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Fifteen years after invasion: egg bank of the predatory cladoceran *Cercopagis pengoi* in the Baltic Sea

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ABSTRACT: We studied the size, distribution and viability of the egg bank of the non-indigenous cladoceran *Cercopagis pengoi* in different parts of the Baltic Sea. During summer, *C. pengoi* can attain high densities by parthenogenetic reproduction, but during most of the year, it survives as sexually produced resting eggs in bottom sediments, and yearly recruitment is dependent on the survival and hatching of these eggs. Sediments were sampled at open sea sites in the Gulf of Finland, the Gulf of Bothnia and the Baltic Proper from 2007 to 2009. *C. pengoi* eggs were most abundant (up to 26×10^3 m^{-2}) in the Gulf of Finland, whereas farther north in the Gulf of Bothnia, the numbers were lower (up to 3×10^3 m^{-2}). This reflects the invasion history of *C. pengoi* in the Baltic Sea, and is in agreement with its average yearly planktonic abundance. Hatching success varied substantially between sites, but at least some eggs hatched from all sites, even those suffering from persistent anoxia. However, as the incubation time needed for hatching was long (average 7 to 74 d), and some of the viable eggs were buried deep in the sediment, recruitment from the open sea sediments is possibly low, especially in the Gulf of Bothnia. *C. pengoi* recruitment in spring or summer originates likely from coastal sites.

KEY WORDS: Fishhook waterflea · Non-indigenous species · Resting eggs · Diapause · Hatching success · Sediments · Gulf of Finland · Gulf of Bothnia

INTRODUCTION

Worldwide, biodiversity is influenced by an increasing rate of invasions of alien species. The Baltic Sea has been subject to both intentional and unintentional introductions for centuries; however, the number of invasions has been accelerating during the last decades (e.g. Leppäkoski & Olenin 2000). To date, 79 identified non-indigenous species are considered as established (Olenin et al. 2012). In the pelagic zone, the most important recent invader, in both ecological and economic terms, is the predatory cladoceran *Cercopagis pengoi* (Ostroumov, 1891) (Leppäkoski & Olenin 2000), which originates from Ponto-Caspian waters (Mordukhai-Boltovskoi 1965, Rivier 1998). *C. pengoi* was first recorded in the Baltic Sea in 1992 in the Gulf of Riga (Ojaveer & Lumberg 1995) and the Gulf of Finland (Ojaveer et al. 2000; Finnish Institute of Marine Research unpublished data). It spread and established rapidly. In 1997 it inhabited the northern Baltic Proper (Gorokhova et al. 2000), and in 1999 it was reported from the northern part of the Bothnian Sea, Gulf of Bothnia (Leppäkoski et al. 2002) and from the Gulf of Gdansk, southern Baltic Sea (Bielecka et al. 2000). Genetic analyses suggest that from the Baltic Sea, *C. pengoi* was further introduced to the Laurentian Great Lakes in North America (Cristescu et al. 2001), where it was first observed in Lake Ontario in 1998 (MacIsaac et al. 1999).

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In the invaded areas, *Cercopagis pengoi* can influence its prey populations (Benoît et al. 2002, Ojaveer et al. 2004, Lehtiniemi & Gorokhova 2008), compete for prey with native zooplanktivores (Benoît et al. 2002, Gorokhova et al. 2005, Lehtiniemi & Lindén 2006) and cause economic loss to fisheries by fouling nets, trawls and other objects (Leppäkoski & Olenin 2000). On the other hand, it has become a food source for fish (Ojaveer & Lumberg 1995, Antsulevich & Välipakka 2000, Gorokhova et al. 2005) and mysids (Gorokhova & Lehtiniemi 2007) in the Baltic Sea.

Cercopagis pengoi has 2 life cycle characteristics considered favourable for invasive species (Panov et al. 2007). During summer, it can reproduce rapidly by parthenogenesis and attain high densities, while in autumn it produces resting eggs as a result of sexual reproduction (Mordukhai-Boltovskoi 1965, Mordukhai-Boltovskoi & Rivier 1971, Rivier 1998). Resting eggs can act as means of dispersal. They are able to survive extreme conditions during transport in ballast water tanks of ships (Panov et al. 2004), such as exposure to high salinities when brackish or fresh ballast water is partially replaced with open-ocean water (Gray et al. 2005). In addition, resting eggs provide an escape from seasonally occurring unfavourable conditions, such as low temperatures. *C. pengoi* is considered a warm-water plankton species: it occurs in the Caspian Sea at 13 to 30°C and in invaded areas at 8 to 26°C (Gorokhova et al. 2000 and references therein).

Krylov & Panov (1998) showed that *Cercopagis pengoi* allocates a larger part of its reproduction to resting eggs in the Baltic Sea compared to its native area. Early and prolonged gamogenetic reproduction may facilitate invasion success, and has been observed in several cladoceran species in the early stages of invasion (Yan & Pawson 1998, Panov et al. 2004, Riccardi et al. 2004). This can be seen as a bet-hedging strategy (cf. Hairston et al. 1985): as the species is not adapted to the new environment, it cannot rely on getting cues for starting resting egg production prior to deterioration of the conditions. Also, sexual reproduction produces new genotypes, which may assist adaptation. Resting eggs can remain unhatched but viable in sediments for extended periods and form 'egg banks' that act as a long-term survival strategy against unpredictable catastrophes (Hairston & De Stasio 1988). The native zooplankton species in the northern Baltic Sea form such egg banks (Viitasalo & Katajisto 1994, Katajisto 1996), but egg banks would be especially advantageous for species settling to new areas where interannual variation in the environmental conditions may in some years lead to complete failure in their reproduction. On the other hand, egg banks also form in sites with environmental conditions that suppress hatching, and analysing samples from those sites can give information on long-term viability of the eggs (Marcus et al. 1994, Hairston et al. 1995, Katajisto 1996) and the invasion history of the studied species (Branstrator et al. 2006).

