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Consequences of invasion of a predatory cladoceran

by

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ABSTARCT

In 1992, a carnivorous species of Ponto-Caspian origin - the cladoceran *Cercopagis pengoi* (Ostroumov, 1891) - invaded the Baltic Sea (Gulf of Riga and Gulf of Finland)). In the NE Gulf of Riga, the abundance of the species has increased linearily in 1992 - 1999. Dependent upon meteorological conditions, the cladoceran is present in the pelgic zooplankton community for 7-20 weeks annually by having several abundance peaks per year. After the invasion of *C. pengoi* the abundance level of its potential prey - *Bosmina coregoni maritima* - has been significantly lower than during the pre-invasion time (t-test, $p<0.01$). Abundance of other native cladocerans (e.g., *Evadne nordmanni* and *Pleopsis polyphemoides*) or *nauplii* of copepods did not exhibit any peculiar changes after the invasion. During 1994-1998, the mean share of *C. pengoi* in the diet of most abundant planktivorous fish - herring, *Clupea harengus membras*, smelt, *Osmerus eperlanus* and three-spined stickleback, *Gasterosteus aculeatus*, remained below 7% (wet weight), whilst in the food of bleak (*Alburnus alburnus*) it constituted 69%. In 1999, *C. pengoi* made an average 59% of herring diet in the open Gulf of Riga, the year of the highest *C. pengoi* population abundance in the record. The introduction of *C. pengoi* to the Baltic Sea probably influence fish stock structure and may prove beneficial to commrecial fisheries production if it enhances transfer of previously less-utilized mesozooplankton production to planktivorous fishes (*Bosmina* → *Cercopagis* → planktivorous fish). Invasion of *C. pengoi* obviously complicates energy flow to higher trophic levels, but probably increases the overall stability of the Baltic ecosystem. Questioning of some taxonomic identification keys of the genus *C. pengoi*, alterations in mesozooplankton community (mainly in the warm season), changes in the diet of several fishes and economic loss to fishers (by chocking fishing gears) are important consequences of this invasion. As this euryhaline species originates from warmer climate conditions, the global warming should favour the extension of its area in the Baltic Sea region and support further increase in abundance.

Introduction

World-wide human-mediated spread of non-indigenous aquatic organisms due to both ecological impacts and economic losses is one of the recent major concerns, amongst others, of scientists, managers and resource users. Phytoplankton, zooplankton, benthic invertebrates, fish, aquatic plants and parasites are all known as potential invaders. Their impacts which are often unpredictable are seen at all trophic levels of aquatic ecosystems, by involving also substantial changes in foodweb interactions, modifications of abiotic habitats, alterations in energy flow patterns and transformations in cycling of contaminants (Carlton 1996, Eno 1996, Dobson and Mackie 1998, Kelleher et al. 1998, Ketelaars et al. 1999, Olenin and Leppäkoski 1999, Reise et al. 1999). Estimated economic losses caused by non/indigenous species may reach to millions of dollars (Glassner-Shwayder 1999).

Invasion history of *C. pengoi* (Ostroumov, 1981), a predatory cladoceran of the Ponto-Caspian origin, dates back to early 1990s. Three years after the first finding in the Gulf of Riga (Baltic Sea), the species was recorded in several locations in the Gulf of Finland (Kivi 1995, Avinski 1997). Later on, expansion of distribution area further north (Gulf of Bothnia) and south (Gulf of Gdansk) took place (Zmudzinski 1999, Leppäkoski pers. comm.). After invasion to Lake Ontario (North America) in 1998, the species was observed in the following year in Lake Michigan and five New York Fingerling lakes (MacIsaac et al. 1999, Makarewitz et al. subm.).

Based on new data mainly from the long-term studies in the Gulf of Riga (Baltic Sea) and the revision of existing knowledge (published literature and manuscripts) from the invaded areas (Baltic Sea and Great Lakes) consequences of invasion of *C. pengoi* are summarised in this paper.

