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Evolutionary and ecological aspects of crustacean diapause

RESTING EGGS IN THE LIFE CYCLE OF CERCOPAGIS PENGOI, A RECENT INVADER OF THE BALTIC SEA

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With 4 figures

Abstract

The Ponto-Caspian predaceous cladoceran *Cercopagis pengoi* was first recorded in the Gulf of Riga in 1992 and in the eastern part of the Gulf of Finland in 1995. The seasonal cycle of C. *pengoi* in the shallow waters off the north-eastern coast of the Gulf of Finland was studied from the end of June to October 1996. In early August females bearing resting eggs constituted 13-67% of the total population of *C. pengoi.* The start of the production of resting eggs corresponded with the period of elevated water temperature and with an increase in population density of *C. pengoi.* A comparison with published data on reproduction of cercopagids revealed a considerable difference in timing and intensity of resting egg production between the Caspian and Baltic populations of *C. pengoi.* The adaptive significance of changes in the mode of reproduction and in the mass production of resting eggs for survival of *C. pengoi* in the novel environment is discussed.

Introduction

Cladoceran crustaceans of the families Podonidae and Cercopagidae comprise one of the most peculiar groups among the autochthonous Ponto-Caspian fauna. While podonids may be considered as descendants of the marine genus *Evadne,* cercopagids of the genera *Apagis* and *Cercopagis* most probably originated from the freshwater *Bythotrephes* (MORDUKHAI-BOLTOVSKOI 1965a, MORDUKHAI-BOLTOVSKOI & RIVIER 1987). Similar to other cla-docerans, these species generally reproduce asexually throughout most of the summer season. In the Caspian Sea, sexual reproduction occurs in late autumn, as water temperature declines. Sexual reproduction of Caspian cladocerans is, however, generally suppressed. For several species, neither males nor sexual females have been described (MORDUKHAI-BOL-TOVSKOI 1967, RIVIER 1969, MORDUKHAI-BOLTOVSKOI & RIVIER 1971, 1987). It has been suggested that, at least in the southern part of the Caspian Sea, asexual females of some species can persist by reproducing parthenogenetically throughout the winter (MORDUKHAI-BOLTOVSKOI & RIVIER 1971, ALADIN 1995).

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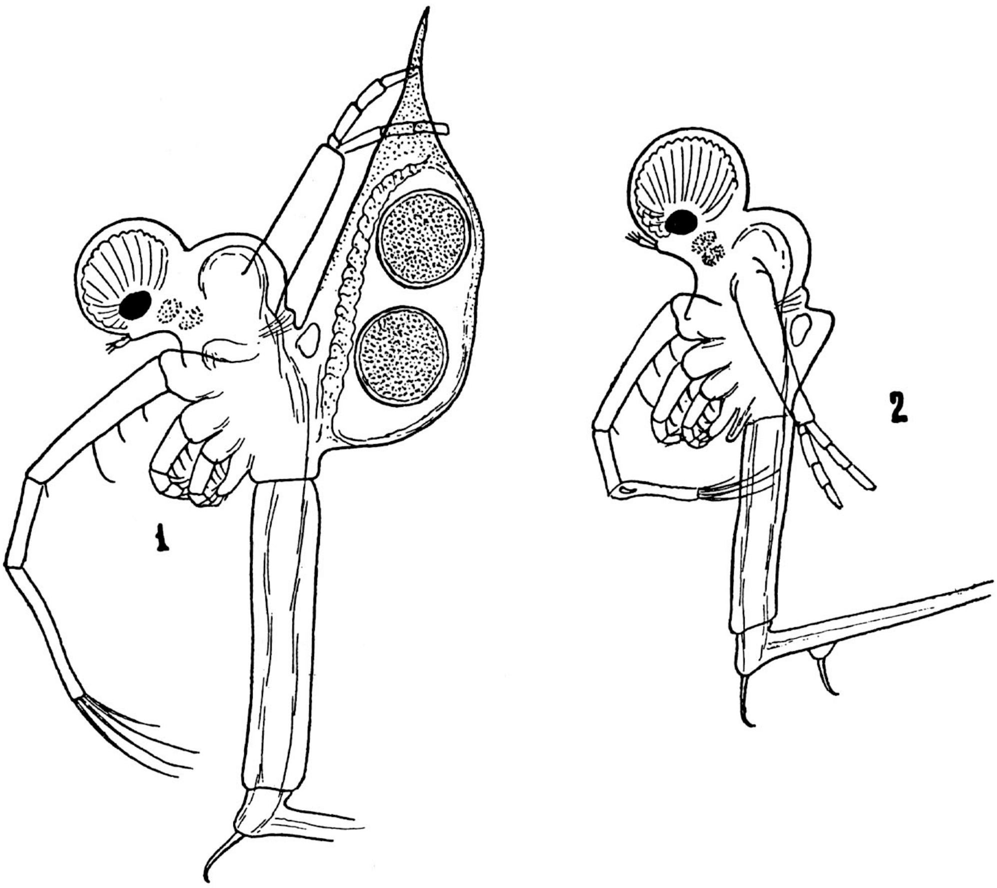

Fig. 1. Female with resting eggs (1) and male (2) of *Cercopagis pengoi* (redrawn from MORDUKHAI-BOLTOVSKOI 1967).

