DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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ARNO PÕLLUMÄE

Spatio-temporal patterns of native and invasive zooplankton species under changing climate and eutrophication conditions

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following papers, which are referred to in the text by Roman numerals:

I. Põllumäe, A., Kotta, J. & Leisk, Ü. 2009. Scale-dependent effects of nutrient loads and climatic conditions on benthic and pelagic communities in the Gulf of Finland. *Marine Ecology*, 30, (Suppl. 1), 20–32.

II. Kotta, J., Kotta, I., Simm, M., Lankov, A., Lauringson, V., Põllumäe, A. & Ojaveer, H. 2006. Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Marine Research*. 60, 106–112.

III. Põllumäe, A. & Väljataga, K. 2004. *Cercopagis pengoi* (Cladocera) in the Gulf of Finland: Environmental variables affecting its distribution and interaction with *Bosmina coregoni maritima*. *Proceedings of the Estonian Academy of Sciences. Biology. Ecology,* 53, 4 276–82.

IV. Põllumäe, A. & Kotta, J. 2007. Factors describing the distribution of the zooplankton community in the Gulf of Finland in the context of interactions between native and introduced predatory cladocerans. *Oceanologia*, 49, 2, 277–290.

V. Põllupüü, M., Simm, M., Põllumäe, A. & Ojaveer, H. 2008. Successful establishment of the Ponto-Caspian alien cladoceran *Evadne anonyx* G.O. Sars 1897 in low-salinity environment in the Baltic Sea. *Journal of Plankton Research*, 30, 7, 777–782.

VI. Ojaveer, H., Kotta, J., Põllumäe, A., Põllupüü, M., Jaanus, A. & Vetemaa, M. 2011. Alien species in a brackish water temperate ecosystem: Annual-scale dynamics in response to environmental variability. *Environmental Research*, in press.

Author's contribution:

The author's contribution to papers **I**, **III** and **IV** was substantial including the generation of the original idea, hypotheses, data collection and analyses, and manuscript preparation. As for publications **II, V** and **VI,** the author's main activities were participation in the data collection and analyses related to mesozooplankton and manuscript preparation.

1. INTRODUCTION

Eutrophication and climate change are ranked among the major threats to the stability of the marine coastal environment and can have severe impacts on near-shore biodiversity and functioning (*e.g.*, McGowan *et al.* 1998; Howarth *et al.* 2000; Jackson *et al.* 2001). Eutrophication may lead to algal blooms, accumulation of organic matter and development of anoxia and consequently cause irreversible changes in ecosystems (Andersen *et al.* 2006; Paerl 2006). The effects of climatic variability on coastal ecosystems are less known due to the mismatch of important scales between climate and biological variables. The effects of climate operate through local weather parameters such as temperature, wind, rain, snow and current patterns, as well as interactions among these (Stenseth *et al.* 2002). Shifts in climatic conditions are known to have profound ecological impacts altering the patterns of distribution, abundance and diversity of species (Hughes 2000; Lotze *et al.* 2006).

Taking this into account there is no single natural scale at which the effects of eutrophication and climate should be studied (Levin 1992; Karlson & Cornell 1998). In order to identify the most important governing factors one needs to determine the scales where the links between eutrophication, climate variables and biotic patterns are the strongest (Steele & Henderson 1994). Although it is recognized that processes affect ecosystems simultaneously at various spatial scales (Steele & Henderson 1994; Denny *et al.* 2004), to date the relative importance of small- and large-scale processes on the formation of marine communities is little known (*e.g.* Hewitt *et al.* 2007). Large-scale environmental stresses and disturbances (*e.g.*, climatically driven changes in seawater temperature, sea level or the intensity of ice scouring) can synchronize population changes over wide geographical areas and define broad patterns of distribution, if they have a direct effect on recruitment or mortality. Within these patterns smaller-scale processes operate at a lower intensity to modify distributions, abundances and functioning of communities (Kotta & Witman 2009). Recently it was shown (Hewitt & Thrush 2009) that the degree of interaction between large-scale environmental factors with smaller-scale variability is not consistent across sites or species. The knowledge on such variability, however, may control our ability to predict effects of nutrient loads and changing climatic conditions on coastal communities (Hewitt & Thrush 2009).

Environmental changes, triggered by both climate and human induced eutrophication, are known to affect ecological properties of marine ecosystems and, therefore, are influencing biological invasions (*e.g.*, Bax *et al.* 2003; Walther *et al.* 2009). Due to the complexity of interactions between abiotic changes and biological responses in the marine environment, such fields deserve a great deal of research in order to understand current patterns and predict future changes (Hoegh-Guldberg & Bruno 2010). Evidence of historical invasions (Carlton 1999; Strasser 1999) suggests that the human-mediated invasion of alien species should be considered at the same historical time scale as several other important anthropogenic factors (*e.g.* Lotze & Worm 2009).

Nevertheless, this field of research has only relatively recently received elevated and systematic attention from both scientific and a wider human community (Shirley & Kark 2006), meaning its comparatively weak incorporation into systematic marine ecosystem studies. However, there is evidence that the effects caused by invasions of alien species in marine environments are very substantial, ranging from impacts on biodiversity (*e.g.*, Bax *et al.* 2003; Leprieur *et al.* 2008) to the structure and functioning of populations, communities and ecosystems (*e.g.*, Wallentinus & Nyberg 2007; Oguz *et al.* 2008; Roohi *et al.* 2010). These are, in general, at comparable levels with those induced by other anthropogenic activities and climate variability.

Earlier studies have indicated that abrupt changes in abiotic conditions may directly alter the survival and growth of individuals but, likewise, biotic interactions may indirectly affect the patterns of distribution (Occhipinti-Ambrogi 2007). However, due to the size and complexity of the ocean, deeper insight is needed to relate environmental variables, timing of introductions and population size and distribution of already established species. Unfortunately, the related knowledge on alien species is relatively limited as yet. This is, at least, partly driven by the lack or limitation of appropriate monitoring data with sufficient spatio-temporal coverage and pre-invasion observations needed to carry out such analyses (*e.g*. Stachowicz *et al.* 2002).

Nevertheless, there is increasing evidence that elevated eutrophication and changing climatic conditions result in higher rates of bioinvasions (Steve 2009; Uitto *et al*. 1999, Strake 2002). Consequently, the non-indigenous organisms have become one of the most serious concerns to the aquatic ecosystems during the last 10–20 years causing unpredictable and irreversible changes in the recipient ecosystems (Carlton 1996; Ruiz *et al.* 1999). Ecosystems in which the biological diversity is naturally low are particularly vulnerable to biological invasions (Stachovicz *et al.* 1999). The Baltic Sea is an example of such an ecosystem: some 70 of 100 previously recorded non-indigenous species have established reproducing populations. While there is a plethora of data regarding the impacts of invasions by benthic species, comparable data on pelagic species are few and far between (Leppäkoski & Olenin 2001; Leppäkoski *et al*. 2002). The transfer of ballast water between ports has served as an important vector, enabling the invasion of many aquatic species to new habitats (Charlton & Hodder 1995). Taking into account the position of the Estonian coastal sea as an active area of international shipping routes and large ports, the high rate of alien species introductions and their possible negative impacts on the environment, the region should be considered as a “hot spot” in the Baltic Sea area.

Due to the large uncertainties about the interplay between the shift in the abiotic environment and community interactions, it is difficult to predict, without proper data analysis, whether the role of invasive species will increase or decrease in the changing climate conditions. Moreover, even nowadays the functional diversity of the alien species in the north-eastern Baltic Sea is high and they represent virtually all trophic levels and a multitude of functions. Several of them have already caused strong impacts (Hulme *et al.* 2009; Kotta *et al.* 2010) and, therefore, have a potential to overwhelm key species and ecosystems.

The interactions between native species and invaders are poorly known. To date we mostly rely on field data and there are a few papers linking experimental and field observations (Parker *et al.* 1999). For the Baltic Sea some information exists on the impacts of benthic invasions (Kotta *et al.* 2001; Kotta & Møhlenberg 2002; Kotta & Ólafsson 2003; Kotta *et al.* 2010) whereas data on pelagic species are rarer (Leppäkoski & Olenin 2001; Leppäkoski *et al.* 2002). Besides, we virtually lack information whether the dynamics of native and non-indigenous species is coupled or governed by different environmental variables. Such information, however, is of utmost value when assessing the spatial extent and temporal intensity of the potential effects of non-indigenous species at community and ecosystem levels.