Materials and Methods

In the Gulf of Riga, zooplankton samples were collected by means of Juday net (90 µm mesh) from bottom to the surface at the fixed station (depth 10 m) weekly during 1973-1999 (Figure 1). The samples were preserved in 4% formaline solution and analysed following the routine methods. Annual means of *C. pengoi* abundance (ind m^{-3}) were calculated for June-September - the period of occurrence of the species in the pelagic mesozooplankton community. Collection of fish for stomach examinations and simultaneous sampling of mesozooplankton was performed during monthly day-time experimental bottom trawl surveys in 1994-1998 (for details see Ojaveer 1997). In 1999, herring was caught by pelagic commercial trawl (trawling depth 0-33 m) in 12 stations over the whole Gulf of Riga during day time from 15 to 20 July (Figure 1).

In the Gulf of Finland, altogether 12 stations were routinely sampled three times a year (May, August and October-November) along the eastern, central and western transects situated at the southern coast until 1992 (see Ojaveer et al. 1999). Since 1993, over 20 stations were sampled along the southern coast of the Gulf of Finland in August. Finding locations of *C. pengoi* (sampled in August 1992 and 1995) are only shown in this paper (Figure 1).

In Väinameri Archipelago (west of Estonia), three mesozooplankton samples in were taken on July 19, 1994.

Fish feeding sample consisted usually of stomachs of 20 individuals which were stored prior to analysis in 4% formaline solution. Stomach analysis were performed by routine methods. For calculation of the mean percent contribution of *C. pengoi* in the fish diet, results of surveys in the main feeding areas of different fish species/age-groups during the essential feeding period (Ojaveer 1997, Ojaveer et al. 1997) were taken into account.

The Ivlev's electivity index of fish for *C. pengoi* was calculated by means of the following formula:

$$E= (N_w-N_s)/(N_w+N_s),$$

where N_e and N_s is the abundance of *C. pengoi* in the environment and fish stomachs, respectively.

Results and Discussion

<u>Population abundance dynamics</u>

As in the Gulf of Riga, *C. pengoi* was first observed in the Gulf of Finland in 1992 - at the southern coast of the basin (Figure 1). However, the cladoceran was not encountered in mesozooplankton samples in 1993 and 1994. In August 1995, the species was observed again at low abundances (<30 ind m^{-3}) in several sites at the southern coast

(Figure 1). Occurrence of *C. pengoi* in the eastern and northern Gulf of Finland in 1995 is documented by Kivi (1995) and Avinski (1997). Thus, by summer 1995, *C. pengoi* colonized the whole Gulf of Finland.

Since the invasion in 1992, the annual mean abundance (A, ind m^{-3}) of *C. pengoi* has increased linearly in the NE Gulf of Riga (r^2=0.64, p<0.05) by reaching the peak in 1999 – 173 ind m^{-3} (Figure 2). No significant correlation was found between the abundance and water temperature during the warm season. This suggests that other factors than abiotic conditions alone are responsible for *C. pengoi* abundance dynamics during the first 8 invasion years. It should be noted that the species has reached higher maximum abundances in the Great Lakes than in the Baltic Sea: 2544 ind m^{-3} in the Lake Ontario (Ojaveer et al., submitted) and 1800 ind m^{-3} in the Gulf of Finland (Uitto et al., 1999) and 800 m^{-3} in the Gulf of Riga (Ojaveer et al., 1998).

Dependent probably upon by climatic conditions (mainly winds and temperature), the cladoceran is present in the pelagic mesozooplankton community in the Gulf of Riga for 7-20 weeks annually by having 1-3 abundance peaks per year. As a long-term mean, *C. pengoi* reached peak densities in the first half of August (mean 231 ind m^{-3}) by exhibiting significantly higher abundances in the first half of the month than most of the remaining vegetation period (Figure 3). Usually, the species appears in pelagic mesozooplankton community at water temperatures over 15 ºC and starts to disappear when temperature falls below 8 ºC. In spring 2000, however, the species was unexpectedly encountered in zooplankton samples in the NE Gulf of Riga at 11 ºC. Similar phenomenon (at 6 ºC) has been observed in the Lake Ontario (H. MacIsaac pers. comm.)