Although the distribution of most members of the Podonidae and the Cercopagidae is limited to the Caspian Sea, a few species have extended their distribution to other water bodies of the Ponto-Caspian basin. *C. pengoi* is the only species of this genus which inhabits the Black, Azov, and Aral Seas, as well as some brackish-water coastal lakes (MORDUKHAl-BOLTOVSKOI & RIVIER 1971, 1987). Originally, the parthenogenetic females of *C pengoi* were described based on specimens from the Azov Sea (PENGO 1879), while the description of gamogenetic females was made on collections from the Aral Sea (ZERNOV 1903), and that of males on a collection from Lake Gebedzhinsko in Bulgaria (VALKANOV 1950). Later, males and gamogenetic females were re-described in detail from the Caspian Sea by MORDUKHAI-BOLTOVSKOr (1967) (Fig. 1).

After the construction of reservoirs on the Don and Dnieper Rivers, *C. pengoi* invaded the Kakhovka, Zaporozhsk, Kremenchug, Tsimlyansk and Veselovsk Reservoirs, demonstrating its ability to establish permanent populations in fresh waters (MORDUKHAI-BOLTOVSKOI 1965b, GLAMAZDA 1971, MORDUKHAI-BOLTOVSKOI & GALINSKIY 1974, GUSYNSKAYA & ZHDANOVA 1978, Vol'vich 1978). In 1992 it was first recorded in the Baltic Sea (Gulf of Riga) (OJAVEER & LUMBERG 1995). By 1995 *C. pengoi* had penetrated into the eastern Gulf of Finland (Kivi 1995, AviNSKiY 1997).

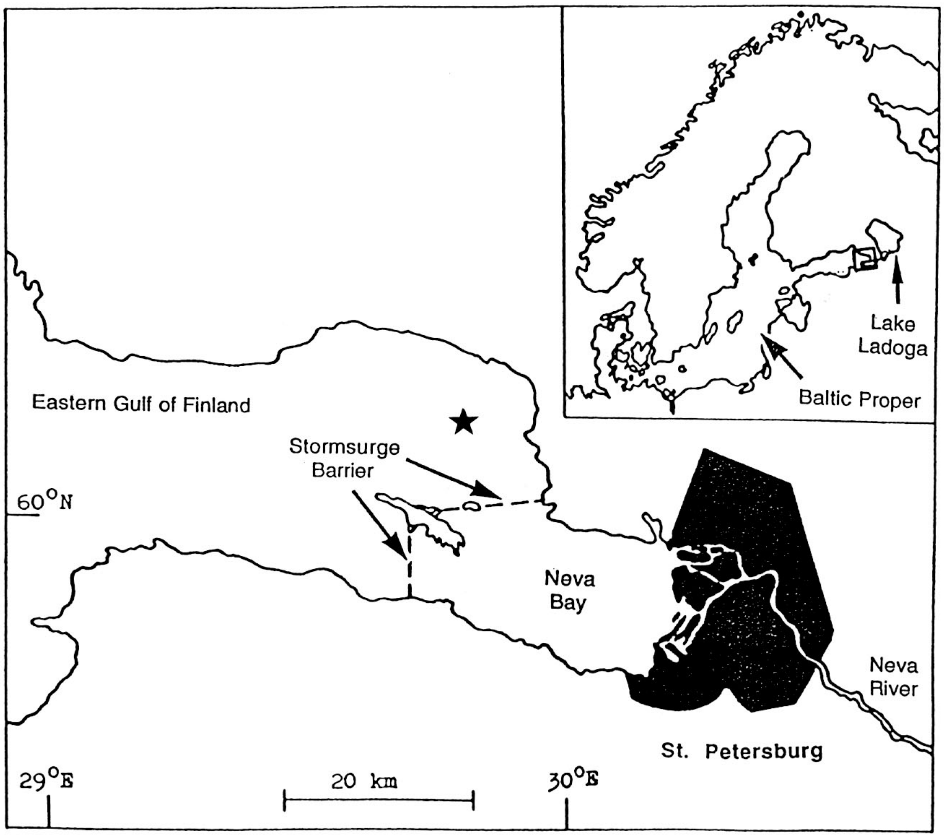

Fig. 2. Position of the main sampling station for the study of seasonal dynamics of *Cercopagis pengoi* in the eastern Gulf of Finland.