In this thesis I evaluate how eutrophication and climate variables estimated at local, gulf and regional scales have contributed to the biomass of native and invasive zooplankton species in a shallow brackish water ecosystem of the Baltic Sea. When assessing the links between environmental variables and biotic patterns, I also identified the existence and timing of population regime shifts in relation to shifts in the abiotic environment. The obtained results should improve our general understanding of the magnitude and direction of modifications of the marine population, community and food web as a result of the interactive effect between environmental variability and alien species invasions in the changing marine ecosystems.

In this thesis I also describe the population dynamics and ecological impacts of four established alien species the cirriped *Balanus improvisus* Darwin, the polychaete *Marenzelleria neglecta* (Sikorski and Bick sp. nov.) and the cladocerans *Cercopagis pengoi* (Ostroumov) and *Evadne anonyx* G.O. Sars in the north-eastern Baltic Sea. The first two species are benthic as adults and have pelagic larvae. The third and fourth species spend the whole life cycle in the pelagic system except for benthic resting eggs.

The specific aims of the studies collected in this thesis were (1) to evaluate how nutrient load and climate variables estimated at different scales contribute to the biomass of zooplankton including recent pelagic invaders, (2) to observe the changes in mesozooplankton communities in relation to the establishment of *Cercopagis pengoi* and *Evadne anonyx*, and (3) to test whether *Cercopagis pengoi* had affected the distribution of its potentially essential prey *Bosmina coregoni maritima*. Although papers **I, II** and **VI** handled both benthic and pelagic community, this thesis is only about pelagic community and all material and analyses concerning benthos was excluded.

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted in the Gulf of Finland and in Pärnu Bay in the Gulf of Riga, northern Baltic Sea (Figure 1). Both study areas are strongly influenced by diffuse and point source nutrient loads. The average depth of the Gulf of Finland is 37 m and maximum 123 m. Sand, silt or sandy clay bottoms dominate. The eastern Gulf of Finland receives fresh water from a huge drainage area, and its western part is a direct continuation of the Baltic Proper; therefore the gulf has a permanent east–west gradient of salinity. The salinity range of stations was 2.2 to 7.3 psu. Two subareas – Tallinn Bay and Narva Bay – are more thoroughly studied in this thesis.

Tallinn Bay is located in the southern Gulf of Finland. The bay is relatively exposed and deep (max depth 100 m). The water exchange between it and the open gulf is good. Seasonal fluctuations in water temperature occur above 30 m depth, mainly from May to November. Maximum temperatures of 22–24°C are usually observed in July. In the deeper parts of the bay the temperature is stable throughout the year at 2–5°C. During the winter, the bay is usually covered with ice. The large urban area of Tallinn is affecting the nutrient status of Tallinn Bay.

Narva Bay, the largest bay in the south-eastern Gulf of Finland, resembles Tallinn Bay as regards exposure, water exchange and temperature regime, but is shallower (although its maximum depth is 80 m, most of it is only 20–40 m deep) and has a longer period of ice cover than the latter. The River Narva is the second largest river flowing into the Gulf of Finland and constitutes the most prominent nutrient source of Narva Bay. The open parts of Narva Bay are influenced by water from the River Neva, the largest river in the whole Baltic Sea catchment area.

Pärnu Bay is the only studied subarea in the Gulf of Riga in this thesis. Pärnu Bay is a shallow semi-enclosed water basin. Its maximum depth gradually increases from 7.5 m in the inner north-eastern part to 23 m in the outer south-western part. The hydrological conditions of the bay are formed under the complex influence of meteorological processes, river discharge (Pärnu River, freshwater inflow 2 km^3 annually), and water exchange with the open part of the Gulf of Riga. During the winter, the bay is covered with ice. The average salinity of the sampling stations is 5 psu, maximum temperatures in summer are 25°C.

2.2. Field sampling

The majority of zooplankton samples were collected within the framework of the Estonian National Monitoring Programme. Additionally some long-term sampling was performed in Pärnu Bay within the fish-larvae monitoring projects (**II**). The samples were collected by means of vertical tows with a Juday closing plankton net (mesh size 90 µm, mouth area 0.1 m^2). The samples were preserved in 4% formaldehyde solution in seawater. At deep stations zooplankton samples were collected separately above and below the thermocline when present.

The sampling frequency varied over the years. A large monitoring cruise with many sampling sites in the Gulf of Finland has been carried out yearly at the end of May or at the beginning of June except 2001, when it was done in August. Three stations in the Tallinn Bay area have been sampled more frequently since 1997 and in Narva Bay since 2001. Those stations are sampled once a month during spring and autumn and fortnightly during summer. The sampling in Pärnu Bay was done weekly during the summer.

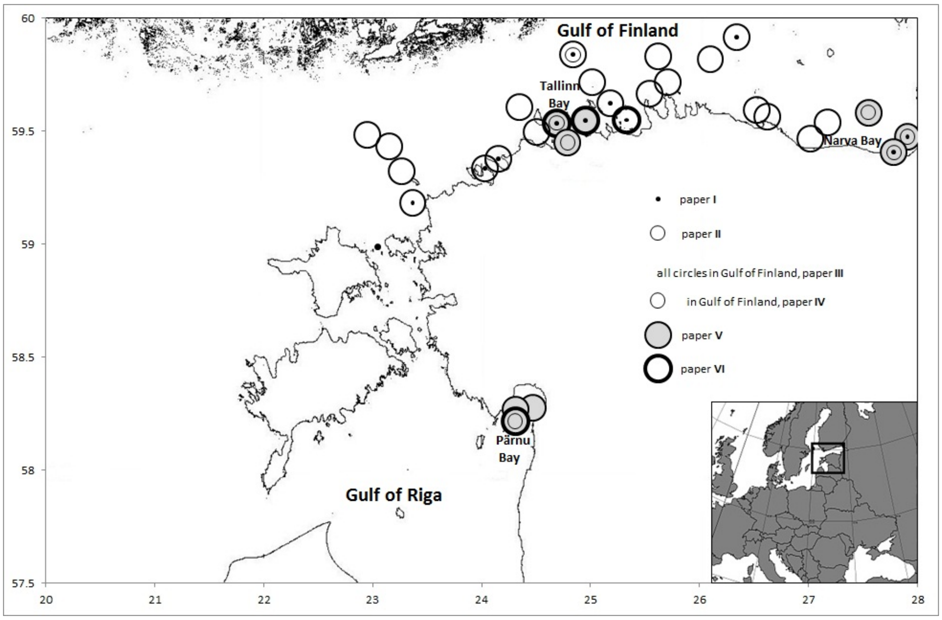

Figure 1. Integrated map of all zooplankton sampling stations used in original publications.

The abundances of zooplankton species were estimated from a number of subsamples according to the methods recommended by HELCOM (1988 and 2010). Biomasses (wet weights) were calculated using the biomass factors for different taxonomic groups and developmental stages (Hernroth 1985). The specimens of *Cercopagis pengoi*, a relatively large-sized species with a tendency to form bundles, were counted in a whole sample to get more precise abundance numbers. Small volumes (24 ml) of concentrated zooplankton samples were stored after analyses. Reanalyses of some samples back until 1997 were done in order to determine the possible occurrence of infrequent specimens of invasive *Evadne anonyx*.

Although the zooplankton sampling was done separately from the layers above and below the thermocline in some deep stations, the abundance of zooplankton in the whole water column is used in all analyses, except in the study where the effect of *Cercopagis pengoi* on the vertical distribution of *Bosmina coregoni maritima* was analysed.

For fish diet analyses monthly daytime experimental bottom trawl surveys were performed at 6–54 m in the central and north-eastern Gulf of Riga during June–September 1994–1998 (for details see Ojaveer 1997). In each sample, stomachs of 20 individuals were analysed according to Melnichuk (1980). Altogether 2074 herring *Clupea harengus membras*, 1117 smelt *Osmerus eperlanus*, 769 three-spined stickleback *Gasterosteus aculeatus*, 80 nine-spined stickleback *Pungitius pungitius* and 71 bleak *Alburnus alburnus* individuals were analysed.

2.3. Other measurements

All basic oceanographic variables (temperature, salinity, water transparency, concentration of nutrients and chlorophyll *a*) were measured or sampled at the same time and in the same stations with zooplankton sampling. For some analyses reference values from the Central Baltic Sea and also winter values have been used. Winter is used as a proxy for eutrophication in the Baltic Sea area because the plankton has not yet taken up the nutrients yet. Inorganic nutrients that have accumulated during the winter are assimilated during the spring bloom. The new production is used directly by either pelagic or benthic herbivores (HELCOM 2002).

The data on the annual point source and riverine loads of total N and total P to the Gulf of Finland in 1996–2005 was obtained from the Estonian Ministry of Environment and from the MARE homepage (http://www.mare.su.se/). The data of annual total N and total P loads and runoff of the River Neva were obtained through Baltic-Nest (http://nest.su.se/nest/) from NW Administration of Roshydromet (Russia).

