* and frequency (F; %) of adults with no oil sacs, b) concentration (WE µg/ind.; mean ± SD) and percentage (WE % DW; mean ± SD) of wax esters (WE) in adult *L. macrurus* during May–September, 2013–2014. Total number of individuals examined each year is shown at the top of the columns.

4.2.3 Seasonal changes in feeding ecology

In literature, *L. macrurus* has been classified as a raptorial omnivore with strong carnivorous tendencies (e.g., Dahlgren *et al.*, 2012; Hiltunen *et al.*, 2014). According to Dahlgren *et al.* (2012) and Warren, (1985), during its early developmental stages, *L. macrurus* feeds mainly on net phytoplankton and later, after entering the fourth copepodite stage, feeds also on rotifers and the nauplii and copepodite stages of cyclopoid and calanoid copepods. In accordance with the literature, in Chapter **III**, adult *L. macrurus* contained FA typical of an omnivorous and carnivorous copepod, which according to Dalsgaard *et al.* (2003), is characterized by high relative amounts of 14:0, 16:0, 18:1(n-9) and low levels of long-chained monounsaturates such as 20:1(n-9). A comparison between pooled plankton samples and *L. macrurus* revealed that the FA composition of *L. macrurus* clearly differ from that of plankton further underlining the species unique status in the plankton community.

The fatty acid trophic marker method (FATM) concept is "based on the observation that marine primary producers lay down certain FA patterns that may be transferred conservatively to, and hence can be recognized in, primary consumers" (Dalsgaard *et al.*, 2003). Therefore, the FATM can be used for example to confirm predator-prey relationships and to identify the main processess that impact dynamics in marine ecosystems. In Chapter **III**, the FATM was used to infer summertime feeding ecology of *L. macrurus* during May–September. A comparison between the FA composition and occurrence of *L. macrurus* and other plankton species suggested that the availability and quality of prey played a role in the formation of *L. macrurus* lipid reserves. During May, *L. macrurus* contained large lipid reserves, which were assumed to be a result of the good feeding conditions, which, according to the plankton samples, were provided by the spring bloom. In May, 22.9% of *L. macrurus* FA comprised of EPA, which in literature is attributed to feeding on diatoms that are rich in this FA, or, alternatively, feeding on herbivorous copepods rich in this FA due to grazing on diatoms (Dalsgaard *et al.*, 2003). Later, during June–September, the FA concentrations of *L. macrurus* changed and the concentration of DHA and 18:1(n-9) in *L. macrurus* increased, whereas the concentration of EPA was at its highest during June. According to the FATM, the changes indicated that there was an increase in carnivorous and detrivorous feeding and that the species fed on cyanobacteria. The species and FA composition of plankton supported this apparent change in the *L. macrurus* diet.

In late summer, by and large, the seasonal variation of WE content and concentration, and the large individual differences in the frequency of oil sacs can imply that food resources were not equally partitioned within the population. The differences could be caused either by individual differences in feeding capabilities, scarcity of food resources and (or) resource competition within the population. In the Gulf of Finland and in freshwater environments, *L. macrurus* has been reported to cease vertical migrations in late summer as a result of high temperatures and the stratification of water (Wells, 1960; Webster *et al.*, 2015). Webster *et al.* (2015) studied the vertical distribution of *L. macrurus* in the Gulf of Finland and suggested that during late summer, the cold-water stenotherm remains at deeper water levels with the trade-off that the population concentrates in a smaller space, where competition for food resources increases. Presuming *L. macrurus* behaves similarly also in the Bothnian Sea, the parallel decreasing trends between the abundance of adults and number of oil sacs could indicate that adults suffered from a scarcity or low quality of food with the result that they became eliminated from the population. The FATM gave some support to this hypothesis by indicating that the diet of *L. macrurus* shifted during July–September, and that the species possibly either fed more on ciliates and cyanobacteria, possibly sinking from the upper water layers, and (or) preyed on copepods occurring also beneath the thermocline.

