DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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MARIA PÕLLUPÜÜ

Ecological relations of cladocerans in a brackish-water ecosystem

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Estonian Marine Institute and Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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Supervisors: Ph. D. Mart Simm, University of Tartu, Estonia
Ph. D. Henn Ojaveer, University of Tartu, Estonia

Opponent: D.Sc. Irena V. Telesh, Zoological Institute of the Russian Academy of Sciences, Russia

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LIST OF ORIGINAL PUBLICATIONS

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

I. 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.

II. Põllupüü, M., Simm, M. & Ojaveer, H. 2010. Life history and population dynamics of the marine cladoceran *Pleopis polyphemoides* (Leuckart) (Cladocera, Crustacea) in a shallow temperate Pärnu Bay (Baltic Sea). *Journal of Plankton Research*, doi:10.1093/plankt/fbq063.

III. Kotta, J., Kotta, I., Simm, M. & Põllupüü, M. 2009. Separate and interactive effects of eutrophication and climate variables on the ecosystem elements of the Gulf of Riga. *Estuarine, Coastal and Shelf Science,* 84, 509–518.

IV. Põllupüü, M., Möllmann, C., Simm, M., Diekmann, R. & Ojaveer, H. Seasonal and long-term dynamics of cladocerans in the Gulf of Riga (Baltic Sea): signals from climate and bioinvasions. Manuscript.

V. Lankov, A., Ojaveer, H., Simm, M., Põllupüü, M. & Möllmann, C. 2010. Feeding ecology of pelagic fish species in the Gulf of Riga (Baltic Sea): the importance of changes in the zooplankton community. Submitted.

Author's contribution:

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

1. INTRODUCTION

Cladocerans (Cladocera, Crustacea) are group of mesozooplankton, which play a major role in freshwater ecosystems. Although they are often viewed as a secondary constituent of marine zooplankton, ranking much below copepods in population density, they are widely distributed in marine ecosystems and may form a significant fraction, and at times the dominant component, of zooplanktonic communities (Bosch & Taylor, 1973a; Platt, 1977; Mordukhai-Boltovskoi & Rivier, 1987; Sherman et al., 1987; Egloff et al., 1997). At northern and temperate latitudes cladocerans are seasonally abundant, with high densities usually in the warm summer months (Ackefors, 1969; Rivier, 1998; Möllmann, 2002; Durbin, 2008; Telesh et al., 2009). However, in subtropical and tropical areas their maximum abundance is shifted to winter-spring and autumn-winter (Rivier, 1998).

Cladocerans have high seasonal variability due to the alternation of parthenogenetic and gamogenetic reproduction modes, the latter with the participation of males and and sexual females. This bisexual reproduction results in the formation of resting eggs, aimed at ensuring survival of the species over the time when environmental conditions are less favorable (Mordukhai-Boltovskoi & Rivier, 1987; Egloff et al., 1997; Rivier, 1998). Cladocerans possess an ability to increase their abundance (by using parthenogenetic reproduction mode) if the environment is favourable. This ability is very characteristic for marine cladocerans and makes them especially adapted to opportunistic utilisation of seasonally changing resources (Brandl, 2002), enables them to achieve seasonally very high abundances and facilitates their significant roles in the diet of various planktivorous fishes and invertebrate predators (Egloff et al., 1997). Therefore, when abundant, they may play an important role in energy transfer to higher trophic levels (Marazzo & Valentin, 2003). However, although marine cladocerans attain high population abundances very rapidly, these are generally sustained only for a short time, followed by a sudden decrease. To identify the factors responsible for an explosive community growth and its sudden decrease, specific investigations on life history (incl. reproduction cycle) are essential. Respective detailed investigations in the Baltic Sea date back to the 1970s–1980s (e.g., Ackefors, 1971; Eriksson, 1974; Kankaala, 1983, 1987; Kankaala & Wulff, 1981).

First observations on the Baltic Sea zooplankton were made at the beginning of the 20th century whilst a continuous systematic monitoring started soon after World War II (Ojaveer & Andrushaitis, 2004). Earlier investigations were mainly confined to spatio-temporal variability descriptions, but in the last decades zooplankton investigations (incl. those on cladocerans) in the Baltic Sea have focussed on other aspects, such as identification of the factors responsible for their long-term dynamics, trophic interactions and invasion of alien species. It has been shown that changes in the species composition as well as in spatio-temporal development are largely controlled by the abiotic environment – first and foremost by the water temperature and salinity (e.g. Vuorinen et al., 1998;

Möllmann et al., 2000, 2003), which, in turn, are determined by the climate variability in the North-Atlantic (e.g., Dippner et al., 2001; Hänninen et al., 2000, 2003; Vuorinen et al., 2003, 2004). The zooplankton communities in the Gulf of Riga, on the contrary, are poorly determined by the variation in the atmospheric circulation at North-Atlantic scale with only the cladoceran summer abundance in the open basin showing a positive link with NAO (North Atlantic Oscillation) winter index (Ikauniece, 2005).

Climate change and eutrophication pose substantial impact essentially on coastal marine ecosystems worldwide. They lead, amongst others, to loss of biodiversity and dramatic changes in ecosystem structure and functioning (e.g., McGowan et al., 1998; Howarth et al., 2000; Jackson et al., 2001; Möllmann et al., 2008). While climate change may alter distribution pattern, abundance and diversity of species and communities (Hänninen et al., 2000; Hughes, 2000; Lotze et al., 2006), eutrophication effects are often manifested in excessive algal blooms, accumulation of large amounts of organic matter and development of anoxia (Granéli & Sundbäck, 1985; Paerl, 2006; Andersen et al., 2006). It is currently believed that climate variables define broad patterns of species distributions. Within these patterns, smaller-scale processes, such as nutrient loading, operate at a lower intensity to modify distributions (Barry & Dayton, 1991; Steele & Henderson, 1994).

Widespread systematic long-term changes in the phenology of ecological events in zooplankton populations have been demonstrated with climate as a responsible factor behind the variability (Edwards & Richardson, 2004; Greve et al., 2004; Richardson, 2008). An important aspect of climate on the scale of an ecosystem is that species interactions are potentially disrupted due to a differential response of interacting populations to abiotic changes. In this respect changes in phenology, i.e. the seasonal timing of the life-cycle dynamics, are of great significance. However, these changes are relatively rarely investigated due to the high sampling effort needed.

Zooplankton serves as an essential link between lower and higher trophic levels. The structuring role of predators of zooplankton communities is evident in both freshwater and marine environments (e.g., Bushek & Allen, 2005; Ojaveer, 2006; Casini et al., 2008). The environmentally induced bottom-up processes in the physically stressed environments through the modified zooplankton (copepod) communities with the dramatic effects on individual growth rate of fish are well known and widely reported (e.g., Rönkkönen et al., 2003). However, there is still relatively little evidence indicating that cladocerans may have substantial roles in the diet of pelagic fish (e.g., Kostrichkina, 1970; Ojaveer et al., 1997) while the signal of the cladoceran abundance/biomass variability at higher trophic levels remains largely unknown as yet.