As a proxy of atmospheric conditions the winter index of the North Atlantic Oscillation was used to relate the global climate pattern to the variation of biological data in the study area (NAO December–March, http://www.cgd.ucar.edu/cas/jhurrell/ nao.stat.winter. html) (Barnston & Livezey 1987; Ottersen *et al.* 2001). The NAO is an alternation in the pressure difference between the subtropical atmosphere high-pressure zone centred over the Azores and the atmospheric low-pressure zone over Iceland. The NAO's connection with the wind, temperature and precipitation fields is strongest during winter. The link between the NAO and sea water temperature may persist over the summer, however, being highly region dependent and should be assessed for each site separately (*e.g.* Ottersen *et al.* 2001). During the years of high NAO there is a substantial increase in the rainfall and consequently the freshwater inflow into the Baltic Sea (Hänninen *et al.* 2000). The increased pressure differences result in higher winter temperatures in the northern Europe (Rogers 1984). As an additional global climatic conditions variable we used the Baltic Sea Index (BSI), which is the difference of normalized sea level pressures between Oslo in Norway and Szczecin in Poland. The BSI is significantly related to NAO and is used as a regional calibration of the North Atlantic Oscillation index (Lehmann *et al*. 2002). The average wind speed and air temperatures at coastal stations were obtained from the Estonian Hydrometeorological Institute.

2.4. Statistical methods

Multivariate data analyses were performed with the statistical program "PRIMER" (Clarke & Warwick 2001; Clarke & Gorley 2006). Environmental variables were normalized prior to analyses. Invertebrate biomass or abundance data were square-root transformed to downweigh the dominant species and increase the contribution of rarer species in the multivariate analysis. The Bray–Curtis similarity measure was used to construct the similarity matrices (Bray & Curtis 1957).

Non-metric multidimensional scaling analysis (MDS) on square-root transformed data of biomasses was used to reveal the dissimilarities between study areas and invertebrate species. Statistical differences in benthic invertebrate and mesozooplankton communities among water bodies were assessed by the ANOSIM permutation test (Clarke 1993). BIOENV or BVSTEP procedures were used to relate the patterns of environmental variables to the biomasses or abundances of invertebrate species. The analysis shows which environmental variables best predict the observed biotic patterns (Clarke & Ainsworth 1993). A Spearman rank correlation (r) was computed between the similarity matrices of environmental data (abiotic variables; Euclidean distance) and different invertebrate species (Bray–Curtis distance). A global BEST match permutation test and RELATE programs were run to examine the statistical significance of observed relationships between environmental variables and biotic patterns.

For univariate analysis the statistical program "Statistica" was used (StatSoft Inc. 2004). Correlation, linear and polynomial linear regression analyses were employed to describe the relationships between abiotic and biotic environmental variables. Polynomial regression results are only reported if significantly better fits were achieved using this method compared with the linear model. The statistical differences between experimental treatments were obtained by ANOVA and *t*-tests (Sokal & Rohlf 1981).

To test the regime shift hypothesis as a step change in the mean level of the studied alien species, we used a parametric method based on sequential *t*-test analysis of regime shifts STARS (Rodionov 2004; Rodionov & Overland, 2005). The method consists in calculating a Regime Shift Index (RSI), which represents the cumulative sum of normalized anomalies relative to a critical value. In this work we used the cut-off length of 10 years and a probability level equal to 0.05.

3. RESULTS AND DISCUSSION

3.1. Links between eutrophication, climate variables and native and invasive zooplankton species at local, gulf and regional scales

Altogether 35 zooplankton taxa were identified in the study area (**VI**). *Acartia* spp., *Eurytemora affinis* and *Synchaeta baltica* were the most frequently detected taxa. The total biomass of pelagic invertebrates in samples ranged from 3 to 62 000 mg wet weight m^{-2}. Ordination of pooled samples showed that small and abundant rotifers were clustered together whereas larger and less dominating copepods kept away from the cluster (**I**).

The analyses on the links between eutrophication, climate variables and mesozooplankton estimated at local, gulf and regional scales showed that mesozooplankton species were often affected by environmental variability at two or all spatial scales. The only exceptions were the biomass of bivalve larvae and *Pleopsis polyphemoides* in May, which were mainly described by environmental variability at local scale. Environmental variability at regional scale was least important but still significant for the most of taxa. Most studied zooplankton species were described by both climate and eutrophication variables (Figure 2). Only *Pleopsis polyphemoides* and bivalve larvae were described only by nutrient load variables and *Bosmina coregoni maritima* and *Keratella quadrata* by climatic condition variables in May. *Pleopsis polyphemoides* was explained by nutrient load variables and *Synchaeta baltica* and *Cyclopidae* by climatic condition variables in August. All other zooplankton species were related to both climatic conditions and nutrient load variables. In the biomass models of zooplankton species the contribution of eutrophication variables increased almost linearly with the contribution of climate variables. For some species such as *Balanus improvisus larvae*, *Cyclopidae* and *Cercopagis pengoi* in May and *Balanus improvisus larvae*, *Limnocalanus macrurus* in August the links between environmental variability and biotic patterns were not statistically significant. We expected that as zooplankton species are mobile and capable of moving both vertically and horizontally in the aquatic environment, their biomasses are influenced by large-scale environmental variability rather than small-scale environmental variability. Interactions between eutrophication and climate variables are likely through changes in the hydrographical regime (temperature, salinity) and benthic habitat disturbance, which may change the development patterns of zooplankton resting stages and affect the population dynamics of benthic invertebrates that have meroplanktonic larvae. Indeed, the results of this thesis suggest that large-scale pressures such as eutrophication and climate change define local patterns of distribution and within these patterns small-scale weather and load patterns modify the response of communities to these large-scale pressures (**I**).

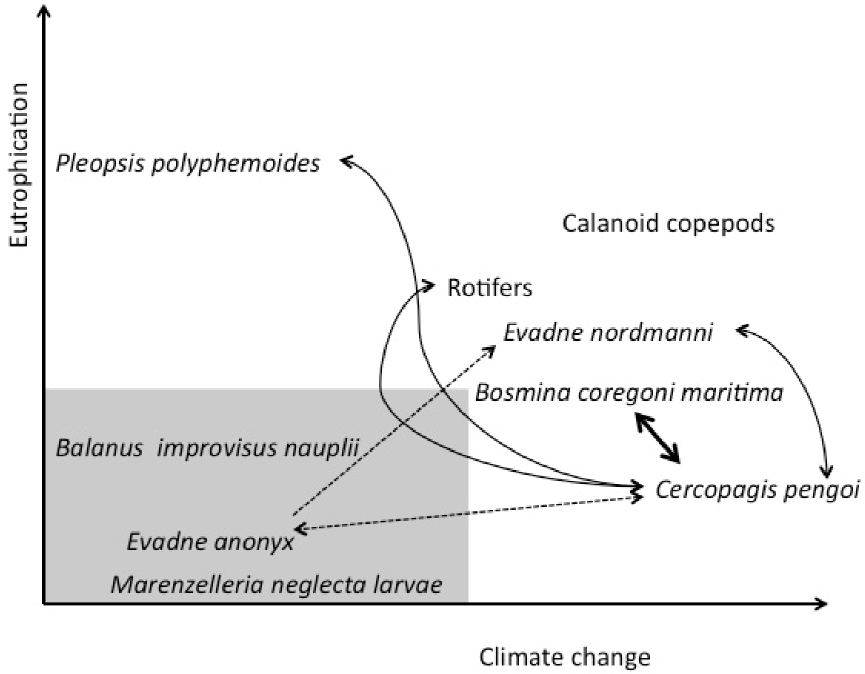

Figure 2. Relationship between eutrophication, climate change and zooplankton taxa in summer (based on Figure 7, **I**). The relationships between species within grey area are unknown or not statistically significant. The interactions between taxa marked as arrows are based on papers **III**, **IV** and **V**.

Until recently it was believed that coastal eutrophication is primarily controlled by the magnitude of anthropogenic nutrient loading. Recent evidence suggests, however, that climate variability also affects the nutrient fluxes to the coastal zone (*e.g*. Justić *et al*. 2005). My results also support the view that both eutrophication and climate variables describe a substantial amount of the variability in the models of mesozooplankton species. On the other hand, the interactive effect of eutrophication and climate variables on mesozooplankton was not significant, *i.e*. did not exceed their separate contribution (**I**). The significance of both eutrophication and climate variables for mesozooplankton was earlier demonstrated in the study area in paper **IV**.