The wide range of optimal salinity (from 2 to 10 psu) does not restrict spreading of *C. pengoi* throughout most of the Baltic Sea. The basic factors limiting the distribution of the species are water temperature and food availability (Avinski 1997). Additionally, stability of the water column may be important: higher abundances have been recorded in sheltered locations (less affected by wind-induced water movements) and in the areas of lack of currents (Ojaveer et al. 1998, Avinski 1997) whereas the species was encountered at minumum abundances (1 ind m^{-3}) in one station in the region of strong currents (Väinameri Archipelago) in 1994 (Figure 1). Significantly higher offshore population abundances of *C. pengoi*, compared to near-coastal areas in Lake Ontario could probably be explained by substantially weaker currents in the open lake (Ojaveer et al. submitted). With regards to coastal-open sea distribution, certain disagrement occurs in the Baltic basins. Avinski (1997) reported avoidance of shallow and most fresh waters by *C. pengoi* in the eastern Gulf of Finland, where species abundance was, an average 22 times smaller that in other locations. In contrast, in the Gulf of Riga, *C. pengoi* shows remarkably larger population densities in shallow and sheltered Pärnu Bay (Ojaveer et al 1998).

C. pengoi prefers warm water environment: its distribution is mostly confined to upper layers both in the Baltic Sea and Lake Ontario during the day and night. However, a few individuals have been recorded in colder waters beneath the seasonal thermocline. Thus, no diurnal vertical migration was evident (Avinski 1997, Krylov et al. 1999, Ojaveer et al. submitted).

<u>Taxonomic identification</u>

Two different morphological forms of cercopagids have been found both in the Gulf of Riga (Simm and Ojaveer 1999) and Lake Ontario (Makarewicz et al., submitted). In spring and early summer, individuals keyed to species *Cercopagis* (*Apagis*) *ossiani* (characterised by straight and relatively short caudal process and forwardly bent tips of barbs) dominated whereas *Cercopagis* (*Cercopagis*) *pengoi*-type individuals (having characteristic loop at the end of the relatively long caudal process and straight or backwardly bent tips of barbs) only occurred the rest of the time. According to taxonomic key of identification, these species belong to the two subgenera of the genus *Cercopagis* – *Cercopagis* and *Apagis* (Mordukhai-Boltovskoi and Rivier 1987). However, based on recent studies in invaded basins, this taxonomic identification has been questioned. Simm and Ojaveer (1999) suggested that *C. ossiani*-type individuals represent the first parthenogenetic generation of the species *C. pengoi*, hatched from resting eggs. This suggestion is in a line with another recent study conducted by Makarewicz et al. (submitted): it was concluded by using the mitochondrial DNA analyses, that *C. ossiani* and *C. pengoi* are morphologically distinctive forms of a single species. Consequently, up to present commonly accepted key of identification (of the genus *Cercopagis*) was questioned in invasion studies. This is, without any doubt, one of the most substantial outcomes of this invasion to date and strongly underlines the continuos need for taxonomic studies (and relevant experts) in biological invasions.

Changes in zooplankton communities

Long-term abundance dynamics of the small-sized cladoceran - *Bosmina coregoni maritima* evidences that significant differences occur prior and after the invasion of the predatory *C. pengoi* (t-test, p<0.01). Although a declining tendency in the abundance of *B. c. maritima* was established before the invasion of *C. pengoi* and a slight increase was recorded during last four years (1996-1999) there were no such a long-lasting low-abundance values recorded since 1973 (Figure 4). In contrast, there are no evidences on similar drastic abundance changes of other cladocerans in the Gulf of Riga - *Evadne nordmanni* and *Pleopsis polyphemoides*. Other suitable and abundant prey for *C. pengoi* - *nauplii* of copepods show continuously increasing tendency since 1986, however, with higher variability and more moderate slope since the invasion of *C. pengoi* in 1992 (Figure 4).

According to Gorokhova (1998), copepods (nauplii and copepodites of *Acartia*, *Eurytemora* and *Temora*), rotifers (*Synchaeta*) and cladocerans (*Evadne*) constituted 60, 20 and 20%, respectively in the diet of *C. pengoi* in the northern Baltic Proper. Thus, in this part of the Baltic Sea, considerable dietary overlap of the cladoceran with abundant planktivorous fish do occur. This may contribute, in case of high *C. pengoi* abundances, to a declined food resource for important commercial fish - herring and sprat. In addition, Uitto et al (1999) argued that if copepod predation by *C. pengoi* is also the case in the eastern Gulf of Finland, it may result in indirect positive effect on ciliates which are regulated by mesozooplankton predation in the Baltic Sea.