Invasion of non-indigenous species is one of the major threats to world oceans as it can significantly alter the structure and dynamics of plankon communities of the invaded ecosystems. To date, there are three alien cladocerans in the Baltic Sea: *Cercopagis pengoi, Evadne anonyx* and *Cornigerius maeoticus maeoticus* (Ojaveer & Lumberg, 1995; Rodionova et al., 2005;

Rodionova & Panov, 2006). Because of their predative behaviour, these non-indigenous cladocerans are suggested to potentially affect the structural and functional diversity of local zooplankton communities. Significant alterations in native species abundance and communities together with implications to overall ecosystem structure and functioning caused by predatory cladocerans have been recorded in several invaded ecosystems (Lehman & Caceres, 1993; Wahlström & Westman, 1999; Lehtiniemi & Gorokhova, 2008). Among invasive cladocerans, *C. pengoi* has been investigated extensively (e.g., Krylov & Panov, 1998; Rivier, 1998; Telesh et al., 2001; Uitto et al., 1999; Ojaveer et al., 2004; Simm & Ojaveer, 2006), but others are relatively poorly studied.

Although there is a tendency to consider the effects of climate change and biological invasions separately, recent research efforts are directed towards identifying synergistic effects (Walther et al., 2009). In general climate change, and especially recently recorded warming, is considered to facilitate the colonization and naturalization of invasive alien species in their new habitats. However, the potential of invasive alien species to significantly alter the established control patterns in a foodweb has not been investigated yet. Research from marine ecosystems has shown that the dominant control can change from bottom-up to top-down control. The change is frequently induced by human-induced changes at the top of a foodweb leading to the uncontrolled rise of mesopredators, being eventually a stronger controlling force than changes of the resource base or variability in the physical environment (Casini et al., 2009). Thus, given that different natural and anthropogenic processes do not act in isolation, changes in the structure of ecosystems are likely driven by changes between the complex interractions of climate and multiple anthropogenic stressors, such as biological invasions and eutrophication (Hughes, 2000; Grall & Chauvaud, 2002; Stenseth et al., 2002; Lotze et al., 2006; Möllmann et al., 2008). There is currently a critical knowledge gap in our understanding on how anthropogenic processes and climate variables interactively impact the dynamics of different ecosystem elements. It is therefore essential that we improve our understanding on how the influence of one forcing factor may modify the action of the others, and thereby determine their combined or synergistic effects.

2. AIMS AND HYPOTHESES

The general task of the present thesis was to identify naturally and anthropogenically induced species-level changes in the cladoceran community of the temperate brackish-water Baltic Sea at different spatio-temporal scales, and to investigate the significance of the variation in the cladoceran biomass in influencing the feeding parameters of pelagic fish.

The specific aims of the present thesis were:

1. To relate the seasonal-scale and spatial changes in the life history and population dynamics of cladocerans to selected key environmental parameters (**I**, **II, IV**).
   The almost exclusive occurrence of cladocerans in warm months has lead to consider, out of the wide array of abiotic factors, temperature as the major factor governing their structural change and abundance dynamics. Still, the quantitative effects of temperature on life history and population abundance dynamics of cladocerans was hypothetical. Therefore, our proposed hypothesis was that temperature variability should essentially impact population dynamics and phenology of cladocerans, but the overall observed cladoceran response to temperature variability is modified by other environmental factors.
2. To estimate the performance of the alien *Evadne anonyx* in the invaded low-salinity environment immediately after the invasion (**I**).
   It has been stated earlier, that *E. anonyx* is unable to survive in low salinity conditions below 5 psu. The abundance dynamics and the selected vital rates of the alien *E. anonyx* since the first year of invasion were investigated and compared with the similar native cladoceran *E. nordmanni*.
3. To explain interannual and multi-decadal trends in cladocerans abundance in relation to the abiotic and biotic environment (**III**, **VI**).
   The effect of climate on zooplankton has been generally related to the standing stock (i.e. abundance/biomass) and zooplankton changes are typically embedded in larger-scale restructurings of ecosystems. However, there is a critical knowledge gap in how the impacts of the key forcings (climate, eutrophication and bioinvasions) interactively affect the dynamics of marine ecosystems. The hypothesis was that long-term abundance of cladocerans is more influenced by large-scale (i.e., climate variables) than small-scale environmental variability (i.e., local nutrient loadings, water temperature, salinity). On the basis of previously accumulated knowledge it was also hypothesised that additional human intervention may be significant and the alien predatory cladoceran *Cercopagis pengoi* may act as an important structuring factor both at the individual species level and at the cladoceran community level.
4. To quantify the importance of cladocerans in the diet composition of the pelagic fish species in the warmest season and to relate the variation in fish feeding parameters to prey availability (**V**).

As cladocerans may reach very high population abundances during the warmest season, their importance in the pelagic fish diet might be significant, but species-specific. The annual-scale variability in prey should be mirrored at least in the diet composition of pelagic fish with adult herring and three-spined stickleback being the fish mostly relying on cladocerans as a food resource.

3. MATERIAL AND METHODS

3.1. Study area

The current thesis is based on studies conducted in two large gulfs situated in the northeastern Baltic Sea: the Gulf of Riga (incl. Pärnu Bay) and the Gulf of Finland (incl. Tallinn and Narva bays) (Fig. 1).

The Gulf of Riga (area 16 330 km^2, volume 424 km^3) is a semi-enclosed sub-basin, which is connected to the Baltic Proper via the Irbe Strait and Suur Strait (Otsmann et al., 2001). The shallow depth of the Gulf of Riga (mean 26, max > 60 m) results in a complete vertical mixing during winter and facilitates oxygen ventilation of the basin (Berzinsh, 1995). Spatial salinity variation in the Gulf of Riga is substantial, ranging from 0.5 to 2.0 psu in the coastal surface layers in spring to over 7 psu at the bottom close to the Irbe Strait (Berzinsh, 1995). In most years the Gulf of Riga is covered by ice in winter. Pärnu Bay, located in the northeastern part of the Gulf of Riga, is a relatively enclosed and shallow area covering approximately 700 km^2 with a volume of 2 km^3. The hydrographic conditions are formed under the complex influence of ice conditions, freshwater inputs and the water exchange with the open part of the Gulf of Riga. In summer, tha average surface temperature has reached 22–23°C during July–August. The area has low salinity (from almost fresh water to 7.5 psu) and is sheltered from winds. The system is influenced by extensive human pressures (Kotta et al., 2004; Wang et al., 2006).

The Gulf of Finland is a continuation of the Baltic Proper without having any separating sill. Investigations were carried out in two small bays at the southern coast of the gulf. Tallinn Bay is a relatively exposed and deep (max depth 100 m) water area located in the central part of the southern Gulf of Finland. Maximum temperatures of 22–24°C are observed in July, whereas in the deeper parts of the bay the temperature is stable throughout the year at 2–5°C. The bay is usually covered with ice in winter. The ecological state of Tallinn Bay is naturally vulnerable and exacerbated by pollution from industry and other activities of the large urban area of Tallinn. Narva Bay is located in the southeastern Gulf of Finland. It is shallower (20–40 m in average) and has a longer period of ice cover than Tallinn Bay. The hydrographic conditions of Narva Bay are influenced by the water exchange with the open gulf and freshwater inputs from the Narva and Neva rivers (Põllumäe & Kotta, 2007).

