

**Factors describing
the distribution of
the zooplankton
community in the Gulf
of Finland in the context
of interactions between
native and introduced
predatory cladocerans***

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Abstract

Mesozooplankton communities were studied monthly at six sites in the Gulf of Finland during six ice-free seasons. The abundances of different zooplankton taxa were related to temperature, salinity, eutrophication level (total nitrogen and phosphorus), phytoplankton (Chl *a*) and density of predatory cladocerans, including the non-indigenous *Cercopagis pengoi* and the native *Leptodora kindtii*. The results indicated that variability in the zooplankton communities was correlated not only with predation by mesozooplankton but also with bottom-up effects. Predation by the non-indigenous *C. pengoi* may significantly affect the dynamics of Cladocera and Rotatoria in the Gulf of Finland during the summer season.

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1. Introduction

Invasive organisms have become one of the most serious threats to aquatic environments worldwide, 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 (Stachovitz 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, Kotta et al. 2006).

One of the most recent planktonic newcomers to the Baltic Sea is the predatory cladoceran *Cercopagis pengoi*, which was first observed in the open sea of the Gulf of Finland in 1992 and in Finnish coastal waters in 1995 (Telesh & Ojaveer 2002). The species originates from the Ponto-Caspian area, and transfer of ballast water between international ports is suggested as a potential vector of this invasion (Leppäkoski & Olenin 2001).

Earlier literature on *C. pengoi* focused on its increasing dominance in the pelagic community (Ojaveer et al. 1998, 1999, Leppäkoski & Olenin 2001) and less on the effect of the invader on food webs (Vanderploeg et al. 2002, Laxson et al. 2003, Kotta et al. 2004, Ojaveer et al. 2004, Gorokhova et al. 2005). The objective of this study was therefore to relate prime abiotic and biotic factors, such as temperature, salinity, water nutrients, phytoplankton biomass and abundance of mesozooplankton taxa, to the abundance of *C. pengoi* in the Gulf of Finland. The studied relationships will indicate if the mesozooplankton is regulated by external nutrient loads and whether the invasion of *C. pengoi* potentially modifies the dynamics of the mesozooplankton. The Gulf of Finland is the northernmost water body in the world where *C. pengoi* has established a permanent population. Thus, information on how environmental variability is related to the dynamics of *C. pengoi* in such a harsh environment is essential for predicting the invasion potential of *C. pengoi* outside its temperature optimum. Moreover, information on significant relationships between *C. pengoi* and other mesozooplankton taxa will indicate the potential impacts of this cladoceran species in the recipient ecosystem.

2. Material and methods

Zooplankton samples were collected within the framework of the Estonian National Monitoring Programme at six stations in the Tallinn Bay area in 1997–2002 and in Narva Bay in 2001–2002 (Fig. 1). Tallinn Bay is

