Distribution, population structure and ecosystem effects of the invader *Cercopagis pengoi* (Polyphemoidea, Cladocera) in the Gulf of Finland and the open Baltic Sea*

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Abstract

Spatial distribution, density, biomass, population structure, predation effects, and the influence of abiotic environmental characteristics (salinity, water temperature, transparency, and depth) on a population of the Ponto-Caspian invasive cladoceran *Cercopagis pengoi* (Ostroumov, 1891) were studied in the Gulf of Finland and the open Baltic Sea (August 1999 and 2004). In our study in 1999, this species was first recorded in plankton of open south–eastern Baltic waters. The age and sexual structure of the *C. pengoi* population were interrelated with population density. The strongest impact of *C. pengoi* predation on the pelagic community in the Gulf of Finland was registered at the stations where the percentage of *C. pengoi* in the total zooplankton biomass was the highest. The calculated impact values of *C. pengoi* exceeded those registered a decade ago, during the first years after *Cercopagis* had invaded the eastern Gulf of Finland.

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1. Introduction

The predaceous cladoceran *Cercopagis pengoi* (Ostroumov, 1891) (Fig. 1) is a native inhabitant of the northern part of the Caspian Sea and the brackish water parts of the Azov, Black and Aral Seas (Mordukhai-Boltovskoi & Rivier 1987). In 1992, this species was first found in the Gulf of Riga and along the south–western coast of the Gulf of Finland of the Baltic Sea (Ojaveer & Lumberg 1995, Ojaveer et al. 2000), and in 1995 it was recorded in the eastern part of the Gulf of Finland (Avinski 1997). Since that time, *C. pengoi* has adapted to new conditions and become distributed widely throughout the Baltic Sea (Fig. 2).

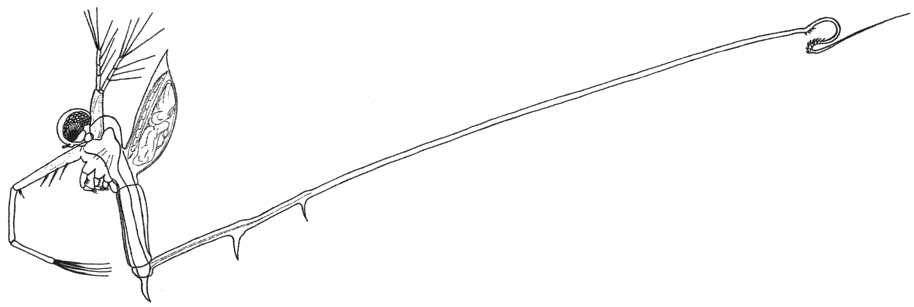

Fig. 1. *Cercopagis pengoi*: parthenogenetic female from the Gulf of Finland, sampled in August 1999 (orig.)

A permanent *C. pengoi* population has been formed in the Gulf of Finland (Avinski & Telesh 1999, Krylov et al. 1999, Telesh et al. 2000, Litvinchuk et al. 2001). In 1997, *C. pengoi* was detected in the Gotland region of the open Baltic Sea (Gorokhova et al. 2000). In the southern part of the open Baltic Sea *C. pengoi* was not detected before 1999. Moreover, in 1999, the species was also found in the south–eastern part of the Baltic Sea – in the Gulf of Gdańsk and the Vistula Lagoon – both in plankton (Bielecka et al. 2000) and in benthos samples (Żmudziński 1999, Naumenko & Polunina 2000, Jurasz et al. 2000). In 2001, *C. pengoi* was recorded in the northern part of the open Baltic Sea (to the north of the Gotland basin) (Avinski & Ryabova 2002). Those investigations, however, did not provide sufficient details on the population structure of *C. pengoi*, and quantitative data were presented only for the Gulf of Finland and the Gotland region. Information about the distribution and peculiarities of the *C. pengoi* population in the vast areas of the Baltic Sea from the eastern part of the Gulf of Finland to the south–eastern part of the open Baltic Sea was lacking.