In summary, the results, in conjunction with other publications from the Baltic Sea (Dahlgren *et al.*, 2010, 2012; Hiltunen *et al.*, 2014; Rajasilta *et al.*, 2014), suggest that *L. macrurus* has a potential role in acting as a mediator of PUFA from the bottom of the grazing chain to higher trophic levels. Although the results of Chapter **III** do not exclude or quantify the possiblity that the observed dynamics in occurrence, lipid content and FA composition were influenced by other factors, such as predation, reproductive effort and (or) individual differences in migration traits, it showed that the summer warming together with the availability of prey were connected to the daytime vertical occurrence and feeding ecology of *L. macrurus*. Together with the previous studies, the current results imply that further warming of water may negatively influence the projected changes in the Baltic Sea by forcing *L. macrurus* to permanently stay in deeper water levels, thereby keeping the species outside the reach of planktivores. Moreover, if also the quality of food is low, then the population growth of *L. macrurus* is most likely suppressed causing the summer period to act as a bottleneck, despite summer being the main production period of its prey organisms (Kuparinen *et al.*, 1996). However, in order to gain a comprehensive understanding of the timing of *L. macrurus* life-cycle events and lipid dynamics, more information are needed on how the dynamics vary during winter and interannually.

4.3 Climate-induced changes in the transfer of energy to higher trophic levels

In order to assess what climate-induced changes have occurred in pelagic food web in the northern Baltic Sea, I set out to study how the changes in hydrography and bottom of the grazing chain (through phyto- and zooplankton) have influenced the transfer of energy to higher trophic levels using the Baltic herring as a case example. The impact of environmental changes on fish populations can be assessed using metrics such as fish body condition (i.e., length-weight relationship of fish) or lipid content. According to Neff *et al.* (2012), changes in fish lipid content may reflect dietary shifts, changes in the physical and chemical characteristics of a habitat or provide insight into the temporal variation of some lipophilic environmental contaminants. Like all clupeid fish, the Baltic herring uses its muscle lipid reserves to provide energy during periods of low food availability (Rajasilta *et al.*, 2015). Over the 19-year monitoring period, the muscle lipid content of spawning herring decreased approximately by 25% (from 6% to 1.7%), and based on additional samples during 2013–2014, the lipid content seems to have remained at a low level also since 2006 (**IV**, Fig. 8). The results of Chapter **IV** showed that the decreasing trend in the Baltic herring lipid reserves was connected to both abiotic and biotic changes in the ecosystem as the decline was negatively correlated with the ca. 10% decrease in salinity, 160% increase in the herring stock size and 1.5°C increase in winter temperature.

4.3.1 Climate-induced increase in the consumption of metabolic energy?

So far, several studies have shown that there is a relationship between salinity and herring condition, estimated from a year-specific length-weight relationship (Casini *et al.*, 2010, 2011; Rönkkönen *et al.*, 2004). Yet, in the literature, salinity has been discussed mainly as a background factor that affects fish indirectly through changes in the prey community and fish diet. Although correlations do not prove a causative link among the variables, the relationship between salinity and decreasing lipid content indicate that the effect must be also mechanistic, as low salinity is known to cause direct energy costs for marine species due to osmoregulation between blood water and electrolytes. The direct effects of salinity on adult Baltic herring are poorly known, but in a laboratory experiment with herring juveniles, the lipid reserves clearly grew with increasing salinity (Rajasilta *et al.*, 2011). Presuming a similar effect in adult herring, the decline of salinity could have forced the fish to allocate more energy to osmoregulation, which, in turn, may have consumed their lipid reserves. In this case, the net energy level, measured here as the muscle lipid content, could have decreased, even if food consumption was stable.

In addition to salinity, the lipid content of spawning females was negatively influenced by winter temperature varying between –0.2 and 2.0°C during the study years. Although the association with winter temperature was slightly variable depending on the used study years, the negative connection may still indicate that the energy consumption of fish increased during mild winters, as wintertime warming of water has been shown to increase the basic metabolic needs of fish (Clarke & Fraser, 2004). In addition, winter warming could have also increased the swimming activity, i.e., speed, of fish through a reduction in the extent of ice cover, and a consquent increase in the penetration and intensity of light (Didrikas & Hansson, 2009).