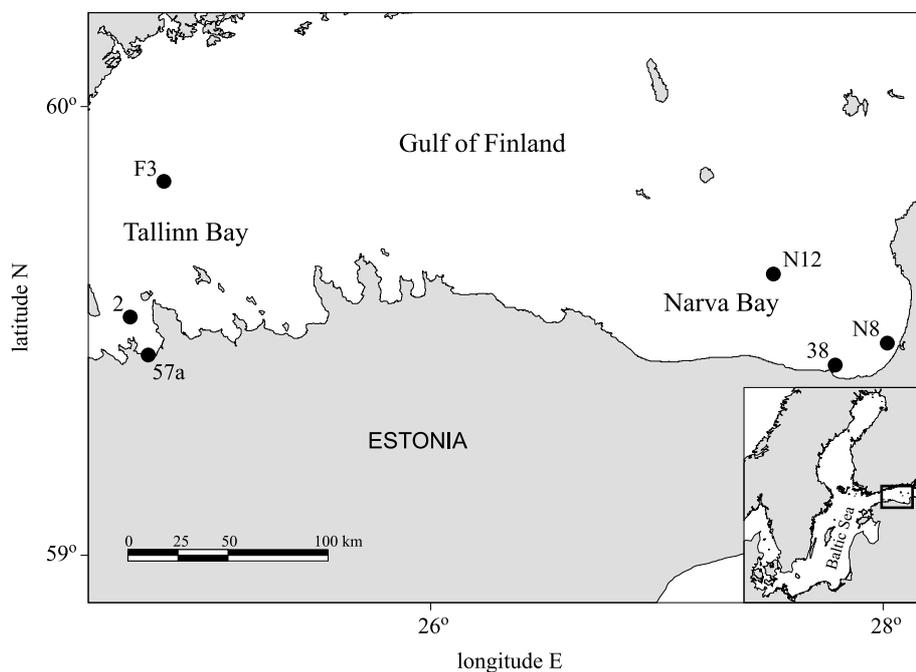


Fig. 1. Study area. Filled circles indicate the zooplankton sampling locations

located in the southern Gulf of Finland. The bay is relatively exposed and deep (max depth 100 m); in addition, 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 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 affects 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 the maximum depth of the bay 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.

The sampling was done during the ice-free period: fortnightly from June to August, and monthly in May and from September to November. The samples were collected by means of vertical tows with a Juday closing plankton net (mesh size 90 μm , mouth area 0.1 m²). At deep stations zooplankton was sampled separately above and below the thermocline

when present. The samples were preserved in 4% formaldehyde solution in seawater. All *C. pengoi* in a sample were counted to calculate abundance. The abundances of other taxa were estimated from a number of subsamples according to the suggestion of HELCOM (1988). Altogether 255 samples were analysed. The following parameters were routinely monitored during zooplankton sampling: temperature and salinity profiles, nutrient concentrations and phytoplankton biomass (Chl *a*).

Winter values are used as a proxy for eutrophication in the Baltic Sea area because the plankton has not yet taken up the nutrients. 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). In this study the concentrations of total phosphorus (totP) and nitrogen (totN) measured annually at each station in the winter period were used to assess the level of eutrophication at the particular site.

The statistical analysis encompassed the raw data of zooplankton abundances and the set of environmental data collected for each site and sampling occasion separately. For univariate analysis the Statistica statistical program was used (StatSoft, Inc. 2004). Multivariate data analyses were performed by the Primer statistical program (Clarke & Warwick 2001). Correlation analyses were employed to describe the relationships between abiotic and biotic environmental variables (Sokal & Rohlf 1981).

The Bray-Curtis similarity measure was used to construct the similarity matrices (Bray & Curtis 1957). Spearman rank correlations ρ were computed between environmental data and the similarity matrices of the coefficients of determination (separate analyses for different zooplankton taxa). The analysis shows which environmental variables best predict the variability in zooplankton densities (Bioenv procedure, Clarke & Ainsworth 1993). The significance of the correlation was determined using the Relate program (Clarke & Warwick 2001).

3. Results

Average water temperatures showed no clear trend in the Gulf of Finland over the period analysed. Average salinities decreased gradually from 1998 onwards. The concentration of totP and totN in winter varied considerably between years. Similarly, Chl *a* concentrations fluctuated strongly and displayed no distinct trend (Fig. 2).

In general, among the cladocerans *Bosmina coregoni maritima*, *Evadne nordmanni* and *Pleopsis polyphemoides* were prevalent in the study area. *Synchaeta* spp. and *Keratella* spp. were the dominant rotifers. The most