We aimed to investigate the size and distribution of the *Cercopagis pengoi* egg bank in the Baltic Sea, and to assess hatching success of eggs from different areas. *C. pengoi* can attain high densities in the open sea, above deep bottoms (>80 m; Lehtiniemi & Gorokhova 2008). It is of interest to know whether the populations develop at these sites from the bottom, or whether they renew every year by migration from shallower waters where near-bottom temperature is higher, possibly accelerating development and hatching of the resting eggs. Also, we compared the egg bank data to the distribution of *C. pengoi* in plankton, assessed during regular national monitoring cruises.

MATERIALS AND METHODS

Benthic eggs

Sediment sampling was conducted in open sea areas in different parts of the Baltic Sea during 3 cruises on RV 'Aranda' in 2007 to 2009 (Table 1, Fig. 1A). With a Gemax dual gravity corer, 2 samples (each consisting of 1 or 2 parallel cores of 90 mm ∅) were taken, and sliced in 1 cm intervals. One of the parallel cores was sliced to 15 to 20 cm depth and the other one to 5 to 6 cm depth (see Table 3). In the harder sediments, slicing could not be performed that deep, and at some sites the sediment was very coarse and included ferromanganese concretions that disturbed exact slicing; at site LL4A, cores from only 1 Gemax sample could be sliced deeper than 2 cm. For these latter sites the results are more reliable in terms of total abundance of the eggs but only indicative of their depth distribution. At site F69 (Åland Sea), methane gas bubbling in the sediment disturbed the depth layers. At each site, water from near bottom was taken with a 30 l water sampler and filtered (Whatman GF/F, nominal pore size 0.7 µm) to be used for the egg hatching incubations. If hydrogen sulphide was detected in the bottom water, the water was taken from higher up in the water column.

Sediment samples were stored at 3°C. Sediment processing was started on board: eggs were extracted (see below) and transferred to 50 ml tissue cul-

Table 1. Sediment sampling sites for *Cercopagis pengoi* eggs. Hydrographical data taken from Finnish Environment Institute and Finnish Meteorological Institute (2012). Sal: salinity; Temp: temperature; na: measurement not available

Sea area	Site	Latitude (N)	Longitude (E)	Depth (m)	Date (dd/mm/yy)	1 m above bottom			
						Sal	Temp (°C)	O_2 (ml l^{-1})	H_2S (µmol l^{-1})
Gulf of Bothnia: Bothnian Bay	CVI	65° 14.02′	23° 33.77′	71	09/06/08	3.3	2.0	7.76	
	BO3	64° 18.12′	22° 20.59′	107	09/06/08	3.7	1.5	8.36	
	F15	63° 31.01′	21° 30.78′	48	13/06/09	4.5	5.4	7.58	
Gulf of Bothnia: Bothnian Sea	F18	63° 18.86′	20° 16.36′	100	10/06/08	6.0	3.4	5.40	
	US3	62° 45.53′	19° 11.74′	177	15/06/09	6.3	4.3	4.91	
	US6B	62° 36.01′	20° 15.78′	82	12/06/09	6.1	4.0	5.28	
	F26	61° 59.01′	20° 03.78′	134	07/06/08	6.3	4.1	4.62	
	Rauxz	61° 21.29′	21° 01.45′	51	11/06/09	5.5	2.3	na	na
	SR3	61° 11.00′	18° 13.80′	72	16/06/09	5.6	2.9	5.71	
	SR5	61° 05.00′	19° 34.78′	122	05/06/08	6.4	3.7	5.41	
Åland Sea	F69	59° 47.00′	19° 55.80′	187	05/06/08	8.5	4.5	3.97	
Baltic Proper	LL19	58° 52.84′	20° 18.65′	166	04/06/08	11.5	6.0	0.00	28
	HA1	56° 56.20′	18° 49.60′	86	03/06/08	9.8	5.4	0.74	
	BY2	55° 00.00′	14° 05.00′	47	02/06/08	14.1	6.1	4.25	
Gulf of Finland	LL12	59° 29.01′	22° 53.81′	83	23/05/07	10.5	5.5	0.00	16
	LL11	59° 35.01′	23° 17.81′	67	23/05/07	8.8	4.5	2.80	
	LL9	59° 42.01′	24° 01.81′	66	23/05/07	9.0	4.7	1.82	
	LL6A	59° 55.01′	25° 01.81′	73	21/05/07	9.7	5.1	0.36	
	LL4A	60° 01.01′	26° 04.81′	59	21/05/07	7.7	4.1	3.63	
	XV1	60° 15.00′	27° 14.82′	66	22/05/07	6.4	3.0	4.93	