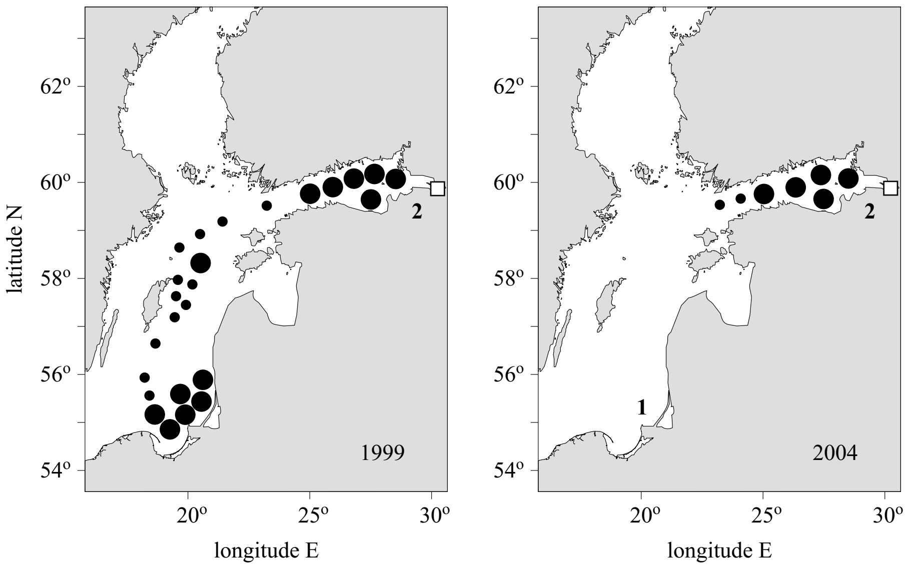

Fig. 2. Distribution of *Cercopagis pengoi* in the Baltic Sea in 1999 and 2004 (large circles – density exceeds 100 individuals per cubic meter); 1 – the south–eastern open Baltic Sea, 2 – Luzhskaya and Koporskaya Bights

The aim of this paper was to study the spatial distribution, density and biomass, population structure, predation effects of *C. pengoi*, and influence of abiotic environmental characteristics on the population of *C. pengoi* in the Gulf of Finland and the open Baltic Sea.

2. Material and methods

Zooplankton samples were collected in 1999 (August, 1–15) and 2004 (August, 1–8) during the cruises of the research vessel 'Sibiriakov' in the Gulf of Finland, the central Baltic Sea (including the HELCOM profile), the open waters of the south–eastern Baltic Sea, and the Bornholm region. In total, 40 and 36 stations were sampled during the two years, respectively.

Samples were taken by vertical hauls with the standard Juday quantitative plankton net (opening diameter 0.2 m, mesh size 138 μm) from 20 m depth to the surface. Such a sampling procedure was used because it is known from literature data that *C. pengoi* prefers to stay above the thermocline – usually in the upper (0–20 m) layers of water that are the warmest, brackish and rich in food resources (Avinski & Telesh 1999, Bolshagin & Krylov 2003). A similar type of vertical distribution of *C. pengoi* was described in the northern part of the open Baltic Sea (Gorokhova et al. 2000) and in the North American Lake Ontario (Laxson et al. 2003), which this species has recently invaded.

All zooplankton samples were collected during the daytime and preserved in 4% formalin. Water transparency (Secchi depth), temperature and salinity profiles (from surface to 20 m depth, at 5 m intervals) were measured during each sample collection. At the majority of sampling stations the thermocline was recorded below 20 m; thus for the correlation analyses of *Cercopagis* distribution the temperature and salinity values were averaged for the 0–20 m water column. *Cercopagis* (as well as other planktonic organisms) were counted and measured under a dissecting microscope in the whole sample (without sub-dividing it into sub-samples). Statistical analysis was carried out using STATISTICA 6.0.

The impact I of a population of an invasive, non-indigenous species on the native community can be determined as the cumulative effect of factors defining the population range size R, population density or biomass A, and some measure of the species' effect E on the community or ecosystem (Parker et al. 1999):

$$I = R\,A\,E. \tag{1}$$

Later it was suggested that the population pressure of *C. pengoi* during its maximum population density can be considered as a measure of the invader's effect on the native community (Telesh et al. 2001) that can be calculated as the ratio of the predator's consumption rate C_i to the production rate of the potential prey organisms P_{hz}:

$$E = C_i/P_{hz}. \tag{2}$$

The abundance of *C. pengoi* A measured as the ratio of the invader's population density N_i to the total zooplankton density N_z was considered a quantitative characteristic providing information on the role of *C. pengoi* in the zooplankton community structure:

$$A = N_i/N_z. \tag{3}$$

The range R of the invasive species is estimated as the ratio of the area occupied by the invader's population R_i to the total area of the water body R_{tot}:

$$R = R_i/R_{tot}. \tag{4}$$

Eqs. (1)–(4) provide the formula for calculating the overall impact I of the predatory invasive species on the zooplankton community (Telesh et al. 2001):

$$I = (R_i/R_{tot})(N_i/N_z)(C_i/P_{hz}). \tag{5}$$

In the Gulf of Finland *C. pengoi* is randomly distributed and thus $R_i/R_{tot} = 1$; we therefore calculated the impact of this predator on the zooplankton community using eq. (6):

$$I = (N_i/N_z)(C_i/P_{hz}). \tag{6}$$

The advantage of the model (5) is the fact that parameter I is a dimensionless value which can vary within the limits between 0 and 1, reflecting variations in the population range size, the role of *C. pengoi* in the zooplankton community structure, and the functional impact of the predator on the ecosystem (Telesh et al. 2001). We applied this model for calculating the predation impact of *Cercopagis* on the zooplankton community in the Gulf of Finland in 2004.

3. Results

3.1. Distribution, population density, and biomass

In August 1999, *C. pengoi* was recorded in all the investigated areas of the Baltic Sea – from the eastern part of the Gulf of Finland to the south–eastern part of the Baltic Sea, except for the Bornholm region (Fig. 2). During this study, *C. pengoi* was first recorded in the plankton of the open waters of the south–eastern Baltic.

In the areas of investigation, the water temperature averaged for the 0–20 m layer varied from 16.7 to 22.6°C in August 1999, and from 13.04 to 16.93°C in August 2004; salinity (averaged for 0–20 m) ranged from 3.51 to 5.90 PSU in the Gulf of Finland, and from 5.90 to 6.90 PSU in the open Baltic waters.

In August 1999, numbers of *C. pengoi* fluctuated within the range 0–260 indiv. m^{-3}. The minimum population density was observed in the central part of the open Baltic. The highest numbers of *C. pengoi* were found in the Gulf of Finland and in the south–eastern Baltic (249 and 262 indiv. m^{-3}, respectively) (Tables 1 and 2).

In the Baltic Sea, *C. pengoi* density decreased with increasing water salinity and depth: $r = -0.4$ and -0.52, respectively, at $p < 0.05$ (Table 3). In the Gulf of Finland, the most important factors influencing *C. pengoi* density were depth, water transparency and water temperature. However, no reliable, sufficiently strong correlations between *C. pengoi* biomass and abiotic factors were found in the Gulf of Finland in either year (Table 4).

In August 2004, *C. pengoi* was absent in the open Baltic and was recorded only in the Gulf of Finland. The population density averaged at 124 indiv. m^{-3} (Table 1); maximum densities (296 and 223 indiv. m^{-3}) were recorded in Luzhskaya Bight and at the station located to the north of Seskar Island.

The density of *C. pengoi* decreased with increasing depth, water salinity and temperature (Table 4). *C. pengoi* density was highest at salinities 4–5 PSU.

Table 1. Density (N), biomass (B), sexual and age population structure of *Cercopagis pengoi* (as % of total density) in the Gulf of Finland (GF), the open part of the Baltic Sea (OB), and the Gdańsk and Kaliningrad regions (G/K) in 1999 and 2004 (**mean**, ± standard deviation, ranges – in brackets)

Year	Area	N [indiv. m^{-3}]	B [g m^{-3}]	Generation: Partheno-genetic females	Generation: Gameto-genetic females	Generation: Males	Age: 1 pair of caudal claws	Age: 2 pairs of caudal claws	Age: 3 pairs of caudal claws
		195.24	**273.33**	**56.83**	**31.83**	**10.83**	**25.83**	**19.00**	**54.67**
	GF	±49.72	±69.61	±8.64	7.39	±4.88	±9.89	±3.90	12.37
		(105–249)	(147–349)	(48–69)	(20–40)	(2–16)	(11–41)	(13–24)	(37–72)
		38.98	**54.57**	**46.40**	**44.40**	**8.80**	**65.80**	**15.40**	**18.40**
1999	OB	±38.07	±53.30	±22.26	±16.09	±8.79	±10.16	±13.33	±6.43
		(2–119)	(2–166)	(18–68)	(23–66)	(0–20)	(52–75)	(4–33)	(8–24)
		184.72	**258.61**	**28.00**	**50.13**	**21.75**	**25.25**	**22.75**	**51.88**
	GK	±72.46	±101.44	±8.21	±7.34	±8.61	±9.57	±7.15	±9.57
		(22–262)	(31–367)	(19–43)	(42–65)	(7–34)	(12–36)	(7–30)	(36–65)
		123.92	**127.58**	**46.53**	**38.99**	**15.28**	**34.91**	**20.80**	**48.17**
2004	GF	±86.18	±80.57	±15.38	±16.01	±7.46	±22.22	±12.44	±22.09
		(24–296)	(44–303)	(15–68)	(22–72)	(10–31)	(10–76)	(6–45)	(12–73)