Low abundance of the small-sized cladoceran – *Bosmina*, accompanied by the invasion of *C. pengoi* since 1992 could be the direct effect of predation by the exotic species. It has already been shown in other invaded ecosystems that drastic changes in zooplankton community, particularily declines in the abundance of small-sized cladocerans have taken place after invasion of another predatory cladoceran similar to *C. pengoi* - *Bythotrephes cederstroemi*, probably due to predation (e.g., Lehman and Caceres 1993, Yan and Pawson 1997). If such direct predator-prey relationship occurs, i.e. the decline in *Bosmina* population abundance in the Gulf of Riga is caused by *C. pengoi* predation, impact of this invasion to the zooplankton dynamics is superior to other, previously documented cause-effect relationships between natural and/or other anthropogenic impacts and mesozooplankton community (e.g., Simm 1976, Sidrevics et al. 1993, Ojaveer et al. 1998, Yurkovskis et al. 1999).

Similarily to the Baltic Sea, but much rapidly, important changes have taken place in zooplankton community of Lake Ontario: decrease in population abundance of *Bosmina* sp. and replacement by *Daphnia retrocurva* was already observed in the first year of invasion of *C. pengoi* (Barbiero et al. submitted).

Consumption by fish

Long-term fish stomach investigations in the main fish feeding areas in the Gulf of Riga during the essential feeding period (June-September) in 1994-1998 revealed that except bleak, the mean share of the predatory cladoceran in fish stomachs did not exceed 7 % (Table 1). However, strong seasonality is evident: the mean percent contribution of the cladoceran in herring stomachs in this period varied from 0 and 0.1 % in June and July to 11.3 and 16.6 in September and August, respectively. However, the situation was different in the Gulf of Riga in July 1999: herring diet consisted in 59% of *C. pengoi* (wet weight) and stomachs of 66% herrings contained this exotic species. It is previously known that *C. pengoi* population was very abundant in the coastal Gulf of Riga in 1999 (see above) which may be one of the reasons. Unfortunately, we lack of zooplankton data from the 1999 cruise which limits the explanation of such high dietary importance of *C. pengoi* in herring diet in the open gulf in July 1999.

Both the minimum and mean size of different fish species having preyed upon *C. pengoi* varied more than twice: 9-spined stickleback 3.4 vs. smelt 7.3 cm, and 9-spined stickleback 4.3 vs. 1+ herring 14.0 cm, respectively (Table 2). Size-dependent consumption of *C. pengoi* by herring and smelt was recorded: the mean length of fish (above the minimum size being able to ingest *C. pengoi*) having *C. pengoi* in stomachs significantly exceeded that of without *C. pengoi* while 0-group herring did almost not feed on this relatively large prey (Table 2). By length groups, herring with L>13 cm consumed notably higher proportions of *C. pengoi* than smaller individuals (Table 3).

However, significant differences were not observed for sticklebacks and bleak (Table 2) suggesting that fish length (above the minimum size) is not the limiting factor for consumption of the cladoceran. The above findings point to a species-specific size-dependent predation by fish on *C. pengoi*. Similarily, studies in the Great Lakes with another recent invader, predatory cladoceran similar to *C. pengoi – Bythotrephes cederstoremi* have shown that (1) *Bhytotrephes* is not a preferred prey for young fish, (2) there is a treshold size of fish that can utilize *Bhytotrephes* and (3) as fish increase in size, they are more likely to consume Bhytotrephes (Barnhisel and Harvey 1995). Therefore, only larger (older) fish are able to ingest *C. pengoi* and gain directly profit from this invasion.

Herring, smelt and sticklebacks do not feed selectively on the cladoceran, evidenced by negative Ivlev's electivity indices: the extremes were recorded for 1+ herring (mean -0.10) while 0-group individuals totally avoid this prey (Table 1). However, with the exception of 0-group herring, if the cladoceran was present in fish stomachs, it was consumed numerically at least by 25% (max. 93) of fish by contributing similar percentage (max. 86%) of the stomach biomass (Table 2). Due to different temperature preferences of *C. pengoi* compared to 1+ smelt and older herring, vertical distribution of those predators and their prey (in difference from sticklebacks and younger herring) do not overlap: the fish inhabit colder waters when the majority of the *C. pengoi* stock remains above the thermocline. Therefore, occurrence of *C. pengoi* in stomachs of those fish probably reflects unsufficient amount of proper food (e.g., large calanoid copepods and mysids) in deeper water layers that forces the fish to perform upward vertical migration for searching energetically profitable diet in the warmer surface waters.