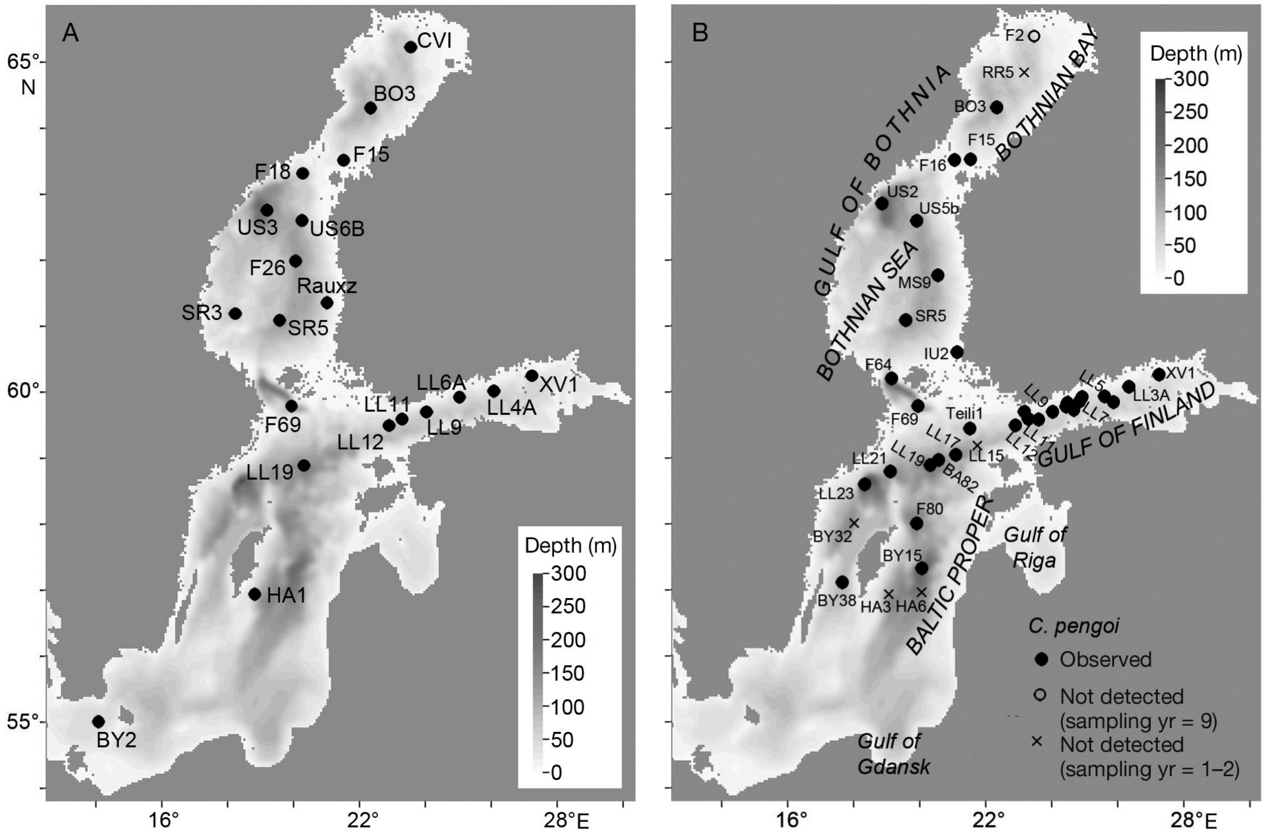

Fig. 1. *Cercopagis pengoi*. (A) Sediment sampling sites for eggs. (B) Distribution in water column in the middle and northern parts of the Baltic Sea observed in August from 1997 to 2008. ●: *C. pengoi* observed in ≥1 sampling year; ○: *C. pengoi* not observed, site sampled nearly every year; ×: *C. pengoi* not observed, site sampled occasionally between 1997 and 2008. In the Gulf of Finland, only those sites are named which are shown in Fig. 4

ture flasks in GF/F filtered seawater and stored at 3°C. At the end of the cruise, the flasks and remaining sediment samples were taken in coolers to the laboratory and stored at 3°C until further processing. Sets of samples were processed in succession, collected eggs stored at 3°C and incubations at 12°C started at the same time for these sets. The surface samples (down to 2 to 6 cm) were processed first, and their incubations were started 9 to 22 d after sampling, whereas the incubations of eggs from the deeper layers were started 17 to 127 d after sampling. The processing of the samples, egg counting and, for most sites, incubations were conducted to depths where (almost) no eggs were found (see Table 3).

Most of the water taken from the sampling sites was spared for the incubations. For sieving the sediment, 100 µm filtered seawater (FSW) from near the laboratory (5 to 6 psu) was taken. This water was adjusted to appropriate salinity either by diluting with tap water or by adding sea salt; the final salinity was checked with a handheld conductivity meter.

The eggs were extracted from the sediments by the sugar flotation method (Onbé 1978; modified by Marcus 1984), which has been successfully used for zooplankton resting eggs in the Baltic Sea (Viitasalo & Katajisto 1994). Sediment samples were sonicated for 1 min to break up sediment clots (cf. Marcus 1984, 1989), washed with FSW on a 200 µm sieve and centrifuged with sugar-water solution (1:1) at 1000 × *g* for 3 min. After centrifugation, the supernatant was poured onto a 200 µm sieve and rinsed carefully with GF/F filtered sampling site sea water. Of most samples from the Gulf of Bothnia and Åland Sea, almost no material was initially left on the sieve, and these samples were not centrifuged.

The samples were checked with a stereomicroscope. *Cercopagis pengoi* eggs were counted and incubated individually in wells of 24-well culture plates at 12°C to reveal hatching success. This temperature was chosen instead of the *in situ* temperatures of the sites (Table 1) in order to be able to compare the viability of eggs at these sites and to speed up the hatching process. The plates were checked in 1 wk intervals for at least 163 d. Empty shells as well as those whose contents had visibly started to decompose were disregarded in the countings. The incubations were started at the Tvärminne Zoological Station in summer and continued in Helsinki (Finnish Institute of Marine Research/Finnish Environment Institute marine laboratory) in autumn.

Onychopod resting eggs develop in distinguishable steps (Onbé et al. 1977, Yurista 1992, Rivier 1998). Prior to hatching, the chitinous outer egg envelope divides into 2 unequal halves which part from each other but are held together by the innermost envelope, stretched into a short cylinder (Fig. 2). *Cercopagis pengoi* eggs stay in this 'pop-up stage' (cf. Yurista 1992) for several days to weeks, depending on temperature (Sopanen 2008, T. Katajisto unpubl. data). At 12°C, the eggs stay in the pop-up stage for ~6 to 7 d, so the eggs were mostly observed to be at the pop-up stage on one observation date and having hatched on the following observation date a week later. A proportion of the eggs died at this stage, and these were not counted as hatched.