No previous studies exist reporting clear evidence on the links between eutrophication variables and zooplankton communities in the Baltic and North Sea areas (*e.g*. Colijn *et al*. 2002). There is some indication that the density of adult *Temora longicornis* increases with the eutrophication level (Fransz *et al*. 1992). In the freshwater ecosystems, however, the nutrient loading is known to raise the biomass of zooplankton and change the species composition of zooplankton (Straile & Geller 1998; Ostoji 2000; Kangur *et al*. 2002). In that respect my result on the significant interactions between eutrophication variables and zooplankton communities in the brackish Gulf of Finland should be treated as exceptional. It is important to stress here that differently from many studies in the marine environment my study does not report just zooplankton total biomass but takes into account the relative proportion of different species in the community. Total biomass is a surrogate of different responses of species involved and it need not capture the links between eutrophication variables and individual zooplankton species (**I**).

Earlier studies have clearly demonstrated the existence of links between climate variables and zooplankton communities in the Baltic Sea area (Hinrichsen *et al*. 2007). Earlier studies have also established the functional relationships between temperature, salinity, species composition and biomass of zooplankton (Ojaveer *et al.* 1998; Vuorinen *et al.* 1998; Möllmann *et al.* 2000). Climate change may also cause replacement of key species (Southward *et al.* 1995) and other major shifts in the community structure (Greve *et al.* 1996; Conners *et al*. 2002; Hays *et al.* 2005; Mackas & Beaugrand 2010). The strong link between climate variables and mesozooplankton taxa may refer to their salinity tolerance. Most invertebrate species of marine origin live near their distribution limit in the northern Baltic Sea. Therefore reduction in salinity (associated to recent mild winters) has large consequences to these species.

Piontkovski *et al.* (2006) demonstrated that the zooplankton community responds to large-scale climatic pressure with a time lag of up to several years. Comparing the correlations they found that the time lag depends more upon the dimensions and geomorphology of the basin than on the distance from the atmospheric pressure systems. The pelagic community responds quicker to climate change in small basins than in large basins. According to the hydrodynamic model by Andrejev *et al.* (2004), the south-eastern parts of the Gulf of Finland have the longest residence time and south-western parts have the shortest residence times of the gulf. As I observed significant relationships between environmental variability and zooplankton communities mainly at gulf and partly at local scales, my observed patterns on the spatial differences in the biomasses of zooplankton likely reflect the east–west gradient in the water circulation patterns of the gulf. This was demonstrated by pooling all biomasses of pelagic invertebrates into same ordination space with data being scattered along the east-west gradients of the Gulf of Finland. ANOSIM analysis confirmed the trend and showed that most water bodies could be distinguished from each other in terms of the biomasses (**I**).

Analyses of temporal dynamics of the abundance and biomass of alien species representing different trophic levels and ecological functions in the Tallinn Bay (Gulf of Finland) and the Pärnu Bay (Gulf of Riga) provided two major results. Firstly, no abrupt population decreases amongst the studied alien species were detected, but some species significantly increased their abundances and biomasses during the course of the study. Secondly, the timing of such shifts in the abundance and biomass of the alien population was clearly species-specific. Other recent studies have evidenced pronounced changes (including regime shifts) in several sub-systems of the Baltic Sea and also elsewhere and timing of these events matched across the ecosystems, especially in the North Atlantic (Diekmann & Möllmann 2010 and references therein). In contrast, the study clearly demonstrated that large shifts in environmental parameters had no uniform consequences to the alien biota in the coastal areas of the Baltic Sea. Instead, these effects were species-specific and due to significant interactions of large-scale environmental variables with the local environment, the inter-annual dynamics of alien species also varied among the studied bays. This supports an earlier view that alterations in the structure of ecosystems are likely driven by changes between the complex interrelationships of environmental forcing and ecosystem elements (Hughes 2000; Stenseth *et al.* 2002). Seemingly, large-scale environmental variables and local forcing (*e.g.*, nutrient loading, biotic interactions) interfere with the communities at similar intensities, show strong interactive effects (Kotta *et al.* 2009) and occur over different spatial and temporal scales (Wu *et al.* 2000; Hewitt & Thrush 2009). The consistency of effects of environmental shifts very likely depends on the degree of the small-scale heterogeneity of communities (**VI**).

The study clearly demonstrated abrupt increases in the range and density of the populations of the existing alien species in the Baltic Sea in recent decades. Such shifts may be attributed to milder winters and warmer summers in the region (virtually all invertebrate models included temperature). This supports the current view that recent accelerated warming of high-latitude environments has increased the chances of species transported from lower latitudes to be able to establish and spread (Stachowicz *et al.* 2002). Recent observations elsewhere indicate that not only changed climate conditions but also local hydrodynamics might have important consequences on the population abundance of alien invertebrates that have been present in the invaded system for more than 50 years (Rigal *et al.* 2010; Witte *et al.* 2010). In addition to generic temperature effects, all models of benthic alien invertebrates included the salinity term. In the Baltic Sea area, milder winters are known to be associated with stronger freshwater inflows from rivers, which directly affect coastal salinities. This all suggests large difficulties in predicting the interplay between environmental setting, spread of invasive species and the potential for large-scale synergisms of these processes in the Baltic Sea area (**VI**).

To conclude, my study demonstrated that eutrophication and climate variables largely explained the observed patterns in pelagic invertebrate communities. Knowledge on the correlation scales between environmental and biotic patterns can provide an insight into how processes generate these patterns. The prevalence of the key processes, however, is further complicated to an unknown extent by regional-scale variability. Together with the increasing research into relationships between eutrophication, climate variables and biotic patterns at multiple spatial scales and in different regions, metaanalyses (*e.g.* Gurevitch *et al.* 2001) can tackle this problem.

3.2. Population dynamics and ecological impacts of alien species

Marenzelleria neglecta, *Cercopagis pengoi* and *Evadne anonyx* are among recent newcomers in the Baltic Sea (Bick & Zettler 1997; Ojaveer & Lumberg 1995; Rodionova & Panov 2006) whereas the invasion of *Balanus improvisus* dates back to the late 19th century (Välikangas 1926; Lindquist 1959). *Balanus improvisus* and *Marenzelleria neglecta* originate from North America, *Cercopagis pengoi* and *Evadne anonyx* from Ponto-Caspian area. The transfer of ballast water between international ports is suggested as a potential vector of these invasions (Leppäkoski & Olenin 2001).

Prior to the invasion of *Balanus improvisus* there was no benthic suspension feeding mode in the northern Baltic Sea where salinity is below 5 psu and the climate is too cold for another non-indigenous suspension feeder *Dreissena polymorpha* (Pallas) (Leppäkoski & Olenin 2001). Thus, the invasion of *Balanus improvisus* potentially increased the energy flows from the pelagic system to benthos and caused a shift from pelagic production to benthic production.

Cercopagis pengoi and larvae of *Marenzelleria neglecta* appeared in plankton samples in 1991 and *Marenzelleria neglecta* appeared in benthos in 1995 (except for occasional findings in the northern Gulf of Riga in 1991 and 1993). *Marenzelleria neglecta* is ranked among the most influential benthic exotics in the Gulf of Riga (Kotta *et al.* 2000). Field experiments (Kotta *et al.* 2001; Kotta and Ólafsson 2003; Kotta *et al.* 2004a) have indicated that *Marenzelleria neglecta* reduces the growth and survival of the native polychaete *Hediste diversicolor* and the growth of the amphipod *Monoporeia affinis*. Adult specimens of the bivalve *Macoma balthica* have a negative effect on the *Marenzelleria* population. Competitive interactions between *Marenzelleria neglecta* and the native fauna may explain why polychaete densities are low when the densities of *Macoma balthica* are high, and why *Monoporeia affinis* has not recovered in areas with a high density of *Marenzelleria neglecta*. Higher sediment chlorophyll *a* content in the presence of *Marenzelleria neglecta* indicates higher biodeposition and/or bioturbating activity of the polychaete as compared to the native fauna. According to Pelegri and Blackburn (1995), polychaetes significantly accelerate nitrogen remineralisation and transformation processes within the sediment. As *Marenzelleria neglecta* burrows much deeper and more actively than the native polychaetes, the amount of reworked sediments, i.e. the availability of nutrients to microalgal growth, is higher in the presence of *Marenzelleria neglecta*. According to these experiments, *Marenzelleria neglecta* should prevail only in such biotopes where it can avoid competitive interactions with *Macoma balthica*. Such areas appear to be adjacent to river mouths, where the food for deposit-feeders is in excess and bivalves are stressed by low salinity, but quite likely also in deeps where the amphipods *Monoporeia affinis* and *Pontoporeia femorata* prey on the bivalve spat. Because *Macoma balthica* is one of the most common species in the soft bottom sediments in the Estonian coastal range, competitive interactions between

Marenzelleria neglecta and *Macoma balthica* appear to be a key factor in keeping the densities of *Marenzelleria neglecta* low in the study area. The pelagic larvae of *Marenzelleria neglecta* have remarkably changed also the zooplankton community in some regions. The share of the *Marenzelleria neglecta* larvae can exceed 90% of the total zooplankton abundance in Pärnu Bay in autumn (Simm *et al*. 2003). The dominance of *Marenzelleria larvae* has never been so evident in more saline waters of the Gulf of Finland. The diversity of other zooplankton groups is higher there and because the larvae of other polychaete species are also present there, *Marenzelleria* has not been counted separately in analysing zooplankton samples (**VI**).