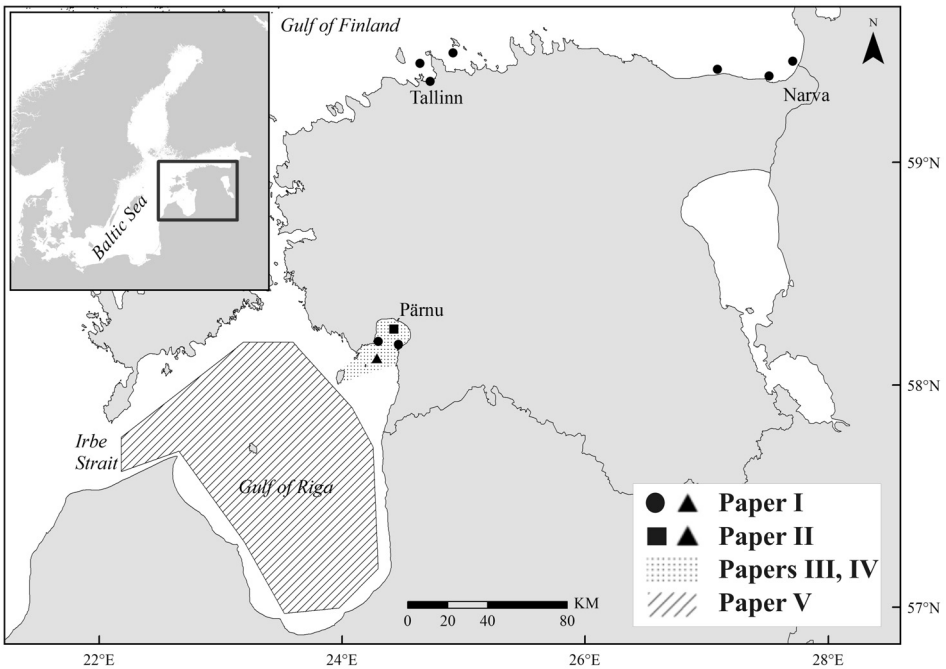

Figure 1. Location of the study areas and sampling sites by individual papers in the Gulf of Riga and the Gulf of Finland (northeastern Baltic Sea).

3.2. Sampling and sample analyses

Mesozooplankton sampling was performed with a standard Juday net (mouth opening 0.1 m^2; mesh size 90–100 μm) integrating the whole water column vertically. Analyses for the abundance calculations fully followed the guidelines outlined by HELCOM (HELCOM, 1988). The samples were preserved in a formalin solution with a final concentration of 4% and subsampled with a Stempel pipette. Individuals of the different taxa were counted in Bogorov's chambers under a binocular microscope. Measurements of water temperature, salinity and chlorophyll *a* were made by means of a CTD sond.

The mesozooplankton samples collected in 1997 to 2006 from the north-eastern Gulf of Riga (Pärnu Bay) and from the southern coast of the Gulf of Finland (Tallinn and Narva bays) were used to estimate the possible occurrence of the alien cladoceran *E. anonyx*. Seasonal abundance dynamics and fecundity analyses of cladocerans are based on 2006 data. All collected individuals of cladocerans were counted by the following categories: parthenogenetic females, gamogenetic females and males. Additionally, the fecundity of parthenogenetic (number of embryos) and gamogenetic females (number of resting eggs) was determined. Body length of cladocerans was measured from the top of the head to the end of the caudal outgrowths. Total length was determined from the top

of the head to the end of the brood pouch (detailed information on conventional measurements of cladocerans is provided in Egloff et al., 1997). Embryonic development in *P. polyphemoides* was divided into four stages (stages I to IV), based on easily distinguishable external characteristics found in Podonidae (Wong et al., 2004; Atienza et al., 2008).

To analyse the long-term and seasonal abundance dynamics of cladocerans in the northeastern Gulf of Riga ecosystem, a time series on cladoceran abundance was derived from sampling during the period of 1957–2006. Zooplankton sampling started in April–May and was generally performed weekly until the end of October. However, during 1957–1972 the sampling intensity was lower (until July), but during 1973–2006 the sampling period was extended, and samples were collected weekly during the ice-free period. Long-term data on daily air temperature, water temperature, salinity, wind and ice conditions and river runoff were obtained from the Estonian Meteorological Institute. The winter NAO (North Atlantic Oscillation) index of Hurrell (1995, data available at http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html# naopcdjfm) was used as a proxy of atmospheric behaviour to relate the large-scale climate pattern to the variation in the biotic and abiotic data in the study area. Time-series of hydrographic variables used in the analyses covered the period from 1957 to 2006. The yearly data on the nutrient load to the Gulf of Riga were obtained from the Estonian Ministry of Environment.

To compare the feeding behaviour of the main pelagic fish species in relation to changes in the prey field, fish stomachs and zooplankton were sampled during hydroacustic surveys designed to estimate the size of commercially important pelagic fish stocks in the Gulf of Riga. Sampling was performed during the second half of July and early August in 1999–2006 with a pelagic commercial trawl. Mesozooplankton prey of pelagic fish was sampled subsequently to trawling. The total length (to the nearest 1 mm) and individual body weight (to the nearest 0.1 g) of herring *Clupea harengus membras*, sprat *Sprattus sprattus balticus*, three-spined stickleback *Gasterosteus aculeatus* and smelt *Osmerus eperlanus* were measured. Stomachs of randomly sampled 20 individuals per species were analysed according to Melnitchuck (1980). To determine the food consumption of the pelagic fish, the following five zooplankton taxa that appeared to play the most substantial role in the fish diet, were subjected to further analyses: the calanoid copepods *Eurytemora affinis* and *Acartia* spp., the cladocerans *Bosmina longispina* and *Cercopagis pengoi* and the podonid *Pleopis polyphemoides* (incl. *Podon leuckarti* and *Podon intermedius*).

3.3. Data analyses

Statistical software "Statistica" was used for univariate data analyses. The significance of differences in the body size of *Evadne* sp. and *P. polyphemoides* was estimated by one-way analysis of variance (ANOVA) and the post hoc Bonferroni test in repeated measures ANOVA. The differences were considered

significant at $p < 0.05$. The *R* package relaimpo (relative importance of regressors in the linear models) method LMG was applied for tests between the abundance, body size, fecundity of *P. polyphemoides* and different continuous abiotic variables.

Multivariate data analyses were performed by the statistical program "Primer" version 6.1.5 (Clarke & Gorley, 2006). BEST analysis (BIOENV procedure) was used to relate eutrophication and climate variables to the abundance of zooplankton. This analysis shows which environmental variables best predict the observed biotic patterns. The relationships between nutrient loads and other abiotic and biotic environmental variables were estimated by correlation, linear and nonlinear regression analyses.

The sequential regime-shift detection method STARS (http://www.beringclimate.noaa.gov/regimes, Rodionov, 2004; Rodionov & Overland, 2005) was used to identify shifts in the time-series of hydrographic variables and occurrence of periods with different cladoceran abundance levels. Decadal changes in the strength of the climate control was assessed by calculating Pearson correlation coefficients (r) between cladoceran abundance and the abiotic variables on a 10-year sliding window. To identify the effect of the invader *Cercopagis* on this relationship, correlation coefficient were related to 10-year running means of *Cercopagis* abundance using GAMs (GAMs; Hastie & Tibshirani 1990).