Statistics were performed with non-parametric tests, as the assumptions for parametric tests were not met. The differences between sea areas (Gulf of Finland and Gulf of Bothnia) in average egg abundance and in the vertical distribution of eggs in the sediment were compared with the Mann-Whitney *U*-test. For the latter, the mean depth of eggs in each Gemax sample at each site was calculated as $\Sigma(n_i \times d_i)/\Sigma(n_i)$, where n_i = number of eggs found at each depth layer and d_i = mid-depth of the respective layer, i.e. 0.5, 1.5 cm etc. The statistical tests were performed with SPSS 15.0 for Windows (release 15.0.1).

Plankton

Sediments are likely to contain eggs deposited during several years and, in the case of a recent invader, may even preserve history from early invasion days to the time of sampling. For comparison with the information derived from sediments, we present data of the distribution and abundance of planktonic *Cercopagis pengoi* in the central and northern Baltic Sea (Fig. 1B). The data were extracted from the zooplankton data collected in 1997 to 2008 during the national late summer monitoring cruises, which are part of the Helsinki Commission (HELCOM) COM-

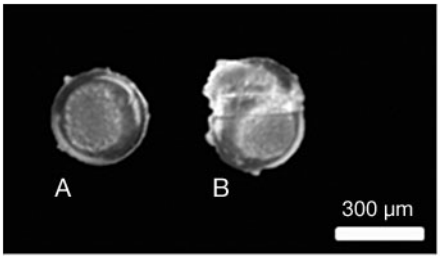

Fig. 2. *Cercopagis pengoi*. Resting eggs from the Baltic Sea sediments. (A) Early stage of development; (B) pop-up stage (see 'Materials and methods')

BINE monitoring programme. Prior to 1997, only 1 specimen of *C. pengoi* had been observed in the samples. Zooplankton was sampled, preserved and counted according to HELCOM Guidelines (HELCOM 2006). In all, samples were taken from 18 stations, but not for each year: 12 stations were sampled 7 to 12 times and 6 stations were sampled 1 or 2 times during the 12 yr, for a total of 123 samples. In 2003 and 2005 to 2007, additional sampling for *C. pengoi* was performed during the same monitoring cruises with a WP-net (200 or 500 µm, 0.255 m^2) with 3 to 4 vertical hauls from 50 m to the surface. These additional samples (n = 68) were taken from 34 stations. The individuals were counted alive on board. In the results, the additional *C. pengoi* samples are combined with the monitoring samples.

RESULTS

Egg abundance

Cercopagis pengoi eggs were found almost everywhere in the sediments in the northern parts of the Baltic Sea (Table 2, Fig. 1A). In the Gulf of Finland, sediment type seemed to determine the occurrence of the eggs: they were found in recently sedimented, organic material. The lowest egg abundances were observed at erosion sites with a thin organic sediment layer on top of sandy and clayish sediment (Sites LL4A and LL11; Table 2, Fig. 1A). In the Gulf of Bothnia, a similar pattern was not observed. The sediment type differed from that in the Gulf of Finland and the Baltic Proper: it was well oxygenated (indicated by brown colour to several cm depth and no visible lamination), and bioturbated by abundant macrofauna (Finnish Environment Institute 2012). In the Gulf of Bothnia and the Åland Sea, the oxygen situation was good near the bottom; in the Gulf of Finland and the Baltic Proper, many sites were anoxic or hypoxic (<2 ml O_2 l^{-1}; Table 1). Bottom temperatures varied between 1.5 (Bothnian Bay) and 6.1°C (southern Baltic Sea).

Cercopagis pengoi eggs were relatively abundant (up to 26×10^3 m^{-2}) in the Gulf of Finland, northern Baltic Proper and Åland Sea, whereas in the Gulf of Bothnia, the numbers were very low (up to 3×10^3 m^{-2}; Tables 2 & 3). Abundance was higher in the Gulf of Finland (pooled with the northern Baltic Proper site) than in the Gulf of Bothnia (pooled with the Åland Sea site; Mann-Whitney $U = 26$, p = 0.000). No eggs were found at the northernmost station (CVI) or at the 2 southernmost stations (BY2 and HA1). Also, the vertical distribution of eggs in the sediments seemed to differ between the areas (Fig. 3). In the Gulf of Finland and the northern Baltic Proper, the highest egg abundance was generally found in the layers near the surface (depth for eggs collected: mean ± SE = 2.2 ± 0.3 cm), whereas in the Gulf of Bothnia and the Åland Sea, eggs were mostly found deeper (4.0 ± 0.6 cm) and at many sites there were no eggs in the surface layers. However, the difference between the sea areas in the vertical distribution of eggs was not statistically significant (Mann-Whitney $U = 72$, p = 0.06).

Table 2. *Cercopagis pengoi*. Resting eggs in Baltic Sea sediments, showing total abundance (mean ± SD in 2 Gemax samples (1 to 2 cores each) from the sampling sites (Fig. 1A)

Site	Egg abundance (m^{-2})
CVI	0 ± 0
BO3	39 ± 56
F15	275 ± 278
F18	3183 ± 167
US3	157 ± 111
US6B[a]	118 ± 56
F26	275 ± 278
Rauxz	0 ± 0
SR3	1100 ± 445
SR5	118 ± 56
F69	11239 ± 222
LL19	4716 ± 667
HA1	0 ± 0
BY2	0 ± 0
LL12	18863 ± 18784
LL11	354 ± 56
LL9	25976 ± 5057
LL6A	14933 ± 2668
LL4A	10099 ± 389
XV1	23343 ± 1556

[a] At this site, 4 samples (1 core each) were collected

Egg hatching

Hatching success of the eggs varied spatially, but at least some eggs hatched from each site (except BO3) where eggs were found (Fig. 3, Table 3). There was no clear trend in hatching success over sediment depth. Oxygen conditions in the water column could not be directly related to hatching success — low hatching success was found at sites with the lowest oxygen concentrations (LL12, LL19, LL6A), but in addition there were sites with good oxygen conditions and low hatching success (XV1) and vice versa (LL9; Fig. 3, Tables 1 & 3). However, there was no benthic macrofauna present at XV1 at the time of sampling (Finnish Environment Institute 2012), indi-