During all my studies *Balanus improvisus* occurred in plankton at high densities along the whole Estonian coastal sea. Since invasion the density of *Cercopagis pengoi* gradually increased until 2002 and then dropped to the level of the early 1990s (**II**) and later increased again (**VI**). The abundance of pelagic larvae of *Marenzelleria neglecta* in Pärnu Bay peaked in 2006 and 2007 (**VI**).

Temperature at the bottom had the best match with the abundance of *Balanus improvisus* larvae (BIOENV). Other variables predicted less than 5% of the variability. The studied abiotic environmental variables (temperature, salinity, nutrient load, ice conditions) did not explain the interannual variability in the seasonal cycles of *Marenzelleria neglecta* and *Cercopagis pengoi* (**II**). More recent analyses performed with longer time series showed significant relationships between the abundance of *Cercopagis pengoi* and a number of several climatic variables in the Gulf of Finland (**I**) and in Pärnu Bay (**VI**). Similarly, the abundance of *Balanus improvisus larvae* was related with chlorophyll *a* in Pärnu Bay and with climatic variables in Tallinn Bay (**VI**).

Cercopagis pengoi and *Bosmina coregoni maritima* tend to share the same habitat in the Gulf of Finland. There were only two samples where the abundance of *Bosmina coregoni maritima* exceeded 1000 ind m^{-3} and *Cercopagis pengoi* was not present. The average abundance of *Bosmina coregoni maritima* in the samples with *Cercopagis pengoi* was 6600 ind m^{-3}. The effect of predatory *Cercopagis pengoi* on the potential prey species *Bosmina coregoni maritima* was estimated by the Spearman correlation product between the abundance of *Cercopagis pengoi* and the percentage of *Bosmina coregoni maritima* above the thermocline. The results revealed that at higher abundances of *Cercopagis pengoi* above the thermocline, the cladoceran *Bosmina coregoni maritima* stayed below the thermocline (**III**).

BIOENV analyses were performed to seek the best combination of environmental variables determining the distribution of *Bosmina coregoni maritima* and *Cercopagis pengoi*. Almost all combinations of zooplankton species with high correlation to *Bosmina coregoni maritima* contained nauplii of *Balanus improvisus* and *Keratella cochlearis*. *Cercopagis pengoi* was often included too. BIOENV including environmental parameters and abundance of *Cercopagis pengoi* only, pointed most frequently to *Cercopagis pengoi* as the prime factor determining the distribution of *Bosmina coregoni maritima* (**III**). On the other hand, the abundance of *Cercopagis pengoi* was best explained by thermal stratification and the densities of selected cladocerans (*Evadne nordmanni* and *Pleopsis polyphemoides*) (Figure 2). The abundance of the native predatory cladoceran *Leptodora kindtii* was correlated with chlorophyll *a*, temperature, salinity and the density of various zooplankton taxa (**IV**).

It is unlikely that the nauplii of *Balanus improvisus* or *Keratella cochlearis* have some direct impact on the vertical distribution of *Bosmina coregoni maritima*. There are probably some other environmental factors that influence all three species in the same way. The predatory *Cercopagis pengoi* may, on the other hand, be one of the main factor causing changes in the vertical distribution of *Bosmina coregoni maritima*. No diurnal vertical migration of *Cercopagis pengoi* has been recorded in the Baltic Sea area and the majority of the population are located in the upper water layer (Gorokhova *et al.* 2000). Hence, the deeper water layers may be considered as a refuge for prey species such as *Bosmina coregoni maritima* (**III**).

In addition to the changed vertical distribution, the annual density of *Bosmina coregoni maritima* and other less abundant cladocerans such as *Evadne nordmanni* and *Pleopsis polyphemoides* significantly declined after the invasion of *Cercopagis pengoi* compared to the pre-invasion period (Figure 3). Previous studies from other basins show that the introduction of *Cercopagis pengoi* has in many cases led to significant changes in the composition and abundance of zooplankton in recipient ecosystems (Kotta *et al.* 2004b; Ojaveer *et al.* 2004). *Cercopagis pengoi* is a voracious predator, which feeds on smaller cladocerans and copepod nauplii (Gorokhova *et al.* 2005; Warner *et al.* 2006). Relying on data available for papers **III** and **IV**, it is impossible to say whether the average abundance of *Bosmina coregoni maritima* has decreased after the invasion of *Cercopagis pengoi* in the Gulf of Finland as it happened in the Gulf of Riga (Kotta *et al.* 2004b; Ojaveer *et al.* 2004). Current data show no significant decline of *Bosmina coregoni maritima* in the Gulf of Finland. Temperature stratification and the density of cladocerans seem to be the most important environmental variables explaining the distribution of *Cercopagis pengoi* in the Gulf of Finland and as indicated in this study, densities of the alien species are high enough to have an impact on the distribution of its potential prey *Bosmina coregoni maritima*. The population of the cladoceran *Bosmina coregoni maritima* has collapsed in the whole north-eastern Baltic Sea including those subareas where the density of *Cercopagis pengoi* was low. My results suggest that the invasion of *Cercopagis pengoi* is at least partly behind this decline.

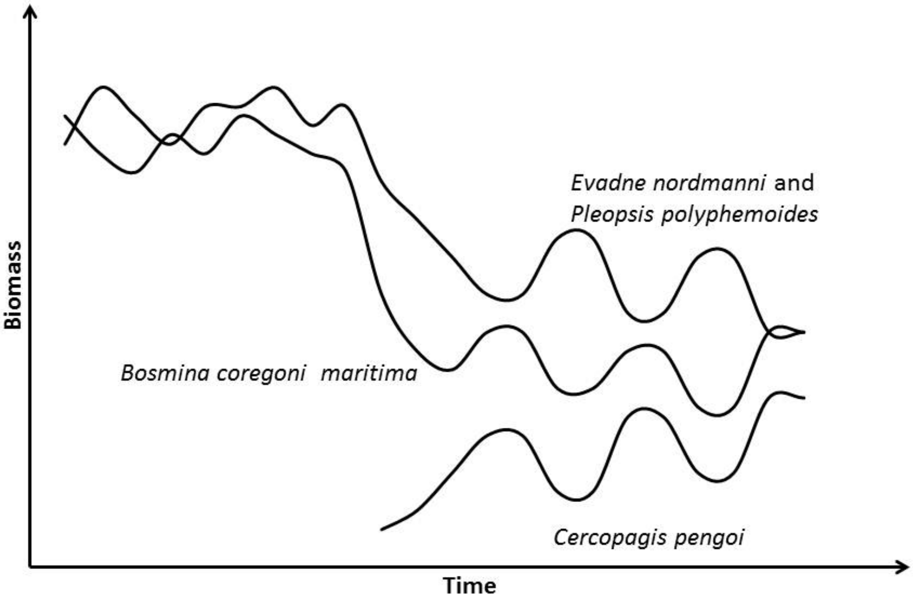

Figure 3. Schematic dynamics of native cladocerans after the invasion of *Cercopagis pengoi* (for correlation coeficents see **IV**).

My results indicate that both intermediate predators and bottom-up effects affect the zooplankton communities to an equal extent and that predation by the non-indigenous *Cercopagis pengoi* may significantly modify the dynamics of Cladocera and Rotatoria in the Gulf of Finland during the summer season. According to the BIOENV analysis, the predatory cladocerans *Cercopagis pengoi* and *Leptodora kindtii* were included in the models of different mesozooplankton taxa on 57% of occasions, whereas the eutrophication level accounted for 50% of the differences. *Cercopagis pengoi* was the only significant variable in the models of *Bosmina coregoni maritima* and *Keratella cochlearis* (Figure 2). Alternatively, the indirect effect of selective predation on other zooplankton taxa may favour the growth of the populations of these species and may explain their rising densities with the increase in *Cercopagis pengoi* (**IV**). However, when the analysis was performed separately for the layers above and below the thermocline, *Bosmina coregoni maritima* tended to remain below the thermocline at greater abundances of *Cercopagis pengoi* in the surface layer. These results suggest the direct predation of *Cercopagis pengoi* on *Bosmina coregoni maritima*. This all points to the need of manipulative experiments in order to detect the causative links between the dynamics of *Cercopagis pengoi* and the native zooplankton communities in recipient ecosystems. My studies indicate that experiments on the predation of *Cercopagis pengoi* on a mixture of zooplankton taxa such as *Bosmina*, *Evadne*, *Pleopsis*, *Keratella* and *Synchaeta* and the behavioural responses of the prey species to the presence of *Cercopagis pengoi* would be particularly rewarding in order to demonstrate the causative links between the dynamics of *Cercopagis pengoi* and other trophic levels in recipient ecosystems.