Table 2. Geographic coordinates and numbers (N [indiv. m^{-3}]) of *Cercopagis pengoi* in the Baltic Sea in August 1999 and 2004 (0 – no *Cercopagis*, '–' = no data)

Latitude (North)	Longitude (East)	N 1999	N 2004
60°00′	29°00′	–	3.92
60°01′	29°24′	–	5.24
60°03′	29°11′	–	13.72
60°06′	29°02′	–	11.76
60°04′	29°02′	–	0
60°01′	29°02′	–	17.64
59°54′	28°37′	–	60.76
60°10′	28°35′	–	58.80
59°50′	28°11′	217.4	295.96
60°07′	28°04′	249.21	113.68
60°20′	28°00′	–	223.44
60°07′	27°23′	–	92.12
59°47′	27°07′	0	1.96
60°00′	27°07′	104.76	139.16
60°10′	27°07′	195.24	107.80
59°58′	26°30′	0	23.52
59°55′	27°37′	220.63	0
59°50′	25°00′	184.13	96.04
59°35′	23°38′	34.92	0
59°20′	21°45′	1.59	1.96
59°02′	21°05′	9.52	0
58°53′	20°19′	46.03	0
58°00′	19°47′	69.84	–
58°00′	19°57′	49.21	–
58°32′	19°49′	119.05	–
58°27′	20°20′	19.05	–
57°26′	19°36′	1.59	–
57°04′	19°43′	0	0
57°05′	19°06′	1.59	–
57°19′	19°55′	0	0
57°37′	19°35′	7.94	–
56°07′	19°04′	0	0
55°00′	20°20′	174.60	–
55°00′	19°00′	180.95	0
55°01′	20°00′	177.78	0
55°06′	20°07′	230.00	–
55°10′	20°20′	250.00	–
55°11′	19°06′	7.94	0
55°15′	20°50′	217.46	0
55°23′	20°35′	261.90	0
55°24′	19°08′	0	0
55°41′	20°36′	22.22	0
55°55′	20°40′	236.51	0
55°07′	18°50′	210.00	0
55°24′	18°33′	206.35	0
55°33′	18°24′	208.00	–
55°43′	18°13′	90.00	–
56°00′	17°54′	5.00	–
55°40′	17°30′	0	0
56°56′	18°52′	0	0
56°29′	18°57′	0	0
56°28′	18°22′	4.00	0

Table 3. Correlation coefficients r between *Cercopagis pengoi* population parameters and abiotic factors (depth [m], water temperature [°C], salinity [PSU], and transparency [m]) in the open Baltic Sea in August 1999 (values in bold are significant at $p < 0.05$)

	Depth [m]	T [°C]	S [PSU]	Transparency [m]
density *C. pengoi* [indiv. m^{-3}]	**−0.52**	0.23	**−0.40**	−0.37
parthenogenetic generation [%]	0.04	**−0.59**	**−0.69**	**0.52**
gametogenetic generation [%]	−0.11	**0.59**	**0.47**	−0.44
juveniles (with 1 pair of caudal claws [%])	**0.88**	−0.27	0.22	**0.48**
adults (with 3 pairs of caudal claws [%])	**−0.79**	0.17	−0.30	**−0.53**

Table 4. Correlation coefficients between *Cercopagis pengoi* population parameters and abiotic factors in the Gulf of Finland of the Baltic Sea in 1999 and 2004 (values in bold are significant at $p < 0.05$)