Table 3. *Cercopagis pengoi*. Eggs recovered and incubated from different sites. Number of parallel cores are given for each Gemax sample. Also shown: maximum depth to which the cores were sliced at each site, depth to which eggs were found and incubated (inc.), total number of eggs recovered (Total found) and incubated (Total inc.) from the 2 samples (3 to 4 cores) at each site, number of hatched eggs during 163 d of incubation, hatched eggs m^{-2} and days to hatch (mean ± SD) of eggs that hatched during the 163 d incubation

Site	Cores per sample	Maximum depth (cm)			Eggs				
		Cores sliced to	Eggs found to	Eggs inc. to	Total found	Total inc.	Hatched (163 d)	Hatched m^{-2} (163 d, Σ all layers)	Days to hatch
CVI	2+2	15	–	–	0	0	–	0	–
BO3	2+2	15	4	4	1	1	0	0	–
F15	2+2	15	10	6	5	3	1	39	31
F18	2+2	15	11	11	48	48	20	786	18 ± 9
US3	2+2	15	4	4	4	4	2	79	67 ± 59
US6B	1+1+1+1[a]	15	4	4	3	3	1	39	45
F26	2+2	15	6	6	7	7	2	79	7 ± 10
Rauxz	2+2	~2[b]	–	–	0	0	–	0	–
SR3	2+2	~6[b]	~6	~6	22	22	9	354	8 ± 3
SR5	2+2	15	4	4	3	3	2	79	14 ± 0
F69	2+2	15	10	10	157	157	5	196	31 ± 10
LL19	2+2	15	9	6	118	116	2	79	43 ± 15
HA1	2+2	15	–	–	0	0	–	0	–
BY2	2+2	15	–	–	0	0	–	0	–
LL12	2+2	20	9	2	448	248	9	354	74 ± 29
LL11	1+2	~2[b]	~2	~2	7	7	1	52	15
LL9	2+2	15	8	5	654	445	102	4008	43 ± 21
LL6A	2+1	16	13	13	281	281	5	262	60 ± 27
LL4A	2+1	4[b]	4	4	191	191	87	4559	31 ± 33
XV1	2+2	20	8	5	536	464	14	550	49 ± 35

[a]Four samples (1 core each) were collected; [b]Slicing of (all) cores was not exact or possible due to sediment properties

cating a history of poor oxygen conditions. In the Gulf of Finland, the highest hatching percentage was achieved at LL4a (with good oxygen conditions), although almost as many viable eggs were found at the hypoxic LL9, which had a higher total abundance of eggs. At totally anoxic stations (LL12 and LL19), hatching success was low but not 0.

Individual eggs hatched after very variable lengths of incubation: from some sites and depth layers, first eggs hatched soon (1 to 2 wk) after the start of incubations, while in others it took 1 to 2 mo before hatching began. Gradual hatching then continued up to 3 to 4 mo. However, even after a long period of inactivity in the incubations, some eggs still hatched. To compare the sites and sediment depth layers, cumulative hatching success is reported after 163 d of incubation (Fig. 3, Table 3).

Plankton

Cercopagis pengoi was observed at least once during the years 1997 to 2008 at 87% of all sampling sites and in almost all areas in the central and northern Baltic Sea (Fig. 1B). Of regularly sampled sites, only at F2 in the northernmost part of the Bothnian Bay the species was not observed. *C. pengoi* abundance in plankton, averaged over sampled years, showed a similar areal pattern to the egg abundance (Fig. 4).

DISCUSSION

We showed that *Cercopagis pengoi* has established an egg bank in the sediments of the northern Baltic Sea. The resting egg abundances of native and invasive predatory cladocerans in marine and lake sediments are often on the order of 10^3 to 10^5 m^{-2} (e.g. Onbé 1985, Viitasalo & Katajisto 1994, Madhupratap et al. 1996, Yurista 1997), comparable with those observed in our study (up to 26 × 10^3 m^{-2}). The egg abundances were highest in the Gulf of Finland (Table 2, Fig. 1A), where *C. pengoi* formed permanent populations in the early stage of the invasion in the Baltic Sea (Krylov et al. 1999, Uitto et al. 1999, Antsulevich & Välipakka 2000). *C. pengoi* has dispersed almost all over the northern and central Baltic

Sea, and although it was occasionally found in substantial numbers nearly throughout the zooplankton monitoring area, high abundances were most repeatedly observed in the Gulf of Finland (Fig. 4). Sampling once a year gives only a rough image of the abundance variations of a strongly seasonal species such as *C. pengoi.* Sampling does not necessarily co-occur with population maxima, the timing of which can vary from year to year and between different sites (Krylov et al. 1999, Antsulevich & Välipakka 2000). Even so, average planktonic abundances over the sampling years correspond with the accumulated egg abundances in the sediments in different sea areas (Fig. 4).

Sediment sampling for resting eggs can provide a useful tool for detecting occurrence or distribution of an invasive species (Branstrator et al. 2006) in a given area when seasonally comprehensive water column monitoring cannot be conducted. Combining the information of the benthic egg distribution with the plankton data, we can reason that *Cercopagis pengoi* occurs all over the northern Baltic Proper and the Gulf of Finland as well as in the Gulf of Bothnia up to the southern Bothnian Bay. In the Bothnian Bay, it probably occurs irregularly; it was found in plankton samples in 2 of the 9 sampling years, and only 1 individual