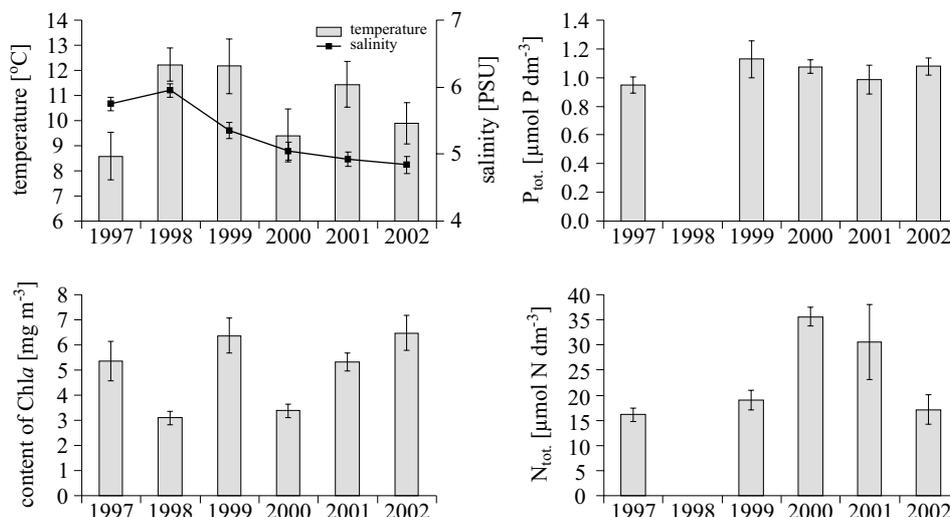


Fig. 2. Interannual changes (average \pm SE) in water temperature [$^{\circ}$ C], salinity [PSU], totP, totN [μ M dm^{-3}] and Chl *a* content [mg m^{-3}] in the Gulf of Finland in 1997–2002

important copepods were *Acartia* spp. and *Eurytemora affinis*. Mero-plankton abundances were low and highly variable, the larvae of *Balanus improvisus* being dominant (Fig. 3, Table 1).

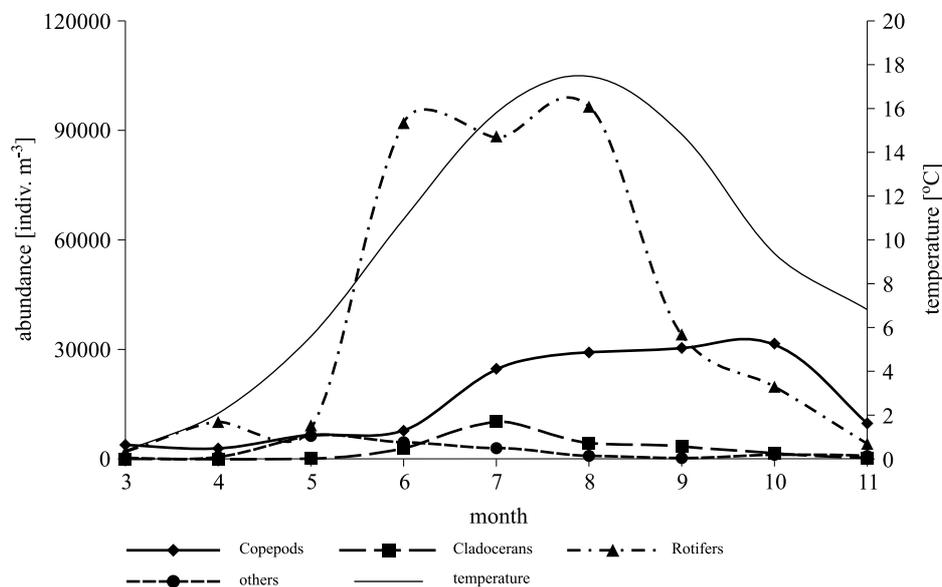


Fig. 3. Seasonal dynamics of temperature and the main zooplankton groups in the Gulf of Finland in 1997–2002

Table 1. Average (\pm SE) and maximum densities of the main zooplankton taxa [indiv. m^{-3}] in the study area during 1997–2002