Thermal stratification was an important variable in the dynamics of *Cercopagis pengoi*: the density of this cladoceran increased with rising temperature stratification (i.e., with decreasing wind stress) (**IV**). Differences in thermal stratification may explain the large-scale variability in *Cercopagis pengoi* populations in the different basins of the Baltic Sea; for example, the southern coastal areas of the Gulf of Finland are hydrodynamically more active than its less exposed northern coasts or the Gulf of Riga. Also, the densities of *Cercopagis pengoi* were about 5–10 times higher in the Gulf of Riga and the less exposed areas of the Gulf of Finland than at our sampling sites (Uitto *et al.* 1999; Ojaveer *et al.* 2004; this thesis). Earlier studies stressed the importance of both temperature and water column stability for the development of *Cercopagis pengoi* in the Baltic Sea area (Avinski 1997; Uitto *et al.* 1999; Ojaveer *et al.* 2004). As the temperature range in our community analyses was very narrow (15–22 ºC), its effect was not significant for *Cercopagis pengoi*. However, when the data for all seasons were included, temperature did become statistically significant, reflecting the species' southerly origin (Leppäkoski & Olenin 2001).

It has been suggested in many papers that the level of eutrophication may explain to a significant extent the spatial differences in the population of *Cercopagis pengoi* (Uitto *et al.* 1999; Strake 2002). In those studies, however, the effect of eutrophication was not quantified. In my thesis, on the other hand, I clearly demonstrated that eutrophication had a minor (**I**) or no (**IV**) significant effect on *Cercopagis pengoi* within a broad range of spatial and temporal variability.

Taking into account the moderate densities of *Cercopagis pengoi*, we may assume that the effect of the species on the exposed ecosystems of the Gulf of Finland is low. Much higher impacts are predicted for the more sheltered easternmost and northern areas of the Gulf of Finland (Uitto *et al.* 1999; Telesh *et al.* 2001). Besides preying on zooplankton, the effects of the species include food competition with fish and probably the reduced efficiency of trophic transfer to upper levels (Antsulevich & Välipakka 2000; Kotta *et al.* 2004b).

The contribution of *Cercopagis pengoi* in the diet of fish was high when the cladoceran was present in the water column (June–September). Nine-spined stickleback started feeding on the cladoceran when it had attained a length of 3.4 cm, three-spined stickleback and herring at a length of 4.1 cm, bleak at a length of 6.2 cm and smelt at a length of 7.3 cm. However, *Cercopagis pengoi* was exceptionally found in the stomach of a herring larva of 2.2 cm (the length of the *Cercopagis pengoi* was 1.0 cm). The consumption of *Cercopagis pengoi* by herring was size-dependent. The share of *Cercopagis pengoi* in the diet of large herring (15–16 cm) reached over 10% by wet weight and exceeded by a factor of 2–3 that of smaller individuals. Significant size-specific differences were not observed for other fish (**II**).

Fish predation on *Cercopagis pengoi* was species-specific and size-dependent. When *Cercopagis pengoi* occurred in the plankton then its share in the diet of fish was noticeable. *Cercopagis pengoi* primarily contributed to the diet of small-sized fish inhabiting coastal areas, for example bleak and nine-spined stickleback, due to a strong overlap of their spatial distribution. The pelagic species herring, smelt, three-spined stickleback, which are abundant in open and deeper areas, consumed less *Cercopagis pengoi*. The consumption of *Cercopagis pengoi* by smelt enhances energy transfer from the surface waters to the cold deeper water layers. This is especially important during the periods of food shortage in deep water layers due to oxygen deficiency and mild winters, which do not favour the formation of abundant cold arctic invertebrate communities in this deep environment (**II**).

Earlier studies indicate that *Cercopagis pengoi* preys on the small cladocerans that are important food items for mysids and fish (Kotta *et al.* 2004b). On the other hand the introduced species is preyed by fish. Thus, the effects of *Cercopagis pengoi* on the pelagic ecosystem are two-sided: competing for food with other pelagic predators and reducing the efficiency of energy transfer to upper trophic levels (**II**).

One of the most recently reported invaders *Evadne anonyx* is morphologically very similar to the native *Evadne nordmanni*. Therefore the new species was not detected during the routine monitoring studies. The re-analysis of the mesozooplankton samples, however, showed that *Evadne anonyx* was first present in Tallinn Bay, in the central Gulf of Finland, already in 1999. In Narva and Pärnu bays, the first individuals were found in samples collected in 2000. Such a pattern suggests that the invasion took place most likely by ship ballast water to different ports almost simultaneously (**V**).

Following the invasion, about a 10-fold increase in the population abundance of *Evadne anonyx* was recorded in the Gulf of Finland in the years 2000–2004. Nevertheless, the abundance of *Evadne anonyx* was relatively low, exceeding 100 ind. m^{-3} only in a few cases. The species is present from late June to mid-September reaching maximum densities in July (Rodionova & Panov, 2006). According to my data, the alien *Evadne anonyx* showed an approximately one order of magnitude increase in abundance in Pärnu Bay until 2006 with its maximum abundance exceeding 120 ind. m^{-3}. In Tallinn and Narva bays, the mean abundance is still below 100 ind. m^{-3}. Despite the recent increase, the abundance of *Evadne anonyx* represents currently only about one-tenth of that of the native *Evadne anonyx* (**V**).

The newcomer *Evadne anonyx* is constantly present in the Baltic mesozooplankton community from July, although one individual was found in late May. The native *Evadne nordmanni* appears in May. *Evadne nordmanni* basically disappears from the plankton at the beginning of August (at a water temperature of 19°C and salinity of 5 psu) while only two individuals were found in late autumn. At the same time, however, the alien *Evadne anonyx* is present until October. In Pärnu Bay, the maximum abundance of *Evadne anonyx* occurs later in the season (in August) than that of *Evadne nordmanni* (in

June). However, in the Gulf of Finland, the abundance of both species reached a peak at the same time, in late June or early July (**V**).

Evadne anonyx occurs constantly in the plankton community when the water temperature exceeds 15°C and salinity 5 psu. Maximum abundances of its population were recorded when the water temperature was 19°C and salinity 5.4 psu (**V**). However, Rodionova and Panov (2006) found maximum abundances of *Evadne anonyx* in the eastern Gulf of Finland at somewhat lower temperatures of 17–18 °C. In its native environment (Caspian Sea), *Evadne anonyx* is present at maximum abundances when the water temperature is 16–20°C and salinity 12–13 psu (Mordukhai-Boltovskoi & Rivier 1987; Rivier 1998). In contrast to my observations that *Evadne anonyx* disappeared from zooplankton samples when the water temperatures below 15°C, Rodionova and Panov (2006) reported finding the species even at temperatures below 12°C.

With respect to the salinity tolerance limits, it is important to mention that before it invaded the Baltic Sea, *Evadne anonyx* was not considered as a high-risk species for low-salinity environments because it was thought to be unable to survive at salinities below 9 psu (Rivier 1998; Panov et al. 1999). However, the results of the current thesis confirm that the species was able to establish itself and is doing relatively well in the low-salinity (around 5 psu) environment (**V**).

For both *Evadne* species, parthenogenetic females dominated the population for most of the season. A decrease in their abundance in late September coincided with the increasing abundance of males and gamogenetic females. Males and gamogenetic females of the alien *Evadne anonyx* appeared in the zooplankton community during the population abundance peak, at the beginning of August at water temperature of 19°C and salinity of 5 psu. The maximum abundance of *Evadne anonyx* males and females with resting eggs was recorded in late September to early October, reaching up to 22% of the total population. Males and gamogenetic females of the native *Evadne nordmanni* appeared after the first peak of population abundance, in mid-June at water temperature of 18°C and salinity of 4 psu, and accounted for up to about 14% of the total population at the beginning of July (**V**).