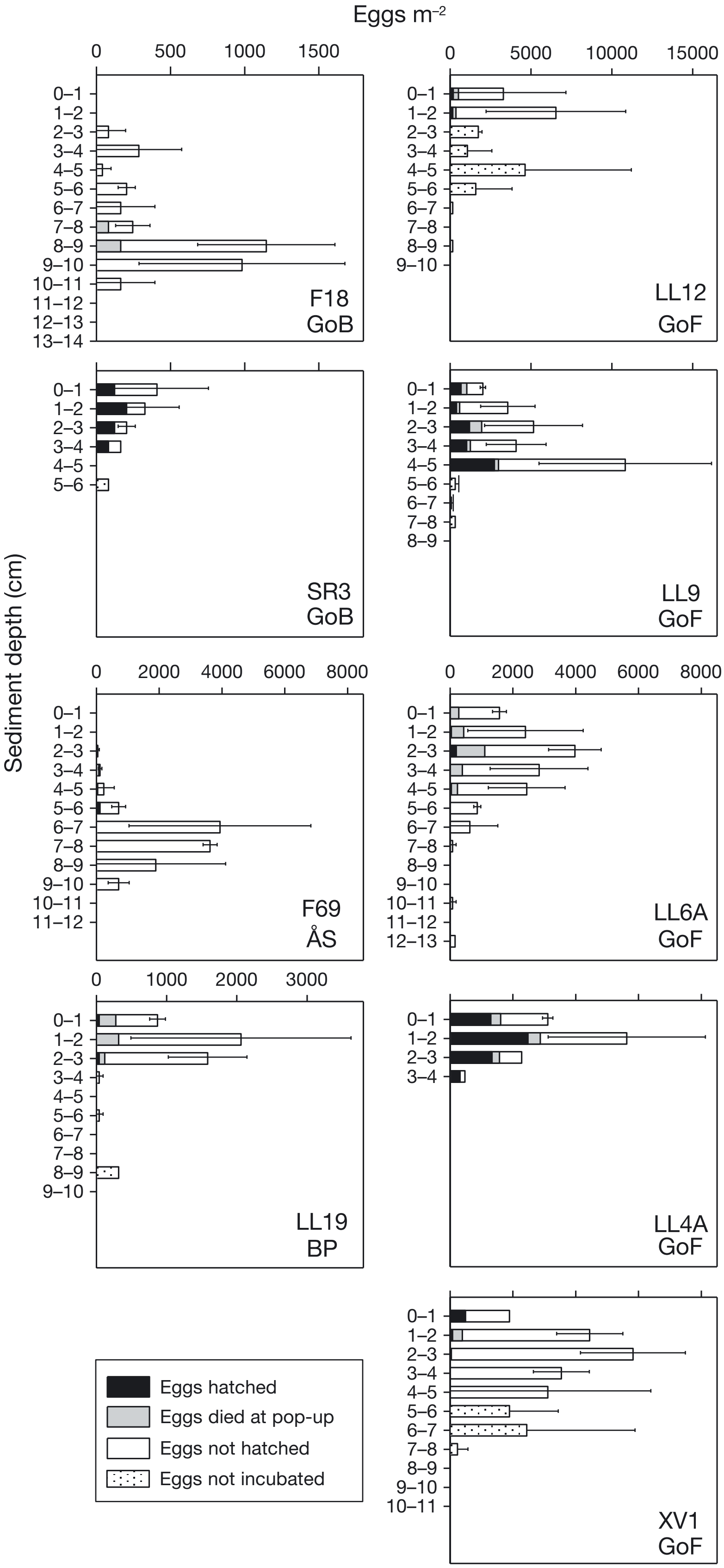

Fig. 3. *Cercopagis pengoi*. Vertical distribution of resting eggs (abundance m^{-2}; means ± SD) in 1 cm sediment layers in 2 Gemax samples (1 to 2 cores each). At LL4A, results beneath 2 cm depth represent only 1 Gemax sample. Shaded areas of the bars (SD not shown for clarity) — black: hatching success during a 163 d incubation at 12°C; grey: proportion of eggs that developed to the pop-up stage but died before hatching; white: eggs that did not hatch during the incubation; dotted bars: layers with no eggs incubated. Note different scales on *x*-axes. Only the sites with >10 eggs (in total) recovered are shown. The actual egg number at each site is given in Table 2. GoB: Gulf of Bothnia; ÅS: Åland Sea; BP: Baltic Proper; GoF: Gulf of Finland