It is concluded here that *C. pengoi* is generally not a favoured prey for planktivorous fishes in the Gulf of Riga. However, being energetically profitable prey (probably due to relatively large dimensions) the cladoceran can periodically make a substantial portion of fish diet. Consumption of *C. pengoi* by some fish with different abiotic preferences (e.g., cold-water preferring and therefore deeper water column inhabiting smelt and older herring) may reflect forced dietary selection of these fish due to shortage or lack of suitable prey in deeper water layers.

Impact on fish production and fisheries

Changes in food-web and energy transfer in lower trophic levels, due to the invasion of *C. pengoi*, will likely impact the structure of fish stocks. Introduction of the cladoceran to the Gulf of Riga may prove beneficial to commercial fish production (mainly gulf herring, but also smelt) if it enhances transfer of less favourable mesozooplankton production to higher trophic levels (e.g., *Bosmina* → *Cercopagis* → planktivorous fish). This is probably most important during the periods of shortage of energetically suitable food that have resulted in decreased individual body weight of herring in the northern Baltic (Flinkman 1999). In the light of studies of Gorokhova (1998) in the northern Baltic Proper, *C. pengoi* may relay on the same food resource as important commercial fish (herring and sprat). This may result in decreased food for these fish and, possibly, declined planktivorous fish production. However, prior to quantification of *C. pengoi* impacts on commercial fish production, experimental studies on predation effects of this predatory cladoceran on different zooplankton communities of the Baltic Sea are badly needed.

The direct impact of this invasion to fisheries is due to chocking of fishing equipment by *C. pengoi*. This may cause substantial harm to fishers - the estimated economic loss in one fish farm in the eastern Gulf of Finland averaged for 1996 -1998 at minimum 50,000 USD (Panov et al. 1999).

General ecosytem impacts

Invasion of this predatory cladoceran obviously increases overall stability and functional diversity of the Baltic Sea by incorporating additional trophic link in the food-web of the invaded sub-systems. Presently, the invasion has additionally resulted in elevated relative importance of the warm-water planktonic invertebrates in the energy flow to cold-water bentho-pelagic fish of the Baltic Sea (through direct predation). In some sheltered coastal shallow areas characterised by high *C. pengoi* but low predator abundance in the warm season, part of the *C. pengoi* production may die and sink to the bottom, and undergo there heterotrophic decomposition processes. This obviously complicates energy transfer to higher trophic levels in these areas. However, studies to date have shown that sinking of dead animals to bottom is probably not intense in deeper areas (e.g., Ojaveer et al. submitted). As this euryhaline species originates from warmer climate conditions, the global warming should favour the extension of its area in the Baltic Sea region and support further increase in abundance.

In the Baltic Sea, *C. pengoi* probably causes comparatively larger ecosystem changes in large gulfs (Gulf of Finland and Gulf of Riga) whereas its impact in other subsystems (e.g., open Baltic Proper) should remain generally insignificant.

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Table 1. Long-term mean contribution (%, wet weight) of *Cercopagis pengoi* in fish diet and Ivlev's electivity index (with S.E. and n) for most abundant pelagic fish in their main feeding areas of the Gulf of Riga during the main feeding period (June-September) in 1994-1998. Each sample consisted of 20 fish.

Fish	%			Electivity		
	mean	S.E	n	mean	S.E.	n
Herring *Clupea harengus membras*						
Adult	6.3	3.0	51	-0.10	0.17	34
0-group	0.1	0.1	20	-1.00	0	6
Smelt *Osmerus eperlanus*						
Adult	6.3	4.4	25	-0.84	0.16	12
Juvenile	3.7	2.7	30	-0.43	0.23	13
Sticklebacks *Gasterosteus aculeatus*	6.1	2.6	27	-0.47	0.19	18
Bleak *Alburnus alburnus*	68.5	20.4	5			

Table 2. Statistics of fish samples where at least 1 fish contained *Cercopagis pengoi* in the stomach. Samples were collected in main feeding areas of the Gulf of Riga during the main feeding period (June-September) in1994-1998. Fish length (total length) is given in cm.