	Depth [m]		T [°C]		S [PSU]		Transparency [m]	
	1999	2004	1999	2004	1999	2004	1999	2004
density [indiv. m^{-3}]	0.63	−0.40	0.42	−0.60	−0.08	−0.40	−0.60	−0.20
biomass [mg m^{-3}]	0.63	−0.40	0.42	−0.60	−0.08	−0.40	−0.60	−0.30
parthenogenetic generation [%]	**−0.86**	0.05	−0.40	0.34	−0.64	−0.17	0.07	0.19
gametogenetic generation [%]	**0.82**	−0.01	0.70	−0.30	0.64	0.21	0.01	−0.15
juveniles (with 1 pair of caudal claws [%])	−0.06	0.41	0.38	0.20	0.49	0.49	0.37	0.35
adults (with 3 pairs of caudal claws [%])	0.03	−0.37	−0.30	−0.12	**−0.52**	−0.37	−0.40	0.43

In August 1999 and 2004, the maximum biomass of the *C. pengoi* population was recorded in the Gulf of Finland and in the open waters of the south–eastern Baltic (Tables 1 and 2).

3.2. Population structure

Population analysis indicated that in August 1999 representatives of the parthenogenetic generation were dominant (on average 57% of the total number of specimens) in the Gulf of Finland. Gametogenetic females and males (72% in total) were relatively most abundant in the south-eastern offshore regions of the Baltic Sea (Table 1, Fig. 3). The highest number

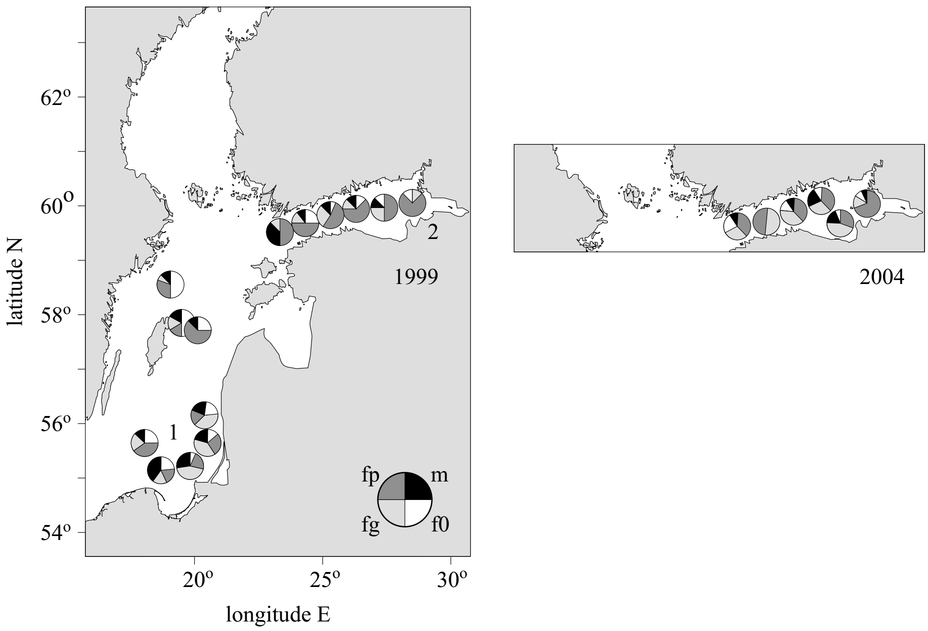

Fig. 3. Population structure of *Cercopagis pengoi* in the Baltic Sea in 1999 and 2004 (percentage of the total number of specimens in samples; white – young females without eggs, light gray – gametogenetic females, dark gray – parthenogenetic females, black – males); 1 – the south-eastern open Baltic Sea, 2 – Luzhskaya and Koporskaya Bights

of adult specimens in the *C. pengoi* population was recorded in the Gulf of Finland and in the south–eastern Baltic: on average, 55 and 52% of the total number of specimens, respectively (Table 1).

In 1999, in the open Baltic Sea the percentage of the parthenogenetic generation decreased with increasing temperature and salinity ($r = -0.59$ and -0.69 at $p < 0.05$, respectively) and the number of parthenogenetic specimens correlated positively with water transparency ($r = 0.52$ at $p < 0.05$) (Table 3). In the Gulf of Finland, the percentage of the parthenogenetic generation was determined by depth ($r = -0.86$ at $p < 0.05$) (Table 4). The share of young specimens in the population of *C. pengoi* correlated positively with depth and water transparency ($r = 0.88$ and 0.48 at $p < 0.05$, respectively) (Table 3). At higher population densities of *C. pengoi* the number of adult specimens and representatives of the gametogenetic generation in the population was the highest ($r = 0.65$ at $p < 0.05$ in both cases) (Table 5).