Gamogenetic females of *Evadne nordmanni* had only a single resting egg in the brood pouch. *Evadne anonyx* had 1.2 ± 0.1 resting eggs on average. For both species, bisexual reproduction becomes most important when parthenogenetic fecundity reaches its minimum. With the onset of sexual reproduction, the population decreases significantly until complete disappearance from the plankton. The parthenogenetic fecundity of *Evadne anonyx* was significantly higher than that of *Evadne nordmanni*: 4.7 vs. 4.0, respectively (**V**).

For both species, the parthenogenetic fecundity was found to be the highest when the species first appeared into the plankton: in July for *Evadne anonyx* and in May for *Evadne nordmanni*. From August to September, the fecundity of *Evadne anonyx* started to decrease with the lowest value in September. The fecundity of *Evadne nordmanni* reached its minimum in July and then increased again in August. Only a few parthenogenetic females of *Evadne nordmanni* were found in September. The parthenogenetic fecundity of *Evadne anonyx* correlated positively with water temperature, but there was no significant correlation with salinity. However, the parthenogenetic fecundity of *Evadne nordmanni* was negatively correlated with both temperature and salinity (**V**).

Although having still low densities, the recent newcomer cladoceran *Evadne anonyx* will most likely further increase in abundance and colonize new areas in the Baltic Sea. Higher reproductive potential of the species may result in a situation where its abundance exceeds that of the native *Evadne nordmanni* (Figure 2). *Evadne anonyx* may become an important food resource of several zooplanktivorous fishes in the region. At the same time, *Evadne anonyx* may also become prey of the predatory cladoceran *Cercopagis pengoi*, which seems to prefer small-sized cladocerans (*Bosmina coregoni maritima*) to all available other prey (Ojaveer et al 2004; Lehtiniemi & Lindén 2006). The fact that *Evadne anonyx* is performing well in the low-salinity environment in the north-eastern Baltic Sea suggests that our knowledge on the tolerance limits of even essential abiotic parameters of marine zooplankton is not sufficient for making predictions of potential new invaders. Finally, due to the continuously accumulating evidence of new invasions worldwide, the current study also points to the need for, and importance of, proper storage of all collected biological samples, to be able, if required, to track the spread and abundance of alien species over previous decades. Further studies should also quantify the changes in the energy flow through the food web as a result of alien species and assess the realised potential of competition between alien invertebrates and native species for the same food and habitat resource.

To conclude, the studied alien species are potentially able to affect biodiversity and modify organic matter and energy transfer pathways compared to the pre-invasion time. The impacts of alien species have large spatial variability. The studies indicated that mesozooplankton communities were more influenced by alien species in shallow areas of Pärnu Bay than in more saline and deeper stations of Tallinn Bay. The effects of environmental factors modulating the role of alien species appeared to be species and area specific, with no clearly identifiable key environmental factors responsible for the population dynamics of all alien species. However, temperature seems to be a common significant forcing factor for the population dynamics of most of the species. Both recently introduced and historically established alien species displayed one or more abrupt increases in abundance and/or biomass during the past two decades. The timing of these shifts was independent of that in the abiotic environment and pointed to the importance of biotic interactions in modifying local communities as a result of bioinvasions. Compared to the native species, the alien species tended to exhibit less diverse annual-scale variability patterns and acted, therefore, as a stable and important structural and functional compartment of the invaded ecosystems.

4. CONCLUSIONS

In my studies I was able to track the annual-scale performance of populations of several alien and native species, representing different trophic levels and ecological functions, over a decade and a half and to identify the environmental factors responsible for the observed variability. My study demonstrated that eutrophication and climate variables largely explained the observed patterns in zooplankton communities and often species were affected by environmental variability at all spatial scales. Both eutrophication and climate variables describe a substantial amount of the variability in the models of mesozooplankton species. On the other hand, the interactive effect of eutrophication and climate variables on mesozooplankton was not significant, that is did not exceed their separate contribution.

My study clearly demonstrated abrupt increases in the density of the populations of the existing alien species in the Baltic Sea in recent decades. The timing of such shifts in the abundance and biomass of the alien population was clearly area and species-specific. Such shifts may be attributed to milder winters and warmer summers in the region since virtually all invertebrate models included temperature. The abundance of *Cercopagis pengoi* was best explained by climate variables and the densities of selected cladocerans while eutrophication had no significant effect on it within a broad range of spatial and temporal variability. The effect of predatory *Cercopagis pengoi* on the potential prey species *Bosmina coregoni maritima* was revealed as changed vertical distribution of the pray species by the presence of the predator. Although it still has low densities and invisible impact to zooplankton community, *Evadne anonyx* will most likely further increase in abundance and colonize new areas in the Baltic Sea. Its higher reproductive potential compared to the native *Evadne nordmanni* may result in a situation where the invader's abundance exceeds that of the native species. The studied alien species on the whole are potentially able to affect biodiversity and modify organic matter and energy transfer pathways compared to the pre-invasion time.

SUMMARY IN ESTONIAN

Kohalike ja invasiivsete zooplanktoni liikide ajalis-ruumiline varieeruvus muutuvates kliima- ja eutrofeerumistingimustes.

Eutrofeerumist ja kliimamuutusi peetakse kaheks väga oluliseks teguriks, mis võivad tõsiselt ohustada rannikumere koosluste stabiilsust. Eutrofeerumine võib põhjustada vetikaõitsenguid ning orgaanilise aine akumuleerumist, mis omakorda võib viia hapnikupuuduse tekkimiseni ning põhjustada sellega ökosüsteemis pöördumatuid muutusi. Klimaatiliste tingimuste varieeruvuse tagajärjed rannikumere ökosüsteemile on vähem selged ja ka vähem uuritud. Mõjude selgitamine on raskendatud eelkõige bioloogiliste ja klimaatiliste muutuste mastaapide erinevusest geograafiliste skaalade erinevuse tõttu. Kliimamuutused avalduvad kohalikul skaalal eelkõige lokaalsete ilmastikunähtuste ja nende omavaheliste seoste kaudu. Samas on teada, et kliimamuutuste ökoloogiline mõju avaldub liikide leviku ja arvukuse muutuste, aga ka liigilise mitmekesisuse muutumise kaudu.

Pole olemas ühte kindlat ruumiskaalat, millel eutrofeerumise ja kliimamuutuste mõju elusloodusele uurida. Üheaegselt mõjutavad ökosüsteemi nii suureskaalalised protsessid kui ka kohalikul tasandil toimunud muutused. Uuringud erinevatel skaaladel toimivate tegurite omavahelistest vastas- ja koosmõjust erinevatele liikidele, kuid ka näiteks erinevates veekogudes, on veel üsna puudulikud.

Nii inimese poolt põhjustatud kui ka looduslikud keskkonnamuutused muudavad ökosüsteemi tihti vastuvõtlikumaks uute liikide sissetungiks. Uute invasioonide tõenäosust on pidevalt suurendatud uute sisserändeteede ja viiside loomisega inimese poolt. Iga uus liik, mis suudab oma uue keskkonnaga kohaneda, võib aga omakorda muuta ökosüsteemi mitmekesisust, stabiilsust ja toimimist. Võõrliikide invasioon on viimastel aastakümnetel muutunud üheks tõsisemaks veeökosüsteeme ohustavaks probleemiks. Eriti muret tekitav on see Läänemere taolistes madala liigilise mitmekesisusega süsteemis. Riimveelisus ja väga tihe laevaliiklus muudavad Läänemere samal ajal just ballastvetega rändavate liikide jaoks eriti tõenäoliseks sishtkohaks. Üle 70 võõrliigi rohkem kui 100-st sissetulnust on Läänemeres püsivalt elama jäänud ja väga mitmed neist on põhjustanud siinses ökosüsteemis ka üsna olulisi muutusi.

Oma töös hindasin ma, kuidas erinevatel ruumiskaaladel toimivad troofsuse- ja kliimamuutujad mõjutavad Soome lahe zooplanktoni biomassi, seda nii kohalike kui võõrliikide puhul. Samuti kirjeldasin ma nelja Läänemerre elama asunud võõrliigi (pelaagilisi vastsestaadiumeid omava tõruvähi *Balanus improvisus* ja hulkharjasussi *Marenzelleria neglecta* ning vesikirbu *Cercopagis pengoi* ja *Evadne anonyx*) populatsioonide dünaamikat ja ökoloogilist mõju Eesti vetes. Esimene neist liikidest on Läänemerre tulnud juba 19. sajandil, ülejäänud kolm aga viimase paarikümne aasta jooksul. Tõruvähk ja hulkharjasuss on pärit Põhja-Ameerikast, vesikirbud Ponto-Kaspia basseinist. Käesoleva töö täpsemaks eesmärgiks on vastata järgmistele küsimustele: 1) kuidas eri skaalades biogeenide lisandumine ja klimaatilised tingimused mõjutavad zooplanktoni, sealhulhgas ka nimetatud võõrliikide biomassi, 2) kas ja kuidas vesikirpude *Cercopagis pengoi* ja *Evadne anonyx* invasioon on mõjutanud zooplanktoni kooslust ja 3) kas *Cercopagis pengoi* on mõjutanud oma potensiaalse saaklooma *Bosmina coregoni maritima* levikut.