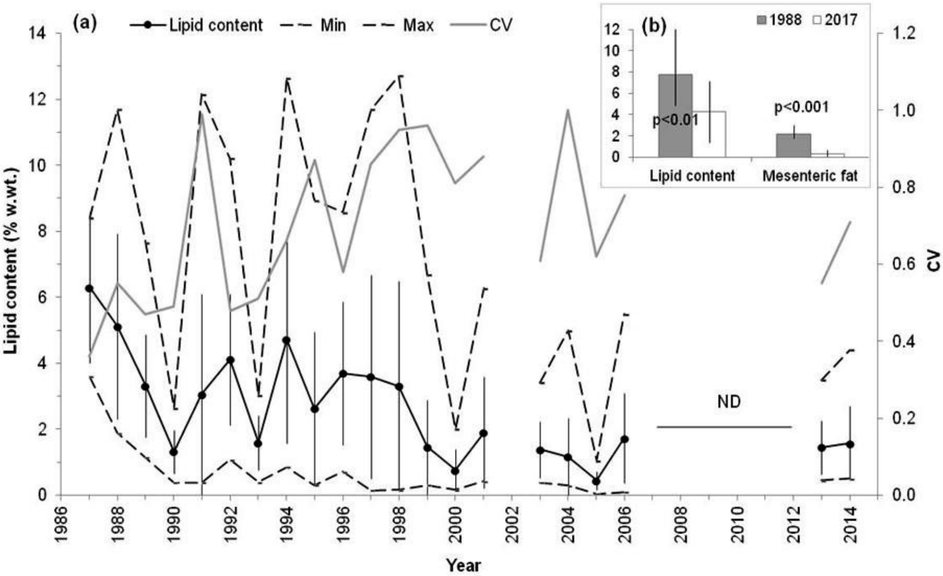

Figure 8. a) Lipid content (% wet weight) of the muscle tissue in spawning Baltic herring females in the Archipelago Sea during 1987–2006 and 2013–2014 and b) lipid content (% wet weight) and amount of mesenteric fat (relative scale from 0 to 4) in herring samples collected during winter from the Archipelago Sea during 1988 and 2017. In the large panel, the bold solid line indicates the sample means with standard deviation (vertical bars), dashed lines are the maximum and minimum values in the samples and the grey line shows the coefficient of variation (CV). In the small panel, values of p indicate the significance level in comparisons between 1988 and 2017 (Mann–Whitney *U* test). ND = no samples were obtained.

4.3.2 Changes in prey availability

Although the changes in the physical environment may have influenced fish directly by increasing the consumption of metabolic energy, the initial size of lipid stores is still determined by the availability of food. In the Central Baltic Sea, an increase in the number of herring was shown to lead to prolonged starvation through an increase in density-dependent resource competition within individuals and possibly also between herring and sprat (Lindegren *et al.*, 2011; Möllmann *et al.*, 2003). Moreover, in Atlantic (*C. harengus*) and Pacific herring (*C. harengus pallasi*), prolonged starvation has been shown to result in a reduction in muscle lipid content (Hay *et al.*, 1988; Wilkins, 1967). Presuming the population increase has had a similar effect on the Baltic herring in the Bothnian Sea, then the decrease in the lipid content may indicate that the fish suffered from prolonged starvation caused by either resource competition and (or) a decrease in prey/fish ratio. This hypothesis is supported by the observation that at the beginning of the monitoring period, the lipid content was characterized by high maximum values, which disappeared from the samples by the end of the 1990s (**IV**, Fig. 8). A decline in the availability of prey could explain the disappearance of the highest lipid values from the samples, as according to Ward *et al.* (2006), when prey organisms become scarce, lipid depositions depend on the individual's competitive abilities as well as genetic differences in the efficiency of food intake and (or) food conversion ratio. As shown by the coefficient of variation (CV) of the lipid content, the individual differences during 1987–2006 were continuously high or even increased during some years. The decrease in the lipid content of overwintering herring also supports this phenomenon. During the winter of 2017, most fish had no mesenteric fat in their body cavity at all, and the muscle lipid content was substantially lower in the samples collected in 2017 than in 1988, when the previous winter samples were analyzed (Rajasilta, 1992). On average, the lipid content of overwintering fish decreased from 7.7% to 4.3% between 1988 and 2017. The decrease in lipid content was of a same magnitude to that in spawning females (**IV**; Fig. 8).

4.3.3 Complex interaction patterns

Neff *et al.* (2012) studied the muscle lipid content of freshwater fish for spatial and temporal trends and concluded that the mechanisms behind lipid trends are usually complex and depend on local conditions. In the Baltic Sea, Lindegren *et al.* (2011) explained the growth of the Bothnian Sea herring stock through an increase in the abundance of *B. longispina maritima, E. affinis* and *L. macrurus*; the former improving the survival of young fish and the latter two increasing the condition and survival of adult fish. The results of this thesis partly agree with this explanation, but also differ in some respects. For instance, the study area in the innermost part of the Archipelago Sea is an important nursery ground for the Bothnian Sea herring, but there, the abundance of *B. longispina maritima* has not increased during the past years (**I**). The food of young herring has not been investigated recently in this area, but in 1988-1990, young herring fed mainly on the copepodite and adult stages of *E. affinis* and *Acartia* spp., and only rarely on *B. longispina* (Rajasilta, 1992). Moreover to the abundance of prey, the survival of young herring depends on prey availability, i.e., that the peaks of the feeding larvae and their prey production match in space and time (Cushing *et al.*, 1990). In the Gulf of Riga, Arula *et al.* (2014), showed that an earlier onset and an improved temporal match between herring larvae and their prey have occurred during the recent decades. In the Archipelago Sea, during the recent decades, small copepods seem to have changed their phenology according to the "earlier when warmer" pattern indicating that the species peak occurred about a month earlier after mild winters compared to colder winters (**II**). It is currently unknown how the herring larvae has responsed to the changes in the seasonal development of zooplankton in the Archipelago Sea, therefore research on the overlap between the mass occurrence of larval herring and its first prey would provide valuable insight into factors influencing the size of herring population in the Bothnian Sea.