Zooplankton taxa	Average	Maximum	\pm SE
<i>Acartia</i> spp.	4377	88 000	593
<i>Eurytemora affinis</i>	6011	56 700	433
Cyclopidae	318	7000	47
Copepoda nauplii	13 373	68 750	426
<i>Bosmina coregoni maritima</i>	2805	75 600	524
<i>Evadne nordmanni</i>	582	8400	89
<i>Pleopsis polyphemoides</i>	4746	104 800	1626
<i>Keratella cochlearis</i>	14 837	312 000	2290
<i>Keratella cruciformis</i>	3606	145 000	1276
<i>Keratella quadrata</i>	41 454	511 000	4130
<i>Synchaeta baltica</i>	8323	123 000	1290
<i>Synchaeta monopus</i>	11 582	205 000	2608
<i>Balanus improvisus</i> nauplii	1644	31 700	228
<i>Fritillaria borealis</i>	7	400	3
<i>Cercopagis pengoi</i>	76	800	7
<i>Leptodora kindtii</i>	14	300	8

Zooplankton abundance peaked in 1998 and 2002. The densities of *C. pengoi* were significantly higher in 1999, 2001 and 2002 than in the other years studied. The dynamics of the native predatory cladoceran *Leptodora kindtii* resembled those of *C. pengoi*, though the densities of *L. kindtii* were ten times lower (Fig. 4).

C. pengoi appeared in the water column when the temperature rose above 15°C (Fig. 5). Therefore, only samples satisfying this temperature condition were used in the subsequent analysis of the potential effects of *C. pengoi* on the zooplankton community.

The abundances of non-predatory Cladocera were best explained by the density of *C. pengoi* (Table 2, Figs. 6 and 7). The density of non-predatory Cladocera either increased (Spearman rank order correlations, $p < 0.05$: *B. coregoni maritima* $r = 0.60$) or decreased with increasing density of *C. pengoi* (*E. nordmanni* $r = -0.74$, *P. polyphemoides* $r = -0.73$). *B. c. maritima* tended to stay below the thermocline at higher abundances of *C. pengoi* in the surface layer ($r = -0.61$, $p < 0.01$). Furthermore, thermal stratification and the abundance of the native predator *L. kindtii* explained the additional variability in the density of non-predatory Cladocera (correlations between variability in temperature and Cladocera were < 0.10 ;

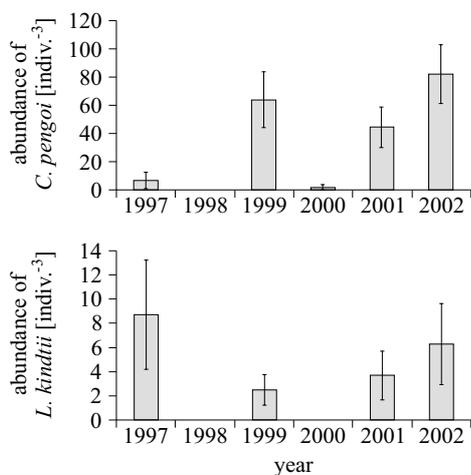


Fig. 4. Interannual changes (average \pm SE) in *Cercopagis pengoi* and *Leptodora kindtii* [indiv. m^{-3}] in the Gulf of Finland in 1997–2002

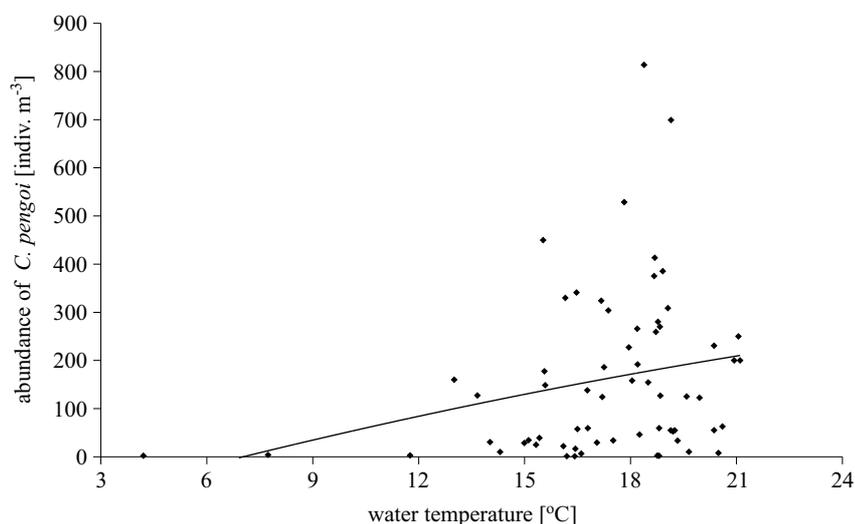


Fig. 5. Relationship between water temperature and density of *Cercopagis pengoi* in the Gulf of Finland in 1997–2002