Töös kasutatud zooplanktoni andmed on suuremas osas kogutud riikliku keskkonaseire raames Soome lahest, proovide kogumise tihedus on olnud suurim Tallinna ja Narva piirkonnas. Lisaks Soome lahe jaamadele on osa andmeid pärit ka Pärnu lahest. Paljud keskkonnaandmed on mõõdetud zooplanktoni proovide kogumise ajal, kuid erinevates ruumiskaalades mõjuvate tegurite analüüsil on lisaks TÜ Eesti Mereinstituudi ja Eesti Meteoroloogia ja Hüdroloogia Instituudi poolt kogutud andmetele kasutatud ka rahvusvahelisi andmebaase.

Zooplanktoni koosluse dünaamika oli mõjutatud nii klimaatiliste tingimuste kui ka eutrofeerumise teguritest ja seda kõikidel uuritud ruumiskaaladel (**I**). Enamike liikide puhul olid kõige vähem mõjuvateks, kuid siiski olulisteks teguriteks just väikseima ehk lokaalse skaala keskkonnatingimused. Samas ei olnud kliima ja eutrofeerumise muutujate koosmõju zooplanktoni liikidele oluliselt suurem kui nende mõju eraldi võetuna (**I**). Käsitletud võõrliikide pikaajalised vaatlused näitavad, et nende biomass on viimastel aastatel näidanud tõusutrendi, eriti võib seda öelda hulkharjasussi *Marenzelleria neglecta* vastsete ja vesikirbu *Cercopagis pengoi* kohta (**V,VI**). Võõrliigi *Cercopagis pengoi* tihedus oli korrelatsioonis nii klimaatiliste tingimustega kui ka näiteks teiste vesikirpude liikidega, kuid olulist seost eutrofeerumisega selle liigi puhul ei leitud (**II, III**). Röövtoidulise *Cercopagis pengoi* mõju oma potensiaalsele saakloomale avaldus peamiselt saaklooma populatsiooni paiknemisena sügavamates veekihtides nendes jaamades, kus röövloom esines suure arvukusega (**III, V**). Värskeima võõrliigi *Evadne anonyx* arvukus on seni jäänud madalaks, kuid arvestades selle liigi suuremat viljakust võrreldes sama perekonna kohaliku esindajaga, võib ta peagi hakata esinema palju kõrgema arvukusega kui *Evadne nordmanni* (**IV**).

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PUBLICATIONS

CURRICULUM VITAE

General

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Date and place of birth: 17.07.1972, Kohtla-Järve
Address: Mäealuse 14, 12618, Tallinn, Estonia
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Position: Estonian Marine Institute, University of Tartu, researcher

Educational History

1998	M.Sc. Hydrobiology, University of Tartu
1995	B.Sc. Hydrobiology, University of Tartu
1990	Toila High School

Languages spoken: Estonian, English, Finnish, Russian, German

Professional employment

2005–...	University of Tartu, Faculty of Science and Technology, Estonian Marine Institute, University of Tartu; Researcher
2001–2006	Tallinn University, Lecturer
2001–2005	Estonian Marine Institute, University of Tartu, Researcher
1996–2000	Estonian Marine Institute, assistant
1995–1996	Estonian Marine Institute, junior researcher
1995–1995	Limnological Station of LakeVõrtsjärv, Institute of Zoology and Botany, lab assistant

Administrative responsibilities

2007–...	Member of ICES/HELCOM WGIAB (Working Group on Integrated Assessment of the Baltic Sea)
2006–2009	member of ICES SGRPOD (Study Group on Baltic Sea Productivity Issues in support of the BSRP)
2005–...	member of ICES WGZE (Working group of Zooplankton Ecology)
2005–...	member of HELCOM MONAS Zooplankton Expert Network

Research History

Research interests:
1. Long-term changes of mesozooplankton in Gulf of Finland and planktonic invasive species in the Baltic Sea, 2. Hasardous substances in the Baltic Sea

Current projects:
1. Interactive effect of small and large scale environmental variability on ecosystem functioning in the Baltic Sea
2. Patterns in productivity and community regulation in marine ecosystems in relation to mesoscale environmental variability
3. Control of hazardous substances in the Baltic Sea region

Supervised master thesises

Karin Lassmann, 2011, (sup) Arno Põllumäe, Mesozooplanktoni pikaajaline muutlikkus Kolga lahes, Tallinn University, Institute of Mathematics and Natural Sciences.

Lennart Lennuk, 2010, (sup) Arno Põllumäe, Invasiivse kammlooma Mertensia ovum arvukus ja levik Eesti merevees, Tallinn University, Institute of Mathematics and Natural Sciences.

Greta Reisalu, 2009, (sup) Arno Põllumäe, Toomas Saat, Mesozooplanktoni biomassi määramine: setteruumala ja individuaalse massi meetodi võrdlus, University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Tartu University, Chair of Hydrobiology.

Katrin Väljataga, 2004, (sup) Arno Põllumäe, Röövtoidulise vesikirbulise Cercopagis pengoi arvukus Soome lahe Eesti rannikuvetes ja selle mõju Bosmina coregoni maritima (Cladocera) arvukuse sesoonsele dünaamikale ja vertikaalsele jaotumusele, Tallinn University, Institute of Mathematics and Natural Sciences.

Publications

Ojaveer, H.; Kotta, J.; Põllumäe, A.; Põllupüü, M.; Jaanus, A.; Vetemaa, M. (2011). Alien species in a brackish water temperate ecosystem: annual-scale dynamics in response to environmental variability. Environmental Research, xx–xx. [in press]

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Keelteoskus: Eesti, inglise, soome, vene, saksa

Teenistuskäik

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2005–...	ICES WGZE (Rahvusvahelise Meruuringute Nõukogu Zooplanktoni ökoloogia töögrupp) liige
2005–...	HELCOM MONAS Zooplankton Expert Network liige

Teadustegevus

Teadustöö põhisuunad:
1. Mesozooplanktoni pikaajalised muutused Soome lahes ja planktilised võõrliigid Läänemeres, 2. Ohtlikud ained Läänemeres

Jooksvad projektid:

1. Keskkonna väikse- ja suuremastaapse muutlikkuse interaktiivne mõju Läänemere ökosüsteemi protsessidele
2. Skaalaspetsiifilise keskkonnamuutlikkuse tähendus mere ökosüsteemidele
3. Ohtlike ainete kontroll Läänemere piirkonnas

Juhendatud magistritööd

Karin Lassmann, magistrrikraad, 2011, (juh) Arno Põllumäe, Mesozooplanktoni pikaajaline muutlikkus Kolga lahes, Tallinna Ülikool, Matemaatika ja Loodusteaduste Instituut, Loodusteaduste osakond, Bioloogia õppetool.

Lennart Lennuk, magistrikraad, 2010, (juh) Arno Põllumäe, Invasiivse kammlooma Mertensia ovum arvukus ja levik Eesti merevees, Tallinna Ülikool, Matemaatika ja Loodusteaduste Instituut, Loodusteaduste osakond, Bioloogia õppetool.

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Põllumäe, A.; Kotta, I.; Kotta, J. (2006). Port biological sampling as a tool for monitoring invasive species in high-risk areas of bioinvasions. Ojaveer, H., Kotta, J. (Toim.). Alien invasive species in the north-eastern Baltic Sea: population dynamics and assessment of ecological impacts (40–46). Tallinn: Eesti Mereinstituut

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Nõges, T.; Kisand, V.; Nõges, P.; Põllumäe, A.; Tuvikene, L.; Zingel, P. (1998). Plankton seasonal dynamics and its controlling factors in shallow polymictic eutrophic lake Vortsjarv, Estonia. International Review of Hydrobiology, 83(4), 279–296.

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Haberman, J.; Põllumäe, A. (1998). Võrtsjärves domineerivad zooplankterid. Eesti LUS aastaraamat (126–154). Tallinn: Eesti Teaduste Akadeemia

Nõges, T.; Nõges, P.; Kisand, A.; Kisand, V.; Tuvikene, L.; Zingel, P.; Põllumäe, A.; Haberman, J. (1998). Ecological studies. T. Huttula & T. Nõges (Toim.). The Finnish Environment (79–135). Suomen Ympäristökeskus

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