The overlap between the occurrence of the predator and its prey is also an important issue for the adult herring. As shown by the muscle lipid data (**IV**), the condition of the herring has decreased over the years, in spite of the high abundance of *L. macrurus* in the environment. Although the results of the current work suggest that the reduction of the energy reserves in herring is connected to increased energy consumption of fish, caused by the warming and freshening of water, it is still an unexpected result in the situation where lipid-rich prey is available in high abundances. As with fish larvae, a possible explanation for the phenomena can be found in the timing of processes. In the Bothnian Sea, adult *L. macrurus* occur abundantly in the upper water layers during spring and early summer when herring are returning to the open sea from heir spawning grounds nearshore. At this phase, fish have used most, if not all, of their energy reserves for reproduction, and they suffer from an increased risk of mortality due to low physical condition. In the feeding grounds, the high availability of lipid-rich prey most likely improves the survival of herring and manifests as an increase in stock number. However, soon after this period, the feeding conditions of the fish change as *L. macrurus* disappears from the upper water layers (**III**) and the herring have to feed on smaller copepods and cladocerans (Flinkman *et al.,* 1992, 1998). With less high-quality prey, it is possible that the density-dependent competition between the fish may have increased with the result that the energy stores of herring are depleted.

In summary, the results of this thesis indicate that the temporal changes in the physical environment of the Bothnian Sea have caused both indirect and direct effects on the energy cycles, which in the monitoring data, appear as a decline in the lipid content as well as a decline in herring body size. That said, more information is needed to fully understand how the lipid reserves of herring in the northern Baltic Sea are formed, as information on the feeding habits of herring in the Bothnian Sea during late summer and autumn is lacking. Also, the degree to which prey diversity has varied in the herring diet, during the recent decades, remains unknown. In the Bothnian Sea, zooplankton monitoring is conducted once a year during August (O'Brien *et al.*, 2011), and therefore information on the seasonal variation of zooplankton and the long-term variation of macroscopic prey, which herring mainly feed on from September onwards, is lacking. Understanding trophodynamics is important, for instance because the size and quality of the lipid content is connected to the survival and reproduction of fish as shown by Laine & Rajasilta (1999). So far, the observed interplay among different environmental variables has most likely provided the herring an opportunity to survive and reproduce, as depleted energy reserves in one year can be restored in another. However, climate models predict that the freshening and warming of water will continue in the future (e.g., BACC, 2008, 2015; Vuorinen *et al.*, 2015) suggesting that the negative effect on the herring lipid reserves is likely also to continue. In a worst case scenario, the described chain-of-events could reduce the reproductive success of herring, as the female lipid content is positively correlated with herring egg survival and hatching success (Laine & Rajasilta, 1999).

However, the decline of lipid reserves is not the whole truth as the quality of female herring lipids (i.e., high concentration of EFA) is believed to have a more important role in reproductive success than lipid quantity alone (e.g., Pickova *et al.*, 1997; Rainuzzo *et al.*, 1997). The results of Chapter **IV**, compared to that of Linko *et al.* (1985) from 1976, indicated that during the recent decades the quality of herring lipids has improved despite the decline in the size. This, together with the similarity of FA patterns between herring and *L. macrurus,* suggests that the hydrograpy changes may have also influenced the herring positively by increasing in the abundance of high-quality prey, i.e., *L. macrurus*, during spring when the females' requirement for EFA is particularly high (Rajasilta *et al.*, 2014). Lind *et al.* (2018) also studied the herring FAs in other areas of the Baltic Sea and similarly showed an increase of n-3 PUFA, supporting the results of this thesis and indicating that there is a general trend in the FA pattern of herring lipids during the past decades.