In addition to species-level calculations of the share of non-fed fish and feeding activity index, the selective feeding behaviour of the different pelagic fish species was described using the fish electivity index (Wootton, 1998) and potential competition for food between the investigated fishes was evaluated as dietary overlap using the Morista similarity index (Horn, 1966). The differences in the abundance of zooplankton taxa between the years were estimated by one-way ANOVA and between periods by t-test. Significant differences of dietary overlap between the fish species were estimated by Kruskal–Wallis one-way ANOVA on ranks.

4. RESULTS AND DISCUSSION

4.1. Species composition

Globally there are eight truly marine cladoceran species belonging to the families Podonidae and Sididae, characterised by a very broad distribution range from tropical to subarctic waters (Giskes, 1971a, 1971b, 1971c; Della Croce, 1974; Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). The cladoceran community of the Baltic Sea is dominated by the following six taxa: the native *Bosmina* spp., *Podon intermedius*, *Podon leuckarti*, *Pleopis polyphemoides*, *Evadne nordmanni* and the alien *Cercopagis pengoi*.

In Pärnu Bay, the dominating taxa were *Bosmina* spp., *P. polyphemoides* and *E. nordmanni*. During the last decades, invasions of two additional cladoceran species, *C. pengoi* and *E. anonyx*, both of Ponto-Caspian origin, have been recorded. *E anonyx* is morphologically very similar to the native *E. nordmanni* and therefore it was initially not differentiated from the native Evadne species during the routine mesozooplankton monitoring. Thus, the current study points to the need for, and importance of, proper storage of collected biological samples, to be able if required, to track the spread and abundance of alien species over previous decades (**I**).

Other species of cladocerans are found either sporadically or are of relatively low abundance. These species include marine podonids *P. leuckarti* and *P. intermedius* (which are morphologically relatively similar to *P. polyphemoides*) and brackish and freshwater species *Leptodora kindtii*, *Diaphanosoma brachyrum*, *Chydorus sphaerichus*, *Daphnia cucullata, D. longispina*, *Ceriodaphnia quadrangula*, *C. pulchella*, *Alona affinis*, *A. rectangula*, etc.

4.2. Phenology and life history of cladocerans

The mass reproduction of all studied cladocerans takes place in summer. The maximum abundance of *P. polyphemoides* and *E. nordmanni* was recorded in June-July, while *Bosmina* spp. were the most abundant in July–August (**I, II, IV**). Comparative study of the two *Evadne* species showed that these species exhibited clearly different seasonal cycles in the Gulf of Riga, where the maximum abundance of *E. anonyx* occurred later in the season than that of *E. nordmanni*. However, in the Gulf of Finland the abundance of both species reached the peak simultaneously – in late June or early July (**I**).

A direct impact of climate on cladocerans through altered seasonal timing was detected. In general, the timing of the population onset of cladocerans is known to be induced by water temperature in spring (Egloff et al., 1997; Rivier, 1998; Marazzo & Valentin, 2003a, 2003b, 2003c) with hatching of parthenogenetic females from resting eggs (Egloff et al., 1997). In Pärnu Bay, the timing of the population onset of cladocerans was related to both water temperature and the timing of the last retreat of the significant ice cover: the earlier the ice

retreated, the earlier the population onset began. Furthermore, the earlier onset of cladocerans during the warm years was found to be accompanied by a shift towards earlier development of the abundance peak (**IV**).

Whilst the development of the cladoceran population in spring seems to be associated with the temperature regime (**III**, **IV**), the drastic decline of the abundance of *Bosmina* spp. and *P. polyphemoides* during summer is probably governed by other factors than alterations in the abiotic environment. It was found to be unlikely that temperature triggered the observed sharp density drop in summer, as population started to decline at the time when water temperature was at or close to its maximum (**II**). Neither was there any relationship between salinity and population abundance. Earlier evidence on the predation-induced mortality of small-sized cladocerans in this region (**IV**; Ojaveer et al., 2004), as well as conclusions from other regions (Gliwicz, 2001; Marazzo & Valentin, 2003c), suggests that predation should be an important factor behind the sharp drop of the abundance of *Bosmina* spp. and *P. polyphemoides* during summer. This suggestion is further confirmed by the fact that the size of parthenogenetic females was significantly smaller at and/or immediately after the seasonal population peak, potentially indicating predation mortality of larger and more easily detectable individuals (**II**).

Cladocerans have high seasonal variability due to the alternation of parthenogenetic and gamogenetic reproduction modes (Egloff et al., 1997; Rivier, 1998). A rapid increase in densities attained as a result of high rates of embryonic and postembryonic growth is characteristic of marine cladocerans. Population development of cladocerans was found to be very seasonal with a strong domination of parthenogenetic females (Fig. 2). Amongst most of the investigated cladoceran populations, the gamogenetic reproduction mode occurred throughout the whole reproductive season being the most intense during or just after the population abundance peak. Exceptionally, the latter was less clearly observed in *Evadne* populations (**I**).

Marine cladocerans attain high population abundances very rapidly, but these are generally sustained over a very short time only. Reasons for a sudden abundance decrease are relatively poorly understood. However, this decrease is typically accompanied by an intensive gamogenetic reproduction (Onbé, 1978), resulting in the production of diapausing (resting) eggs at the end of the reproductive season. This has been suggested to be triggered by changes in environmental conditions and aimed at ensuring survival of the species over the winter (Egloff et al., 1997; Rivier, 1998). In contrast, no relationship was found between the appearance of gamogenetic females and the abiotic environment (**II**). This is probably because no clear shift between the two reproduction modes was detected and the cladocerans were found to reproduce both parthenogenetically and gamogenetically almost throughout the whole reproductive season. However, significant differences were found between the temperature regulation of the fecundity of the native and alien cladocerans. While the parthenogenetic fecundity of the native *P. polyphemoides* and *E. nordmanni* was inversely correlated with water temperature, the relationship was positive

for the alien *E. anonyx*. As the fecundity of the alien *E. anonyx* significantly exceeds that of the native *E. nordmanni*, it is suggested here that the population abundance of *E. anonyx* will very likely increase in the future and the species may colonise new areas in the recently invaded ecosystem (**I**).