In 2004, the share of parthenogenetic neonates and mature females in the Gulf of Finland was on average 47% and reached 68% in Koporskaya Bight.

Table 5. Correlation coefficients between age, sexual population parameters and population density (N [indiv. m^{-3}]) of *Cercopagis pengoi* in the Baltic Sea in 1999 and 2004 (values in bold are significant at $p < 0.05$)

	1999	2004
juveniles (with 1 pair of caudal claws [%])	**–0.71**	0.52
adults (with 3 pairs of caudal claws [%])	**0.65**	–0.47
parthenogenetic generation [%]	–0.05	**–0.47**
gametogenetic generation [%]	**0.65**	**0.65**

Representatives of the *C. pengoi* gametogenetic generation were dominant (82%) in Luzhskaya Bight (Fig. 3). The percentage of parthenogenetic females decreased with increasing population density ($r = -0.74$ at $p < 0.05$). Gametogenetic females dominated in the *C. pengoi* population when species numbers were the highest ($r = 0.65$ at $p < 0.05$) (Table 5).

In August 1999 and 2004, the percentage of representatives of the gametogenetic generation of *C. pengoi* in the Baltic Sea correlated positively with population density ($r = 0.63$ at $p = 0.00006$) (Fig. 4).

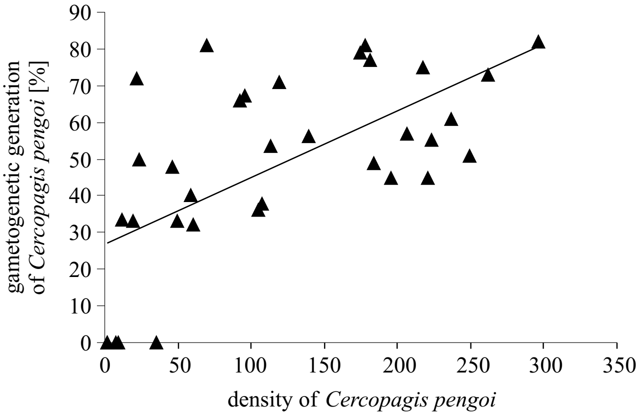

Fig. 4. Correlation between the population density [indiv. m^{-3}] and the percentage of the gametogenetic generation of *Cercopagis pengoi* in the Baltic Sea in August 1999 and 2004 ($r = 0.63$, $p = 0.00006$)

3.3. Impact of predation by *C. pengoi*

The mesozooplankton community in the Gulf of Finland during the study periods consisted of copepods, cladocerans, rotifers and meroplanktonic larvae of benthic invertebrates. Dominant zooplankton species were *Keratella quadrata*, *K. q. platei*, *Synchaeta* sp., *Pleopis polyphemoides*, *Eurytemora affinis*, and *Centropages hamatus*.

During the evaluation of predation pressure by *Cercopagis* in August 2004, the total zooplankton density in the Gulf of Finland ranged between 5.4 and 182.2 x 10^3 indiv. m^{-3}. The strongest impact of *C. pengoi* on the pelagic community in the Gulf of Finland was registered at the stations where the role (percentage) of *C. pengoi* in the total zooplankton biomass was the highest. In Luzhskaya Bight and at the station located to the north of Seskar Island, the impact of *Cercopagis* predation on mesozooplankton reached maximum values: parameter I ranged from 0.46 to 0.70 (Fig. 5).

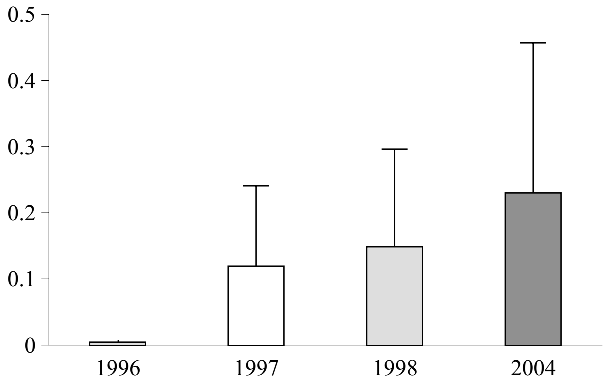

Fig. 5. Impact of the *Cercopagis pengoi* population on the zooplankton community in the Gulf of Finland (in 1996–1998 and 2004)

4. Discussion

In 1999, *C. pengoi* was distributed in all the areas investigated throughout the open Baltic Sea. During our study, this species was first recorded in the pelagic zooplankton communities of the south–eastern part of the Baltic Sea. In the same period, this species was also recorded in the Gulf of Gdańsk and the Vistula Lagoon by other researchers, who found *C. pengoi* in the pelagic community (Bielecka et al. 2000) and in benthos samples (Żmudziński 1999, Naumenko & Polunina 2000, Jurasz et al. 2000). Recent publications provide additional information on the presence of *C. pengoi* in the zooplankton of the south–eastern Baltic in 1999 (Karasiova et al. 2004, Zhigalova et al. 2005).