	Min. length with *Cerc.*	Mean length with *Cerc.*	Mean length without *Cerc.*	Difference	% of fish with *Cerc.*	% of *Cerc.* in diet (wet wt.)	n
Herring (1+)		**14.0**	13.3	P<0.05	53.6	45.7	256
0-group	4.1	**5.2**	5.1	ns	7.7	1.4	40
Smelt (1+)		**13.1**	10.5	P<0.001	25.0	40.8	78
0-group	7.3	**8.1**	7.9	ns	33.3	33.7	60
3-spined stickleback	4.1	5.0	**5.3**	P<0.05	25.0	26.9	94
9-spined stickleback	3.4	4.3	**5.0**	P<0.001	51.1	44.7	60
Bleak	6.2	9.8	**10.2**	ns	93.4	85.7	70

Table 3. Relative importance (%) of *Cercopagis pengoi* in herring diet on wet weight basis (mean, S.E., n) and abundance basis (the share of fish with *C. pengoi* in stomachs) in the Gulf of Riga in July 1999.

	Length interval (cm)								*Total*
	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	17.0-17.9	10.0-17.9
Mean	25.7	42.8	33.7	64.0	65.1	79.8	76.9	77.8	59.1
S.E.	16.7	8.0	6.6	7.9	7.8	5.3	8.4	14.7	3.0
n	7	36	48	29	33	54	23	9	239
Abund. %	28.6	50.0	39.5	75.9	72.7	85.2	82.6	77.8	65.7

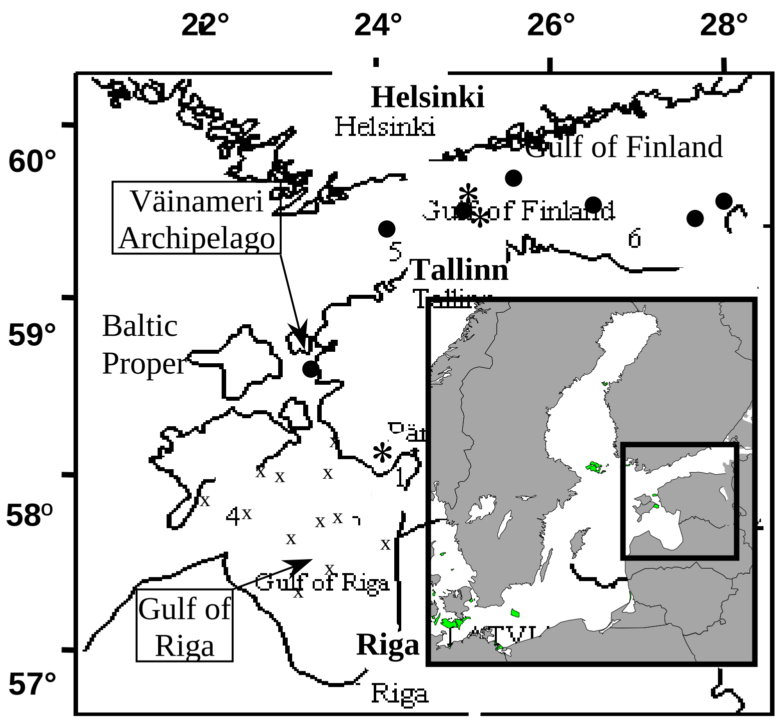

Figure 1. Finding sites of *Cercopagis pengoi* in the Gulf of Finland and Gulf of Riga in 1992 (asterisks), in Väinameri Archipelago in 1994 and Gulf of Finland in 1995 (filled circles), zooplankton long-term monitoring station in the NE part of the Gulf of Riga (asterisk) and sampling stations of herring for feeding analysis in the Gulf of Riga in 1999 (crosses).