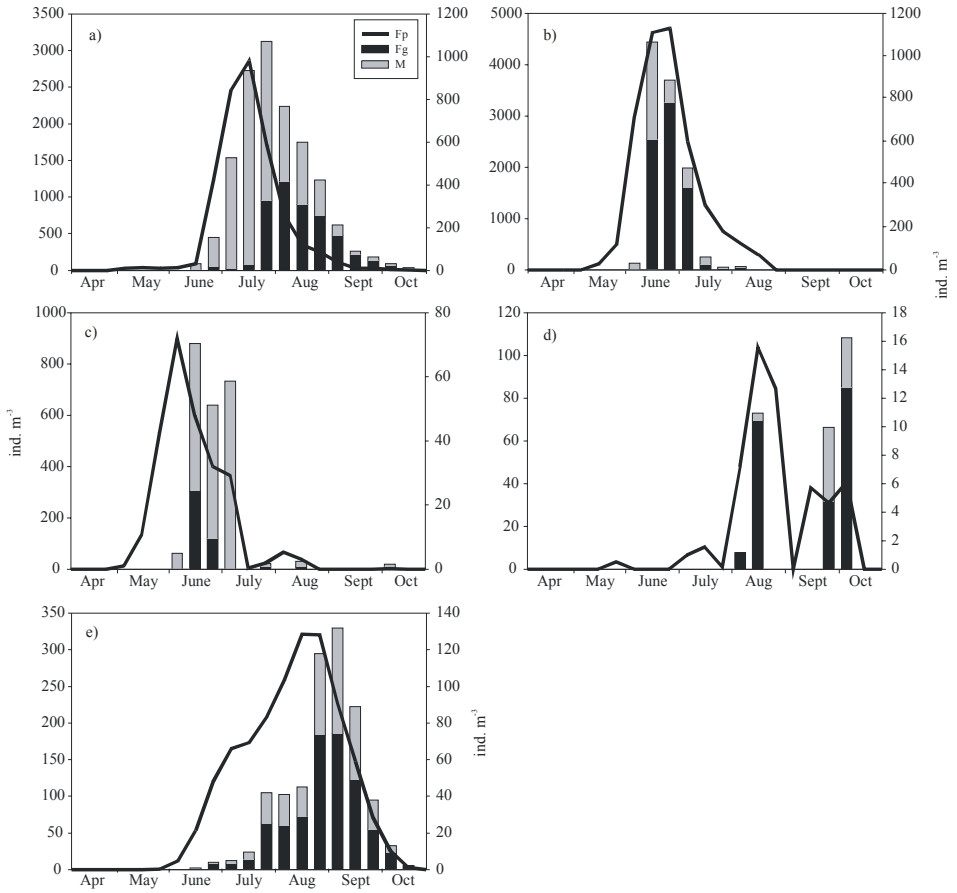

Figure 2. Seasonal abundance dynamics of parthenogenetic females (solid line, left scale), gamogenetic females (black columns, right scale) and males (grey columns, right scale) of (a) *Bosmina* spp., (b) *Pleopis polyphemoides*, (c) *Evadne nordmanni*, (d) *Evadne anonyx* and (e) *Cercopagis pengoi* in the Gulf of Riga in 2006.

The populations of *P. polyphemoides* and *Evadne* spp. in Pärnu Bay before the abundance peak when the water temperature increased rapidly, was characterised by the presence of relatively large parthenogenetic individuals, which were found to be generally more fecund than smaller individuals (**I**, **II**). This was evidenced by a significant positive correlation between parthenogenetic fecundity and the total female length. A positive relationship between the total

length and fecundity was expected, as the total length is mainly determined by the reproductive phase and number of embryos in a brood pouch (Marazzo & Valentin, 2003c). However, the body length of native species *P. polyphemoides* and *E. nordmanni* was not related to fecundity characteristics. In contrast, alien *E. anonyx* exhibited again a difference from native species by the relationship between the body length and the number of embryos (**I**).

During the daytime, most of the embryos found in female brood pouches of *P. polyphemoides* were in stages II and III, while the share of fully developed embryos (i.e., stage IV) was very low (**II**). This was also confirmed for the other investigated cladocerans. It is known for marine cladocerans that the eyes of the embryos become pigmented at the final stage when embryos are fully developed (Platt & Yamamura, 1986). Because planktivorous fish are selecting for the pigmented structures (Zaret & Kerfoot, 1975; Flinkman et al., 1992), it was suggested that the reason for the release of neonates by cladocerans at night is the decrease in fish predation (Wong et al., 2004). However, whether this was due to nocturnal release of neonates and predation remains unclear and should be investigated in the future.

4.3. Long-term dynamics of cladocerans

Annual-scale variability in the abundance of the four dominating cladoceran taxa exhibited both strong similarities and remarkable differences during the about 50 years of investigations in Pärnu Bay. The abundance of the three native taxa – *Bosmina* spp., *P. polyphemoides* and *E. nordmanni* – showed a significant increase in the mid-1970s. For *Bosmina* spp. and *P. polyphemoides*, the period of high abundance lasted until the beginning of the 1990s, since when it has remained at very low levels (**III**, **IV**). This decrease coincides with the invasion of the predatory cladoceran *C. pengoi* in 1991, which reaches very high abundance values in the study area during the warm season (Ojaveer et al., 2004; Kotta et al., 2004). For *E. nordmanni,* however, a high population abundance level was observed for a considerably longer period – until the early 2000s (Fig. 3). One of the latest arrivals to the Baltic Sea is *E. anonyx*, found in the study area in 2000 (I). With respect to the salinity tolerance limits, it is important to mention that before invading the Baltic Sea, *E. anonyx* was not considered as a high risk species for low-salinity environments because of inability to survive at salinities below 9 psu (Panov et al., 1999; Rivier, 1998). However, the results of the current study confirm that the species is successfully adapted to the low-salinity (around 5 psu) environment. Although *E. anonyx* was able to establish itself in the new environment, its abundance succeeded to reach during the very early stages of invasion only about a tenth of that of the native *E. nordmanni* (**I**).

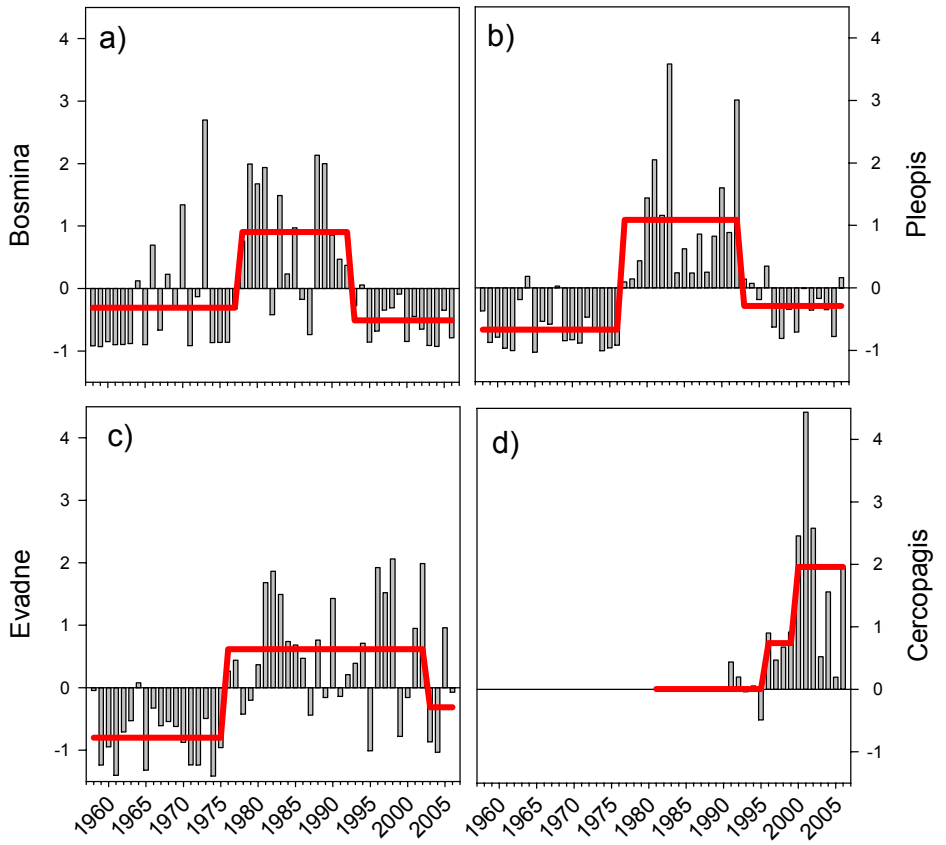

Figure 3. Long-term abundance (in z-scores) dynamics of (a) *Bosmina* spp., (b) *Pleopis polyphemoides*, (c) *Evadne nordmanni* and (d) *Cercopagis pengoi* during 1957–2006. The bold lines indicate significant shifts in population abundance.