In August 1999, the *C. pengoi* population density was highest in the Gulf of Finland and the south–eastern Baltic. The central part of the open Baltic was characterized by the highest depth, transparency and water salinity, and a lower water temperature in comparison with that in the gulfs, where the density of *C. pengoi* was the lowest. These data are in agreement with results from other regions of the Baltic Sea. For example, in the northern

Baltic proper, in the Gulf of Finland, and in the Gulf of Riga, the density of *C. pengoi* correlated negatively with depth, water salinity and water temperature (Gorokhova et al. 2000, Telesh et al. 2000, Litvinchuk et al. 2001, Ojaveer et al. 2004).

In 2003 and 2004, cold, saline water intrusions were registered in the Baltic Sea and in the Gulf of Finland (Averkiev et al. 2004). They might have been responsible for the almost complete absence of any correlations between *C. pengoi* population parameters and abiotic environmental factors in August 2004. In 1999, when water temperatures were higher than in 2004, *C. pengoi* was more abundant and widely distributed in the Gulf of Finland and in the open part of the Baltic Sea.

The age structure of the *C. pengoi* population depended on population density: the highest percentage of adult specimens was observed at maximum population density, as we and some other authors had already shown earlier (Litvinchuk & Rivier 1999, Gorokhova et al. 2000, Telesh et al. 2000). In 1999, adult specimens of *C. pengoi* dominated in the Gulf of Finland and the south–eastern Baltic, while in the open Baltic, at lower population densities, juveniles of *Cercopagis* were predominant.

In the south–eastern Baltic, the number of representatives of the gametogenetic generation reached a maximum in 1999, which was the first year of the *C. pengoi* invasion in this region of the Baltic Sea. During both years of our investigation, 1999 and 2004, the highest percentage of individuals belonging to the gametogenetic generation correlated positively with the density of *C. pengoi*, which is a feature characteristic of cladocerans in general.

Hydrological conditions in the Baltic Sea vary significantly. Thus, of especial value is the evaluation of the influence of environmental factors on the population parameters of *C. pengoi* obtained in this study. Recently, similar data has become available for the *C. pengoi* population in the Gulf of Riga (Ojaveer et al. 2004). Additionally, these authors provide good correlations between the abundance of *C. pengoi* and other mesozooplankton organisms in this area of the Baltic Sea on a long-term scale (1992–2001).

So far, the eastern Gulf of Finland remains the only area in the Baltic Sea where the overall impact of *Cercopagis* predation on zooplankton community has been evaluated and monitored since 1996 (Telesh et al. 2001). The impact values during the first year after the invasion of *C. pengoi* in the Gulf of Finland were negligible; however, these values increased during the succeeding vegetative seasons. In the present study the impact values were significantly higher than those recorded in the Gulf of Finland during the first years immediately after *Cercopagis* had invaded the eastern Gulf of Finland (Fig. 5). Calculations using the same model applied to the *C. pengoi* population in Lake Ontario (North America) resulted in higher values of its impact in the first years after the invasion of this planktonic predator in the Great Lakes of North America (Laxson et al. 2003). Nevertheless, as in the Gulf of Finland, those maximum impact values were registered in Lake Ontario only when the share of *Cercopagis* in the total zooplankton community biomass was the highest.

In the Gulf of Finland, monitoring of the impact of *Cercopagis* on the zooplankton community at present shows a tendency for its predation pressure to increase exponentially. Such a tendency may cause a reduction in the overall filtration and sedimentation activities of planktonic herbivores and suspension-feeders owing to their elimination by the predator, which in turn is likely to result in an accumulation of phytoplankton in the system (Telesh et al. 2001). Consequently, this diminished self-purification ability of pelagic communities will be followed by changes in organic matter and energy fluxes through the Gulf of Finland ecosystem, thereby exacerbating its eutrophication (Telesh 2004).

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