P. polyphemoides vs *L. kindtii* $r = -0.52$, *E. nordmanni* vs *L. kindtii* $r = -0.55$).

Among the Rotatoria *Keratella cochlearis*, *Synchaeta baltica* and *S. monopus* correlated primarily with *C. pengoi* (*K. cochlearis* vs *C. pengoi* $r = 0.59$, *S. baltica* vs *C. pengoi* $r = -0.59$, *S. monopus* vs *C. pengoi* $r = 0.09$). Other rotifer species were related to salinity, temperature, thermal stratification, eutrophication level, Chl *a* or *L. kindtii*. The strength and direction of the relationship varied between the species under scrutiny.

Table 2. Results of BIOENV analysis showing the best environmental variables predicting the abundances of different mesozooplankton taxa. The abbreviations of the variables are as follows: EUTR-P – eutrophication level (P_{tot}), EUTR-N – eutrophication level (N_{tot}), S – salinity, T – water temperature, ΔT – thermal stratification, CHL – content of Chl *a*, ZOOPLANKTON – total abundance of zooplankton, LEPTODORA – abundance of *Leptodora kindtii*, CERCOPAGIS – abundance of *Cercopagis pengoi*, CYCLOPIDAE – abundance of Cyclopidae, PLEOPSIS – abundance of *Pleopsis polyphemoides*, EVADNE – abundance of *Evadne nordmanni*

Zooplankton taxa	Significant environmental variables	Spearman ρ
<i>Acartia</i> spp.	EUTR-P, S, ΔT	0.188
<i>Eurytemora affinis</i>	EUTR-P, S, ΔT , LEPTODORA	0.286
Cyclopidae	EUTR-P, S	0.406
Copepoda nauplii	EUTR-P, CHL, ΔT	0.225
<i>Bosmina coregoni maritima</i>	CERCOPAGIS	0.328
<i>Evadne nordmanni</i>	ΔT , CERCOPAGIS, LEPTODORA	0.567
<i>Pleopsis polyphemoides</i>	ΔT , CERCOPAGIS, LEPTODORA	0.566
<i>Keratella cochlearis</i>	CERCOPAGIS	0.370
<i>K. cruciformis</i>	EUTR-P, S	0.143
<i>K. quadrata</i>	EUTR-P, CHL, T, ZOOPLANKTON, LEPTODORA	0.363
<i>Synchaeta baltica</i>	S, ΔT , CERCOPAGIS, LEPTODORA	0.292
<i>S. monopus</i>	CHL, T, CERCOPAGIS	0.011
<i>Balanus improvisus</i> nauplii	EUTR-N, EUTR-P, S, T, ZOOPLANKTON	0.215
<i>Fritillaria borealis</i>	T	0.058
<i>Cercopagis pengoi</i>	T, EVADNE, PLEOPSIS	0.543
<i>Leptodora kindtii</i>	EUTR-N, EUTR-P, S, T, CYCLOPIDAE	0.435

With the exception of *E. affinis* ($r = -0.24$), Copepoda did not correlate with *C. pengoi*. The variability in *E. affinis* was explained not only by *C. pengoi*, but also by salinity ($r = 0.29$), eutrophication level ($r < 0.10$) and *L. kindtii* (*E. affinis* vs *L. kindtii* $r = -0.51$). The variability in Cyclopidae (adults, copepodids) was explained by salinity ($r = -0.67$), eutrophication level ($r_{N_{tot}} = -0.25$, $r_{P_{tot}} = 0.20$) and *L. kindtii* ($r = 0.68$). Thermal stratification ($r = -0.55$), salinity ($r = 0.45$), eutrophication level