Several earlier studies have indicated significant changes in the distribution and annual abundance dynamics of the major Baltic mesozooplankton taxa, especially cladocerans and copepods, which have mostly been attributed to altered hydrographical conditions, but also to increased eutrophication (Hernroth & Ackefors, 1979; Lumberg & Ojaveer, 1991; Sidrevics et al., 1993; Yurkovskis et al., 1999; Ikauniece, 2001, 2006; Möllmann et al., 2002). On the basis of long-term monitoring data, separate and combined impacts of nutrient loading, temperature, salinity and wind conditions on cladocerans were quantified (**III**). It appeared that the annual-scale abundance dynamics of *Bosmina* spp. was related to both eutrophication and climate, suggesting that the joint effect of climate and nutrient loading is the likely reason of zooplankton dynamics in the Gulf of Riga.

Earlier studies found that the population dynamics of cladocerans in the Baltic Sea is influenced by temperature and salinity (Viitasalo, 1994, 1995; Vuorinen et al., 1998; Möllmann et al., 2001). Our findings indicated that climate variables explained the dynamics of zooplankton better than eutrophication variables (**III**). The single key abiotic variables that explained the interannual differences in the abundance of cladocerans were water temperature and winter NAO (**IV**). *Bosmina* spp. exhibited a better relationship with temperature than with NAO, and the relationship was stronger when the population size was greater. The time trend observed for *P. polyphemoides* was similar to that of *Bosmina* spp.; however, the NAO was more important than for *Bosmina* spp. Such difference between those two species could be attributed to the earlier appearence of *P. polyphemoides* in spring.

While the sharp abundance increase of all native cladocerans took place prior to the invasion of *C. pengoi* at the same time, the decrease of the two most abundant cladocerans (*Bosmina* spp. and *P. polyphemoides*) has happened after the invasion of *C. pengoi* substantially earlier than that of *E. nordmanni*, the timing coinciding with the invasion of *C. pengoi* (**IV**). Additional findings on the reversal of the positive relationship between *Bosmina* spp. abundance and water temperature after the invasion of *C. pengoi* and the dependence of the *Bosmina* spp. and *P. polyphemoides* abundance/NAO relationship on *C. pengoi* density (**IV**) contribute to a substantially advanced understanding on how human-mediated invasion of alien species may interact with climate-driven changes in marine ecosystems, providing also additional evidence on the magnitudes of these changes. These results suggest that synergistic effect of the human-mediated invasion of the predatory cladoceran through the direct predator-prey interactions and climate-induced changes in the abiotic conditions now determines the abundance dynamics of the small-sized native cladocerans and this effect bears species-specific nature (**III**, **IV**). Direct predation of the small-sized cladocerans (incl. *Bosmina* spp.) by *C. pengoi* is also confirmed by laboratory experiments (Lehtiniemi & Lindén, 2006; Simm et al., 2006; Pichlova-Ptacnikova & Vanderploeg, 2009). However, in the case of *E. nordmanni* no significant change in the relationship between its abundance and abiotic conditions was detected before and after the invasion of *C. pengoi* (**IV**). This could be attributed to a considerably lower abundance of *E. nordmanni* compared to that of *Bosmina* spp. and *P. polyphemoides* and thus, most likely point to its negligible importance as a dietary item for *C. pengoi*.

4.4. Feeding of pelagic fish as a function of cladoceran variation

It has been suggested that cladoceran populations are, in addition to predation by invertebrates, regulated by the top-down control through the direct predation by fish (e.g., Horsted et al., 1988; Põllumäe & Kotta, 2007). Predation pressure on zooplankton should be high in the investigated area (i.e., Gulf of Riga), which is biologically very productive and supports relatively large fish catches. It appeared that the most important food items amongst cladocerans for the pelagic fish species (young and adult herring, sprat, young smelt and three-spined stickleback) during the warmest season of the year were *B. longispina*, *C. pengoi* and *Podon* spp. (**V**). While copepods dominated in the diet of herring, the largest part of the diet of three-spined stickleback and juvenile smelt consisted of *B. longispina*, which was far the most abundant cladoceran in the Gulf of Riga. *Podon* spp. were present in the diet of adult sprat, three-spined stickleback and juvenile herring in rather moderate quantities only. Amongst the five studied fish groups, the alien cladoceran *C. pengoi* was highly preferred and served as a substantial energy source for adult herring and three-spined stickleback. Remarkably, this large cladoceran contributed on average about 30% of the adult herring diet.

The variation in the abundance of the cladoceran *B. longispina* substantially affected the diet composition of adult sprat, juvenile smelt and three-spined stickleback, which all were strongly selective for this small cladoceran (**V**). During the study period (1999–2006), *B. longispina* was found in extremely high densities in 2001 and 2002 and extremely low densities in 2003–2004 and 2006, exhibiting far the largest annual-scale variation amongst the more important prey items of pelagic fish. All fish species compensated for the low *B. longispina* contribution through increased consumption of copepods *E. affinis* and *Acartia* spp. Compared to copepods, *Bosmina* is less evasive and therefore easier to capture by zooplanktivores (Viitasalo et al., 2001). However, the observed changes in zooplankton abundance (incl. significant annual-scale variation in cladoceran abundance and biomass) did not initiate any consistent alterations in fish feeding activity and, therefore, also in the total amounts of zooplankton consumed. Adult sprat and three-spined stickleback switched to preying on other planktonic food in case the most preferred food was limited while adult herring may have adapted its feeding mode depending on the availability of the preferred prey (**V**). These results contrast with several other much longer-term annual-scale studies where it was found that a drastic decrease in prey densities had resulted in declined feeding activity and caused reductions in individual growth of fish (Lankov & Raid, 1997; Möllmann et al., 2004; Carruthers et al., 2005).