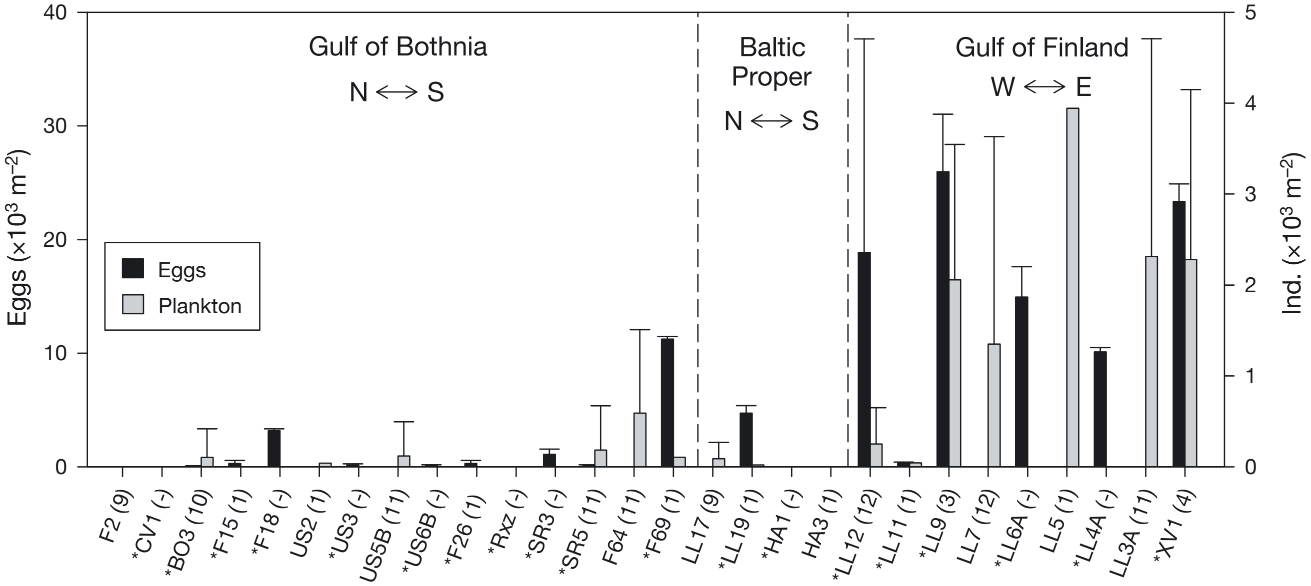

Fig. 4. *Cercopagis pengoi*. Comparison between the abundances (means ± SD) of resting eggs in the sediments (black bars; 2 samples), sampled once in 2007 to 2009, and individuals in the water column (plankton) in 1997 to 2008 (grey bars; 1 sample yr^{-1}, number of sampled years in parentheses after each site), sampled in late summer in the middle and northern parts of the Baltic Sea. If 2 samples were available from the same site in a given year, the higher estimate was used. As there were no plankton data from all of the sediment sampling sites, plankton data from the same sea area are shown next to the sediment data. Sampling sites are organised from north to south in the Gulf of Bothnia and Baltic Proper and from west to east in the Gulf of Finland. Sediment sampling sites are marked with an asterisk (*)

egg was found in the sediment samples at Site BO3. However, not detecting eggs in sediment samples is not conclusive evidence that a species has not been present in the water body. For example, Branstrator et al. (2006) failed to find eggs of the invasive cladoceran *Bythotrephes longimanus* in some lakes in which its occurrence was otherwise verified. Thus, although *C. pengoi* was not found in either plankton (F2) or sediment (CV1) samples in the northern Bothnian Bay (Fig. 4), it cannot be entirely ruled out that it has sometimes extended its occurrence there too. Interestingly, at CV1, eggs of *B. longimanus* were fairly abundant (1800 m^{-2}) although it has only once (in 2002) been found in the zooplankton monitoring samples from F2 since 1979 (Finnish Environment Institute 2012). The species is known to prey upon *C. pengoi* (Witt & Cáceres 2004) but is not likely to exclude it from an area (Cavaletto et al. 2010).

Eggs were found down to 2–7, 4–10 and 3 cm depths in the sediments at different sites in the Gulf of Finland, Gulf of Bothnia and the Baltic Proper, respectively (Fig. 3, Table 3). Solitary eggs were found in samples from deeper sediment layers, but it is not possible to say whether they represented contamination from the upper layers or whether they had been in the deep layers before sampling. In the Baltic Sea, the average sediment accumulation rates have been estimated to be highest in the Bothnian Sea and lowest in the Baltic Proper (Mattila et al. 2006), which may partly account for the observed egg depth distributions. In addition, all of the Gulf of Bothnia sites as well as the 1 in the Åland Sea had a high abundance of benthic fauna (Finnish Environment Institute 2012), and due to bioturbation, vertical mixing of the sediment is strong (K. Lukkari pers. comm.). It is not known to what extent the activity of benthic animals affects eggs of *Cercopagis pengoi*, but bioturbation has been shown to translocate copepod eggs (Marcus & Schmidt-Gengenbach 1986) and cladoceran ephippia (Viitasalo 2007) vertically in sediments.

The egg bank at the easternmost site in the Gulf of Finland, XV1, is of special interest since Sopanen (2008) sampled some nearby sites in the early stage of the invasion, in 2001. Estimates on average yearly accumulation rates of sediment in the area, measured by using ^{137}Cs distribution in sediment cores and observing lamination, range from 1.7 to 8.1 mm yr^{-1} (Kankaanpää et al. 1997, Mattila et al. 2006, Kotilainen et al. 2007). We found eggs down to 7–8 cm sediment depth at XV1. Applying the mean accumulation rates from the above-mentioned studies, we estimate that these eggs were on average 11 to 13 yr old, i.e. they derive from the early invasion days into the Gulf of Finland. This seems plausible, and therefore we used the average accumulation rates to compare our results with the previous study. Sopanen (2008) found 7600 to 8800 *Cercopagis pengoi* eggs m^{-2} in a 0–6 cm deep sediment layer at 3 sites at a depth range of 29 to 46 m in the coastal area near XV1. On average, 3.8 cm (cf. Kankaanpää et al. 1997, Mattila et al. 2006, Kotilainen et al. 2007) of new sediment should have accumulated in the area during the 5.5 yr between the sampling by Sopanen (2008) and our study. We found 7700 eggs m^{-2} beneath 4 cm, which is close to the total egg pool size found in the earlier study. If the resting egg production has been fairly similar throughout the area, this means that egg loss or recruitment from the site has been small. This is supported by low hatching success of eggs from the site observed by us (Fig. 3, Table 3). Also, the lamination of sediments in the northern coastal basins of the eastern Gulf of Finland indicates that these basins have suffered from at least seasonal anoxia for years (Kotilainen et al. 2007), which would have prevented hatching of the eggs. At the time of our sampling, the oxygen conditions were good (Table 1), but hypoxic conditions have been measured between the 2 sampling occasions (Finnish Environment Institute and Finnish Meteorological Institute 2012). If the conditions continue to remain similar, it seems plausible that the egg bank at the site will be more of a sink than a source of reproduction for *C. pengoi*.