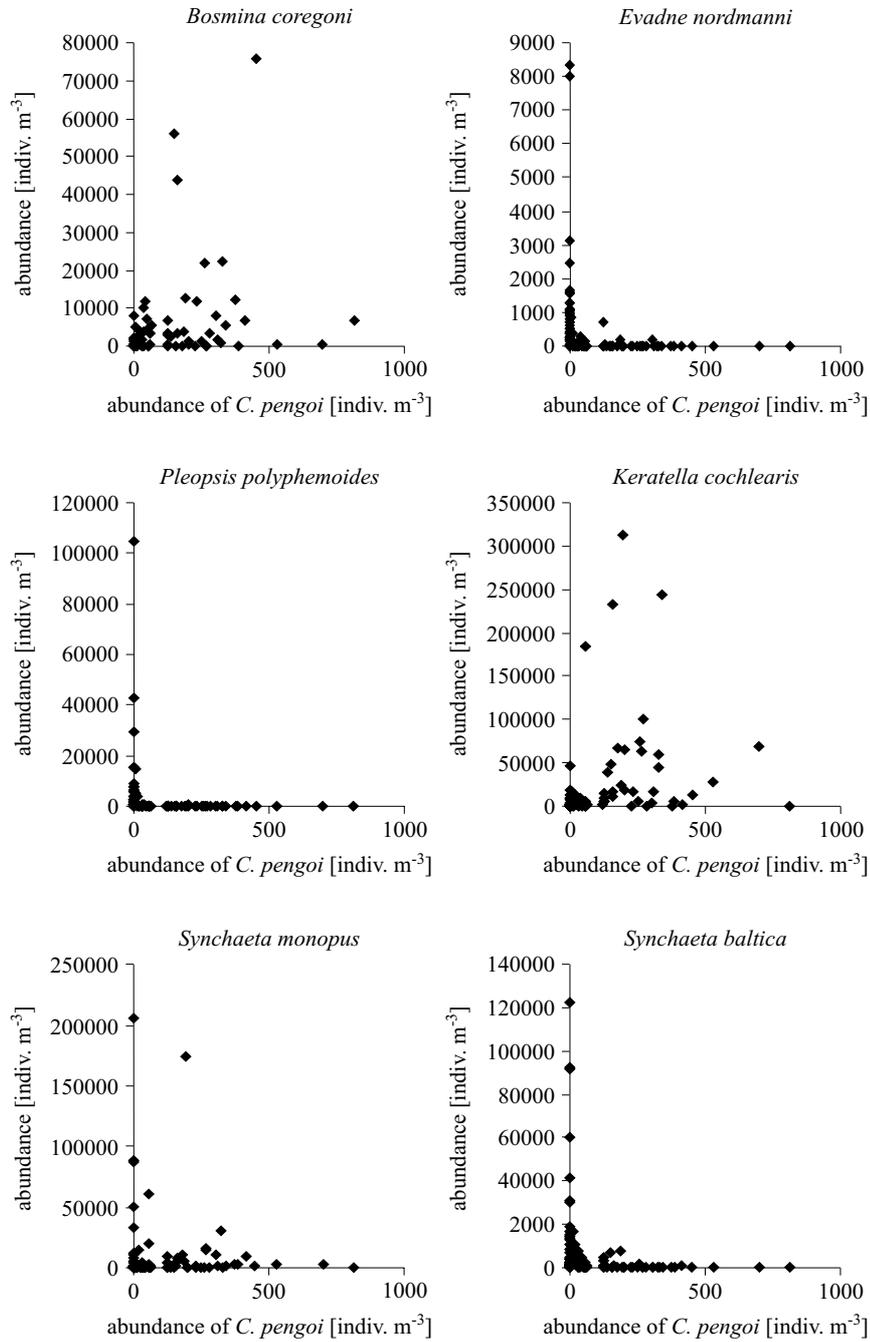


Fig. 6. Scatterplots between the abundances of *Cercopagis pengoi* and other zooplankton taxa in the Gulf of Finland in 1997–2002. Only those taxa were selected that were significantly related to the abundance of the predatory cladoceran in the Bioenv analyses