5. CONCLUSIONS

The main findings of the study are as follows:

1. Population development of cladocerans was found to be very seasonal with a strong domination of parthenogenetic females. Direct climate impacts on the phenology of cladocerans act through the timing of the onset and modification of the length of the time cladocerans need to reach the peak. The change from parthenogenetic to gamogenetic reproduction was found to be influenced neither by water temperature, salinity nor chlorophyll *a* concentration. Diet availability or predation pressure might induce the abundance drop in the warmest season.
2. Contrary to expectations, the alien cladoceran *Evadne anonyx* endured successfully the low-salinity environment and exhibited an about 10-fold increase in abundance during the first few invasion years. The observed high fecundity of *E. anonyx* compared to the native *E. nordmanni* indicates that this alien species has a potential to significantly increase in abundance in the future and modify the local foodweb. The fact that *E. anonyx* is performing well in the low-salinity environment suggests that our knowledge on tolerance limits for even essential abiotic parameters of marine zooplankton is not sufficient for making predictions and performing risk analysis of potential new invaders.
3. Climate and eutrophication interactively affected cladoceran abundance at multi-annual scale with climate being better descriptor than eutrophication. In addition, human-mediated invasion of the predatory cladoceran *Cercopagis pengoi* has resulted in a disruption of the previously existing ecological relations of the dominating native small-sized cladoceran species. However, these alterations have been insufficient to cause additional significant shifts in population abundance, but sufficient to hamper recoveries from losses through direct predation.
4. Major annual-scale variation in the important prey of the pelagic fish species was associated with the dynamics of *Bosmina longispina*. This significantly influenced feeding parameters of those species that strongly selected for this small cladoceran. However, the observed annual-scale variation in cladoceran abundance and biomass did not to initiate any consistent alterations in fish feeding activity and, therefore, also in the total amounts of zooplankton consumed.

SUMMARY IN ESTONIAN

Vesikirbuliste ökoloogia riimveelises ökosüsteemis

Merelised vesikirbulised moodustavad olulise osa Läänemere mesozooplanktoni arvukusest ja biomassist suvel. Vesikirbulistel toimub partenogeneetilise (neitsisigimine) ja gamogeneetilise paljunemise vaheldumine. Ebasoodsates keskkonnatingimustes produtseeritakse püsimunad, mis ladestuvad põhjasetteisse ja võimaldavad vesikirbulistel üle elada ebasoodsad keskkonnatingimused. Keskkonnatingimuste paranedes, näiteks kevadel vee soojenedes, kooruvad püsimunadest partenogeneetilised emased isendid andes alguse uutele põlvkondadele. Tänu partenogeneesile on vesikirbulised võimelised saavutama soodsates keskkonnatingimustes kiiresti suure arvukuse, mis annab neile eelise kohanemiseks kiiresti muutuvates keskkonnatingimustes. Massilise arengu ajal on vesikirbulised oluliseks toiduks kaladele ja röövtoidulistele selgrootutele. Vaatamata kiiresti saavutatavale suurele arvukusele on vesikirbulised võimelised seda säilitama suhteliselt lühikest aega. Vesikirbuliste arvukuse plahvatusliku kasvu ning sellele järgneva arvukuse kiire languse põhjuste selgitamine eeldab nende elutsükli (s.h. paljunemise) detailseid uuringuid.

Mesozooplanktoni varasemad uuringud Läänemeres on peamiselt keskendunud ajalis-ruumilise varieeruvuse kirjeldamisele. Viimastel aastakümnetel on üheks olulisemaks zooplanktoni (s.h. vesikirbuliste) uurimise aspektiks olnud nende pikaajalise dünaamika kirjeldamine ja seda põhjustavate tegurite selgitamine. Kliimamuutuste ja eutrofeerumise kõrval on üheks oluliseks planktonikoosluste struktuuri ja dünaamikat mõjutavaks teguriks ka võõrliikide invasioon kusjuures just tulnukvesikirbulised on seni olnud Läänemere ökoüsteemis olulisemad planktilised võõrliigid. Tulnuk-vesikirbulised on reeglina röövtoidulised ja neid on peetud võimalikuks ohuks kohalikele zooplanktoni kooslustele.

Erinevad looduslikud ja inimtekkelised mõjurid ning neist põhjustatud protsessid mõjutavad mereökosüsteemi eluskomponente nii üksikult kui ka teineteisega seostatuna ning muutused ökosüsteemides on tõenäoliselt põhjustatud nende koosmõjust. Kliima ja inimese poolt põhjustatud muutusi pelaagilistes ökosüsteemides on reeglina uuritud eraldi ning üle kogu maailma on seni suhteliselt vähe töid nende koosmõju kohta.

Käesoleva doktoritöö eesmärgiks on selgitada Läänemere vesikirbuliste koosluses liigilisel tasandil toimunud ajalis-ruumilisi muutusi sõltuvalt keskkonnatingimuste varieeruvusest, mis on põhjustatud nii looduslikest (kliima) kui ka inimtekkelistest (eutrofeerumine, võõrliikide invasioon) teguritest ja protsessidest. Töö põhineb Läänemere kirdeosast, Liivi ja Soome lahest, kogutud materjalil. On analüüsitud keskkonnategurite mõju vesikirbuliste arengule, paljunemisele ja populatsiooni dünaamikale (**I**, **II**). On hinnatud tulnukvesikirbulise *Evadne anonyx*'i arvukuse dünaamikat ja paljunemist sissetulekule vahetult järgnevatel aastatel võrreldes kohaliku vesikirbulise *Evadne nord-*

manni'ga (**I**). Pikaajaliste, alates 1957. aastast pärinevate andmeridade alusel on uuritud eluta- ja eluskeskkonna tingimuste mõju vesikirbuliste arvukuse dünaamikale ning fenoloogiale (**III**, **IV**). On hinnatud vesikirbuliste olulisust pelaagiliste kalade toidubaasina ja uuritud kalade toitumisspektrite aastatevahelist varieeruvust sõltuvalt vesikirbuliste populatsiooni parameetritest (**V**).

Läänemeres on kõige arvukamateks vesikirbulisteks *Bosmina* spp., *Pleopis polyphemoides* ja *Evadne nordmanni*. Teised vesikirbuliste liigid, eeskätt mageveelised, esinevad juhuslikult ja vähearvukalt eeskätt suuremate jõgede suudmealadel. Viimastel aastakümnetel on lisandunud tulnukliikidena kolm Ponto-Kaspia päritolu vesikirbulist, *Cercopagis pengoi*, *E. anonyx* ja *Cornigerius maeoticus maeoticus* (viimane neist leitud vaid Soome lahe idaosas). Vesikirbuliste intensiivseim paljunemine ja kõrgeim arvukus on reeglina suvel: liikidel *P. polyphemoides* ja *E. nordmanni* juunis-juulis ning *Bosmina* spp. juulis-augustis. Pärnu lahes täheldati kahe *Evadne* liigi puhul erinevat sesoonset esinemist – võõrliigi *E. anonyx* maksimaalne arvukus esines hiljem (augustis) kui *E. nordmanni*'l. Samas, Soome lahes esines mõlema liigi arvukuse maksimum samal ajal – juuni lõpus või juuli alguses.

Vesikirbuliste kevadine areng on otseselt mõjutatud jää sulamise ajast ja sellega kaasnevalt ka veetemperatuurist. Veetemperatuuriga on seotud ka vesikirbuliste arvukuse maksimumi ajastatus suvel, kui populatsioonis domineerivad eeskätt partenogeneetilised emased. Samas, vesikirbuliste arvukuse järsk langus kesksuvel on tõenäoliselt põhjustatud muudest teguritest kui muutustest elutakeskkonna parameetrites. On ebatõenäoline, et veetemperatuur võiks olla vesikirbuliste kiire arvukuse languse põhjuseks suvel, sest arvukuse langust täheldati ajal kui mõõdeti kõrgeim (või sellele ligilähedane) veetemperatuur. Vesikirbuliste arvukuse järsk vähenemine kesksuvel on tõenäoliselt põhjustatud kas sobiva toidu puudumisest või nende suremusest läbi ärasöömise kas selgrootute kiskjate või kalade poolt. Usaldusväärset seost ei leitud partenogeneetiliste isendite arvukuse vähenemise ja gamogeneetiliste isendite ilmumise ning veetemperatuuri, soolsuse ja klorofülli *a* sisalduse vahel. Võrreldes partenogeneetiliste isendite arvuga, oli gamogeneetiliste ehk püsimune kandvate emaste isendite osakaal populatsioonis oluliselt väiksem. Siiski, vesikirbulised paljunesid gamogeneetiliselt peaaegu kogu sesooni jooksul, kõige intensiivsemalt arvukuse maksimumi ajal või vahetult peale seda.