5. Conclusions

During the process of this thesis, I have showed that the warming and freshening of seawater in the northern Baltic Sea coincide with ecological changes, despite that the changes are only minor compared to what is expected by the end of the century. Specifically, in the Archipelago Sea, the species composition and seasonal timing of zooplankton has changed alongside the warming and freshening of the surface water (**I**–**II**). By and large, the largest changes in the zooplankton community occurred at the turn of the 1990s. Out of the studied taxa, marine taxa were the most sensitive to the experienced hydrography change, whereas brackish-water taxa were more tolerant to the changing conditions and adapted also to changes in the length of the summer season. In conjunction with other publications (Lindegren *et al.*, 2011; O'Brien *et al.*, 2011; Rajasilta *et al.*, 2014), my findings (**III**–**IV**) imply that the climate-induced changes in water quality have influenced the transfer of energy in the food web through complex interaction patterns. Although the warming and freshening of water seem to have improved condition of herring and enabled the positive development of the herring stock in the Bothnian Sea by increasing the abundance of lipid-rich copepod at a key period, the changes have also increased the energy consumption of fish and caused a decline in the availability of prey resulting in a reduction of its lipid reserves.

Understanding these bottom-up changes is important, as they can have implications not only for the functioning of the ecosystem but also for management and fisheries. Like the results of this thesis have shown (**I**–**III**), zooplankton abundance and community composition can quickly reflect changes in the abiotic environment. In particular, changes in the abundance and availability of lipid-rich species, such as the *L. macrurus,* can have high significance for the growth and survival of planktivores. In literature, the observed reduction of body size has been shown to be a way to diminish the costs of energy, but according to Rideout & Tomkiewicz (2011), fish may also save energy in other ways, for instance by abandoning their normal reproductive cycle, i.e., choose not to reproduce until the energy reserves have replenished. In addition, herring may adjust their behavior by changing their annual migration patterns because the migration between spawning and feeding areas consumes a great deal of energy (Slotte, 1999; Varpe *et al.*, 2005). For example, in the study areas, herring might choose not to migrate to their normal overwintering areas after spawning, but instead stay closer to their spawning grounds. In addition, low lipid content of fish stocks can have various effects further on in the food web, as species preying upon it need to feed more to acquire the same amount of energy as in the 1980s, especially as the size of the fish has also decreased. According to Van Deurs *et al.* (2016), these type of changes can bring about detrimental effects on the food web and fisheries, as they may disconnect the energy flow and transportation of FA from one area to another.

5.1 Future directions for research and monitoring

Whether the observed dynamics will persist in the future remains unknown, but environmental monitoring nevertheless provides an important and a powerful tool for detecting and projecting gradual and abrupt changes in the ecosystem and for identifying relationships among biological variables and environmental forcing. However, in order to separate climate change signals from natural variation, it is essential that the data are collected consistently and at a sufficient sampling frequency as the time lags and relationships between environmental and biological factors alone complicate the interpretation of the data. In this thesis, I utilized several environmental monitoring series available in the study area. The results revealed some limitations in the data and highlight the importance of conducting long-term monitoring with an optimal sampling intensity. For example, the zooplankton data in the Archipelago Sea are collected with a monthly sampling interval that, according to Klais *et al.* (2016), is sufficient to portrait the seasonal variance of sexually reproducing copepods, but probably underestimates the seasonal variance of cladocerans and rotifers, i.e., species capable of rapid parthenogenetic reproduction. Although the monthly data was able to reveal both interannual and phenological shifts in the zooplankton occurrence, it remains unknown to what degree the sampling regime contributed to the presented interannual and seasonal variability. Nevertheless, the zooplankton dynamics presented in this thesis resemble large-scale patterns reported in other subbasins, e.g., from the Gulfs of Finland and Riga (e.g., Ojaveer *et al.*, 1998) and the Baltic Proper (e.g., Möllmann *et al.*, 2005). These findings also concur with future population projections for the Baltic Sea (Vuorinen *et al.*, 2015) giving support that the analyzed long-term data do suffiently portray large-scale ecological processes occurring in the northern Baltic Sea.

Environmental monitoring is often a compromise between sampling intensity and financial and human resources, and routine sampling is rarely able to consider all aspects related to species life-cycle, such as vertical migration. At the moment, zooplankton composition is monitored at the Bothnian Sea only once a year during August, and seasonally resolved information on zooplankton dynamics in the area is lacking in addition to detailed information on herring feeding and on the effect of selective predation on the formation of the zooplankton community. Therefore, I conclude that at minimum, seasonally and spatially comprehensive monitoring, involving their entire habitat, should be pursued for ecologically and economically important species like the Baltic herring and the lipid-rich copepod *L. macrurus* to foresee climate-induced changes in the ecosystem and to provide a more accurate picture of the related dynamics.

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