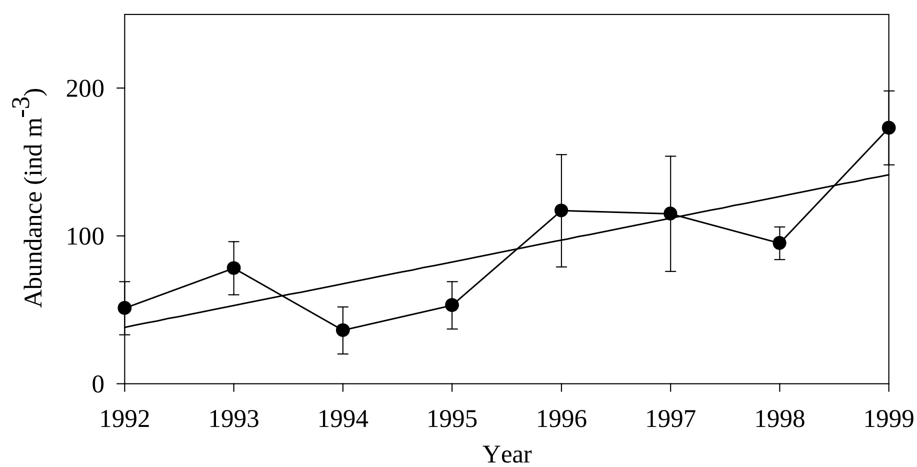

Figure 2. Abundance dynamics of *Cercopagis pengoi* (annual means with S.E. bars and linear regression line) in zooplankton monitoring station in the Gulf of Riga during 1992-1999.

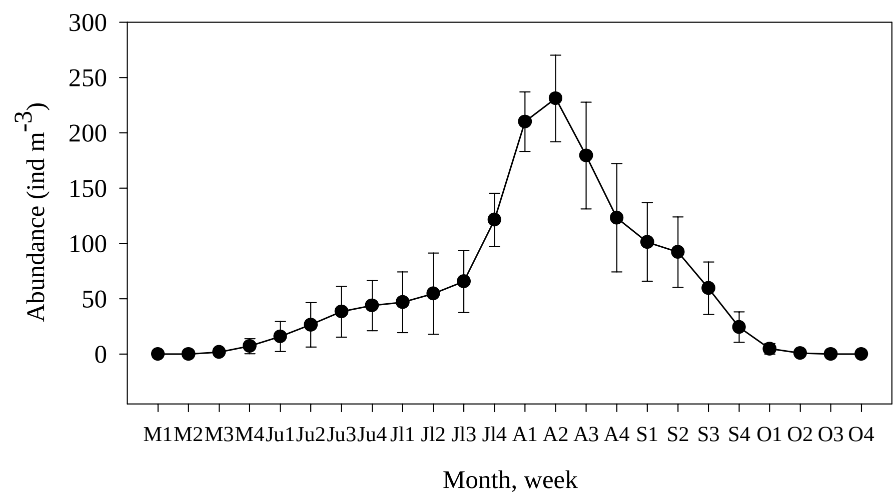

Figure 3. Abundance dynamics of *Cercopagis pengoi* (weekly means with S.E. bars) in the long-term zooplankton monitoring station in the Gulf of Riga during May-October 1992-1999

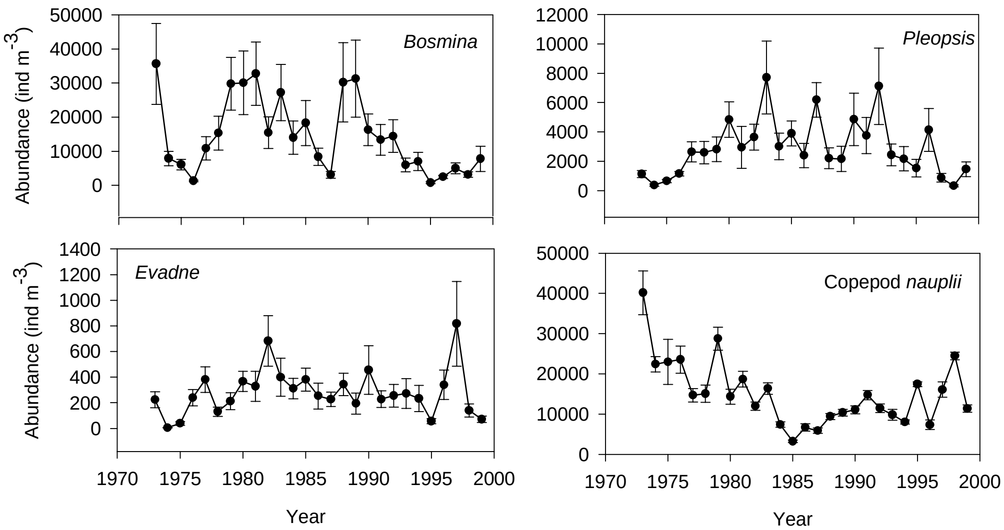

Figure 4. Long-term abundance dynamics of selected mesozooplankters in the norteastern part of the Gulf of Riga during 1973-1999.