Enne vesikirbulise *E. anonyx* ilmumist Läänemerre, arvati, et see liik pole võimeline taluma soolsust alla 9 psu. Erinevalt seni teaduskirjanduses toodust on aga tulnukvesikirbuline *E. anonyx* edukalt kohanenud Läänemere madala soolsusega (umbes 5 psu) ning seega ei tohiks madal soolsus olla sellele liigile levikubarjääriks. Samas, kuigi sissetulekule vahetult järgnevatel aastatel on *E. anonyx* arvukus suurusjärgu võrra kasvanud, jääb tema arvukus siiski oluliselt madalamaks kohaliku liigi *E. nordmanni* omast. Kuid *E. anonyx*'i oluliselt suurem viljakus, võrreldes *E. nordmanni*'ga, võib põhjustada tema arvukuse edasist suurenemist ja seega juba lähitulevikus tunduvalt suurendada tema osatähtsust kohalikus toiduahelas.

Vesikirbuliste arvukuse muutused ligi poole sajandi pikkusel ajaskaalal on mõjutatud mitmete tegurite, nagu kliima, eutrofeerumise ja bioinvasioonid, koosmõjust, kusjuures eraldi võttes selgitavad kliimatingimused arvukuse muutlikkust paremini kui eutrofeerumine. Kõigi uuritud kohalike vesikirbuliste üheaegne arvukuse suurenemine 1970-ndatel viitab, et toimunud muutuste põhjused on ilmselt sarnased ja ei erine liikide tasandil. Erinevalt *E. nordmanni*'st, kelle arvukus on vähenenud 2000. aastate algusest, täheldati kahe arvukama vesikirbulise *Bosmina* spp. ja *P. polyphemoides* arvukuse järsku langust oluliselt varem, toimudes samaaegselt võõrliigi *C. pengoi* invasiooniga 1990. aastate alguses. Lisaks täheldati varemesinenud positiivse seose katkemist *Bosmina* spp. arvukuse ja veetemperatuuri vahel peale *C. pengoi* invasiooni, ning *Bosmina* spp. ja *P. polyphemoides* arvukuse ja NAO seose sõltuvust *C. pengoi* arvukusest. *E. nordmanni* puhul ei täheldatud erinevust liigi arvukuse ja eluta keskkonda iseloomustavate parameetrite vahel võrrelduna enne ja pärast *C. pengoi* invasiooni. See võib olla põhjustatud tema madalamast arvukusest võrreldes *Bosmina* spp. ja *P. polyphemides*'ga ning seega tema väiksemast tähtsusest *C. pengoi* toiduobjektina. Laboratoorsed katsed on kinnitanud, et Pärnu lahes eelistab *C. pengoi* toiduks just väikesemõõdulisi vesikirbulisi (s.h. *Bosmina* spp.). Ilmselt toiduahela suhete tõttu (kisklus) on röövtoidulise võõrvesikirbulise *C. pengoi* invasioon põhjustanud varemesinenud seose katkemise kohalike domineerivate väikesemõõduliste vesikirbuliste ja elutakeskkonna vahel. Antud tulemused täiendavad oluliselt meie teadmisi sellest, milliseid muutusi, mis mahus ja milliste protsesside tõttu võib inimtegevusest põhjustatud võõrliikide invasioon põhjustada mereökosüsteemides.

Suvel on Liivi lahe pelaagilistele kaladele (räim, kilu, tint ja ogalik) kõige olulisemateks toiduobjektideks vesikirbulistest *Bosmina longispina*, *C. pengoi* ja *Podon* spp. (s.h. *P. polyphemoides*). Kuigi räime toidus domineerisid aerjalalised, siis suguküpse tindi, ogaliku ja noore kilu puhul oli kõige olulisemaks toiduobjektiks vesikirbuline *B. longispina*, kes oli ühtlasi ka arvukaim vesikirbuline Liivi lahes. Suurimad aastatevahelised muutused pelaagiliste kalade toidubaasis olid seotud nende olulise toiduobjekti *B. longispina* arvukuse dünaamikaga. Vesikirbulise *B. longispina* arvukuse aastatevaheline varieerumine mõjutas oluliselt suguküpse tindi, noore kilu ja ogaliku suvist toitumist, kes selgelt valisid toiduks just seda väikesemõõdulist vesikirbulist. Eelistatud toiduobjekti puudumisel olid kõik kalaliigid võimelised toituma teistest liikidest, kompenseerides *B. longispina* vähese kättesaadavuse suurema tarbimisega aerjalalistest *Eurytemora affinis* ja *Acartia bifilosa*. Seega, registreeritud aastatevaheline varieeruvus *B. longispina* arvukuses ja biomassis ei osutunud siiski piisavaks, et põhjustada püsivaid muutusi kalade toitumisaktiivsuses ning tarbitud zooplanktoni kogustes.

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PUBLICATIONS

ELULOOKIRJELDUS

I. Üldandmed

Ees- ja perekonnanimi:	Maria Põllupüü
Sünniaeg ja koht:	19.01.1982 Harjumaa
Kodakondsus:	Estonian
Aadress, e-post:	Mäealuse 14, 12618 Tallinn, Estonia, maria.pollupuu@ut.ee
Haridus:	B.Sc. bioloogia (merebioloog-keskkonnaspetsialist), Tallinna Ülikool, 2005. a. M.Sc. hüdrobioloogia, Tartu Ülikool, 2006
Keelteoskus:	eesti, inglise
Teenistuskäik:	2006 Tartu Ülikooli Eesti Mereinstituut, laborant 2007 – ... Tartu Ülikooli Eesti Mereinstituut, teadur

II. Teaduslik ja arendustegevus

Peamised uurimisvaldkonnad

i) Läänemere mesozooplankton: populatsiooni dünaamika ja toitumissuhted ökosüsteemis
ii) Vesikirbuliste (s.h. võõrliigid) paljunemise ja arengu iseärasuste ja seaduspärasuste selgitamine
iii) Läänemere võõrliigid: populatsiooni dünaamika ja ökoloogiline mõju

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2. Põllupüü, M., Simm, M., Ojaveer, H. „Life history and population dynamics of the cladocerans in the NE Gulf of Riga." 7th Baltic Sea Science Congress, 17.08.–21.08.2009, Tallinn, Eesti.
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5. Põllupüü, M. „Long-term dynamics of mesozooplankton community in the NE Baltic Sea in relation to climate variability and different antropogenic forcings" *EUR-OCEANS suvekool*: Climate changes impact on marine ecosystems 14–26.08.2006, Ankara, Türgi.

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