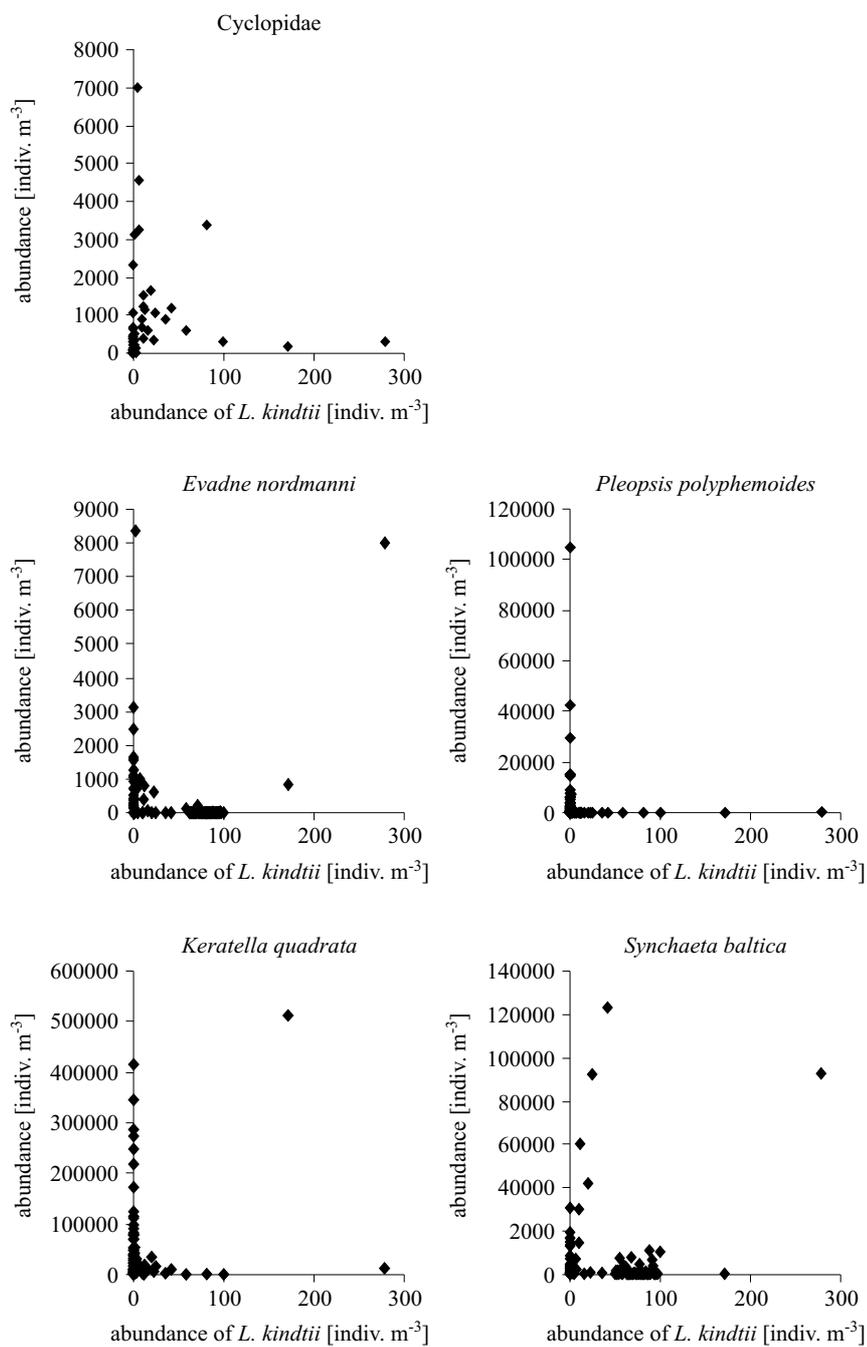


Fig. 7. Scatterplots between the abundances of *Leptodora kindtii* and other zooplankton taxa in the Gulf of Finland in 1997–2002. Only those taxa were selected that were significantly related to the abundance of the predatory cladoceran in the Bioenv analyses

($r < 0.10$) and Chl *a* ($r < 0.10$) affected *Acartia* spp. The nauplii of Copepoda correlated with thermal stratification ($r = -0.41$) and Chl *a* ($r = 0.33$).