In the early stage of invasion, many species invest more into resting egg production than they do in the native area: seasonally early and prolonged gamogenetic reproduction has been observed in several cladoceran species (Yan & Pawson 1998, Panov et al. 2004, Riccardi et al. 2004), including *Cercopagis pengoi* in the eastern Gulf of Finland (Krylov & Panov 1998) and the southern Baltic Sea (Polunina 2005). After establishment, the species have often been observed to shift to more typical, late production of resting eggs (Panov et al. 2004). However, comparison of egg abundance in the sediment reported in our study to that in the early invasion stage (Sopanen 2008) does not suggest that resting egg production of *C. pengoi* would have yet diminished in the eastern Gulf of Finland. *C. pengoi* egg abundance in the surface layer (0–2 cm), which represents the sediments of the most recent 2 to 3 yr (cf. Kankaanpää et al. 1997, Mattila et al. 2006, Kotilainen et al. 2007), was not markedly different in our study (6300 m^{-2}) compared to 2001 (maximum 5500 m^{-2}; Sopanen 2008). In the earlier study, lower abundances (1400 to 1500 m^{-2}) were found at the shallower sites. Abundance of *C. pengoi* in plankton can be patchy (Uitto et al. 1999), but high abundances occur both near shore and in more open sea, although peaks occur at different times (Krylov et al. 1999). In 1997 to 2007, the abundances in the eastern Gulf of Finland were mostly high and without any observable trend. Deeper sites may, however, accumulate more eggs via resuspension and sedimentation.

Hatching success was variable, but it was mostly <50% (Fig. 3). This is at the same level as measured by Sopanen (2008) for *Cercopagis pengoi* eggs derived from surface sediments of a coastal site in the western Gulf of Finland. Simm & Ojaveer (2006) reported only 13 to 28% hatching success for eggs released by field-collected females, but the authors noted that the eggs might not have been far enough developed when released due to the non-natural and stressed conditions for the females. Also, they did not mention for how long the eggs were monitored after they started to hatch. Hatching of resting eggs can be highly asynchronous (De Stasio 2004, Katajisto 2006), as observed in *C. pengoi* eggs extracted from sediments (Table 3; Sopanen 2008). There are no other published results on hatching success of *C. pengoi* resting eggs. Similar or somewhat higher hatching success has been reported for other predatory cladocerans: 23 to 63% for *Podon* (*Pleopsis*) *polyphemoides* and 11 to 79% for *Evadne nordmanni* from sediments in the southern Baltic (Madhupratap et al. 1996) or up to 80% for *P. polyphemoides* from sediments in Japan (Onbé et al. 1977). In comparison, hatching success of copepod diapause eggs is often high, e.g. 90% for eggs from females and sediments (Madhupratap et al. 1996, De Stasio 2004, Katajisto 2006).

At most sites, eggs from the deepest layers did not hatch, but there was no linear correlation between sediment depth and hatching success (Fig. 3). This can imply sediment mixing, but it can also mean that viability does not decline rapidly and survival is more dependent on the environmental conditions than egg ageing. Hairston et al. (1995) suggested that annual egg survival of the copepod *Diaptomus sanguineus* in sediments may be as high as 99%. In a survival experiment, hatching success of *Cercopagis pengoi* eggs did not decline during 3 yr of storage (T. Katajisto unpubl. data). Egg survival time is limited by metabolic rate and energy reserves of eggs. Andrew & Herzig (1984) measured metabolic rate of the resting eggs of 2 predatory cladocerans, *Leptodora kindti* and *Bythotrephes longimanus,* in normoxic conditions and calculated their potential survival time to be 286 to 446 d at 2 to 4°C, taking into account their energy reserves. However, the potential resting period can be lengthened in low oxygen conditions by metabolic rate depression (Clegg 1997, Marcus & Lutz 1998). Therefore, burial in anoxic sediments may lengthen the life expectancy of resting eggs. We found no indication that low oxygen conditions would lengthen survival. High hatching success was achieved at the bioturbated Gulf of Bothnia sites with well oxygenated sediment, whereas eggs from many of the hypoxic or anoxic sites had low success. On the other hand, eggs buried deep down in bioturbated sediment are not necessarily very old. In the Gulf of Finland, poor oxygen conditions of the bottom water could suppress hatching, which may have led to accumulation of eggs at the bottom.

There are different types of dormancy. Resting eggs of *Cercopagis pengoi* are diapause eggs, i.e. they must go through a genetically controlled arrest in development. After the so-called refractory period, when development does not resume even under favourable conditions, the eggs can hatch or continue dormancy depending on the conditions (Grice & Marcus 1981). The exact length of the refractory period required by diapause eggs of *C. pengoi* is not known; in the experiments of Simm & Ojaveer (2006), eggs released by females started to hatch after 150 to 160 d at 6°C, indicating a refractory period of <5 mo. Our samples were taken in early summer when *C. pengoi* had not yet appeared in the water column, and thus the eggs in the sediment had been produced during the preceding autumn (i.e. at least 7 mo earlier), or in previous years. Therefore, it can be presumed that they would have completed their refractory period. If so, the variable incubation times observed prior to hatching in *C. pengoi* (Sopanen 2008, present study) may indicate that development is very slow even after breaking the dormancy, and eggs that hatched in a relatively short time had already started developing in sediments. This explanation was supported by the fact that some eggs in the pop-up stage were observed when processing the samples soon after sampling. However, it is also possible that the length of the refractory period varies a lot between eggs, as observed in copepods (De Stasio 2004, Katajisto 2006).

The results of the benthic egg survey and our plankton data on *Cercopagis pengoi* support each other. The egg bank was larger and average plankton abundance was higher in the Gulf of Finland than in the Gulf of Bothnia, which most probably relates to the history of invasion, redistribution and establishment of *C. pengoi* in the Baltic Sea. The dissimilar environmental conditions between the sea areas may have further increased the difference by affecting hatching from benthic eggs and burial of the eggs into sediment. On the whole, *C. pengoi* recruitment from the open sea areas in the northern Baltic Sea seems to be low. Hatching was slow at almost all sites, although experiments were conducted at higher than the prevailing *in situ* temperatures, and a substantial part of the viable eggs were buried too deep in the sediment to be able to contribute to recruitment. In addition, large areas in the Baltic Proper and the Gulf of Finland commonly suffer from anoxic or hypoxic conditions, during which the benthic eggs cannot hatch. The role of coastal and archipelago areas for the recruitment of *C. pengoi* in the northern Baltic Sea may be important and calls for further studies.

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