The abundance of meroplankton was explained by temperature ($r < 0.10$), salinity ($r = 0.34$), eutrophication level ($r < 0.10$) and zooplankton density ($r = 0.60$), but not by the density of the predators studied. The abundance of *C. pengoi* was best explained by thermal stratification ($r = -0.24$) and the densities of selected cladocerans (*E. nordmanni* and *P. polyphemoides*; for *r* values, see above). The abundance of *L. kindtii* was correlated with Chl *a* ($r = 0.33$), temperature ($r = 0.36$), salinity ($r = -0.64$) and the density of the eight zooplankton taxa (for *r* values, see above).

4. Discussion

The results indicated that both intermediate predators and bottom-up effects affect the zooplankton communities to an equal extent and that predation by the non-indigenous *C. 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 *C. pengoi* and *L. kindtii* were included in the models of different mesozooplankton taxa on 57% of occasions, whereas the eutrophication level accounted for 50% of differences.

Separate correlations between the density of *C. pengoi* and the native herbivorous mesozooplankton were either positive or negative. The positive interactions between species may be a consequence of the similar seasonal dynamics (e.g. *C. pengoi* vs *B. coregoni maritima* or *K. cochlearis*), whereas the negative values may be due to the different seasonality (e.g., *C. pengoi* vs *E. nordmanni* or *P. polyphemoides*).

C. pengoi was the only significant variable in the models of *B. coregoni maritima* and *K. cochlearis*. Alternatively, the indirect effect of selective predation on other zooplankton taxa may favour the population growth of these species and may explain their rising densities with the increase in *C. pengoi*. However, when the analysis was performed separately for the layers above and below the thermocline, *B. c. maritima* tended to remain below the thermocline at greater abundances of *C. pengoi* in the surface layer. These results suggest the direct predation of *C. pengoi* on *B. c. maritima*. No diurnal vertical migration of *C. pengoi* has been recorded in the Gulf of Finland, and the majority of the population is located in the upper water layer (Gorokhova et al. 2000). Hence, the deeper water layers may be considered a refuge for prey species such as *B. c. maritima*.

Previous field observations and laboratory trials showed that *C. pengoi* is able to feed on cladocerans (Laxson et al. 2003, Kotta et al. 2004, Ojaveer et al. 2004), earlier developmental stages of copepods, rotifers (Gorokhova

1998) and cirriped larvae (M. Simm, personal comment). The results of our study indicate that cladocerans and rotifers represent the most likely prey for *C. pengoi* in the Gulf of Finland.

Thermal stratification was an important variable for the dynamics of *C. pengoi*: the density of this cladoceran increased with rising temperature stratification (i.e., with decreasing wind stress). Differences in thermal stratification may explain the large-scale variability in *C. 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 *C. 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 study). Earlier studies stressed the importance of both temperature and water column stability for the development of *C. 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°C its effect was not significant for *C. 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 *C. pengoi* (Uitto et al. 1999, Strake 2002). In those studies, however, the effect of eutrophication was not quantified. Our study, on the other hand, clearly demonstrated that eutrophication had no significant effect on *C. pengoi* within a broad range of spatial and temporal variability.

Taking into account the moderate densities of *C. 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. 2004). Our study indicates that manipulative experiments on the predation of *C. 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 *C. pengoi* would be particularly rewarding in order to demonstrate the causative links between the dynamics of *C. pengoi* and other trophic levels in recipient ecosystems.

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