During summer and autumn 1996, the second year of the *C. pengoi* invasion of the Gulf of Finland, a survey of its seasonal abundance and distribution was conducted (KRYLOV et al. in press). The preliminary observations showed a significant shift towards sexual reproduction corresponding with the mid-summer period of elevated water temperature and with an increase in population density of *C. pengoi.* The aim of this paper is to examine the reproductive behaviour of *C. pengoi* in the novel environment and to discuss possible factors responsible for summer induction of resting egg production.

Materials and methods

C. pengoi were sampled from the end of June to mid-October 1996. Sampling intervals ranged from 3 to 12 days in July-August and from 10 to 20 days in September-October. For the seasonal dynamics study, one main station (depth 15 m) and one to three additional stations in the neighbouring waters (depths 5-12 m) were sampled (Fig.2). Samples were taken by vertical hauls of a plankton net (mesh size 150 µm, diameter opening 20 cm) drawn from the bottom to the surface. Usually, two to three vertical hauls taken at each station were combined into one composite sample. All samples were collected during daytime (11 A.M. - 2 P.M.). Surface water temperature and Secchi depth were measured at each sampling station.

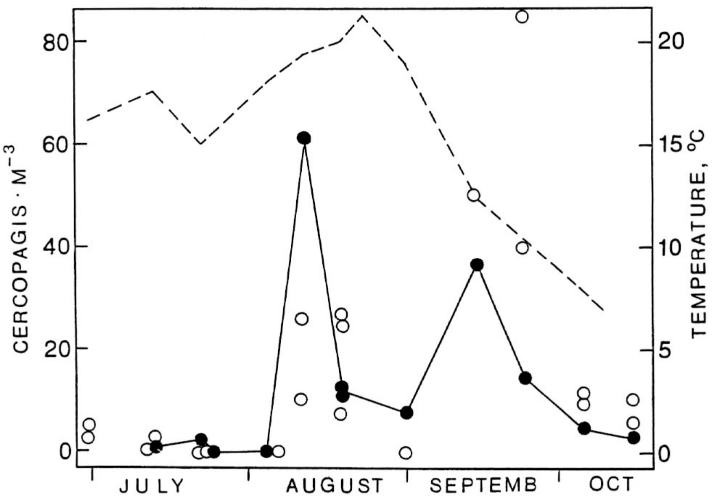

Fig. 3. Seasonal changes in abundance of *Cercopagis pengoi* at the main station (black circles) and additional stations in neighbouring waters (open circles) in the eastern Gulf of Finland in 1996. Broken curve represents surface water temperature.

Besides sampling at these permanent stations, *C. pengoi* were collected during four sampling cruises carried out on 17-18 August, 22-23 August, 22-24 September and 13-17 October 1996. Altogether 29 stations were sampled in August, 15 stations in September and 11 in October. Samples were taken by vertical hauls of a closing plankton net (mesh size 120 μrn, diameter opening 25 cm). At inshore stations net hauls were initiated at 1.5-2 m off the bottom and drawn to the surface. Except at one station on 18 August, all stations were sampled during the day (11 A.M. - 7 P.M.). All samples were preserved in Formalin (final concentration 4%).

C. pengoi were counted and measured using a dissecting microscope. The entire sample was enumerated in all cases. Individuals from all samples were combined for the analysis of seasonal changes in age structure and presence of sexual stages in the *C. pengoi* population. Age-specific morphological stages of *C. pengoi* were distinguished by the number of lateral spines (paired barbs) on the caudal spine (appendage). Similarly to *Bythotrephes, Cercopagis* neonates possess one pair of barbs. Typically, a new pair is added at each moult until a total of three occurs (MORDUKHAI-BOLTOVSKOI & RIVIER 1987). Besides enumerating developmental stages (or "barb stages"), all *C. pengoi* were sorted into juveniles, parthenogenetic females, gametogenetic females and males. Until August, the total number of individuals in samples was not high enough to allow the calculation of age and sex composition. Thus, only data from August to October were used in the analysis of population structure.

Results

C. pengoi was present in plankton samples from the beginning of the period of observations (30 June 1996). However, until 5 August their density did not exceed 4.2 individuals per cubic meter (Fig. 3). The density had increased considerably (up to 61 ind.m^{-3} at the main station) by 11 August. The second peak of *C. pengoi* abundance (up to 88 ind. m^{-3}) was observed in mid-September. The absolute maximum of *C. pengoi* population density (303.2 ind.

m^{-3}) was recorded in the August cruise at the station near Berezovy Island. Later in the season, the abundance of *C. pengoi* gradually decreased. On the last sampling date (15 October), numbers fluctuated between 3 and 10 individuals per cubic meter depending on the sampling station.

The age composition of *C. pengoi* population in the area studied was relatively uniform throughout the season (Fig.4, upper panel). Individuals with one, two and three pairs of caudal barbs were present in plankton in comparable numbers.

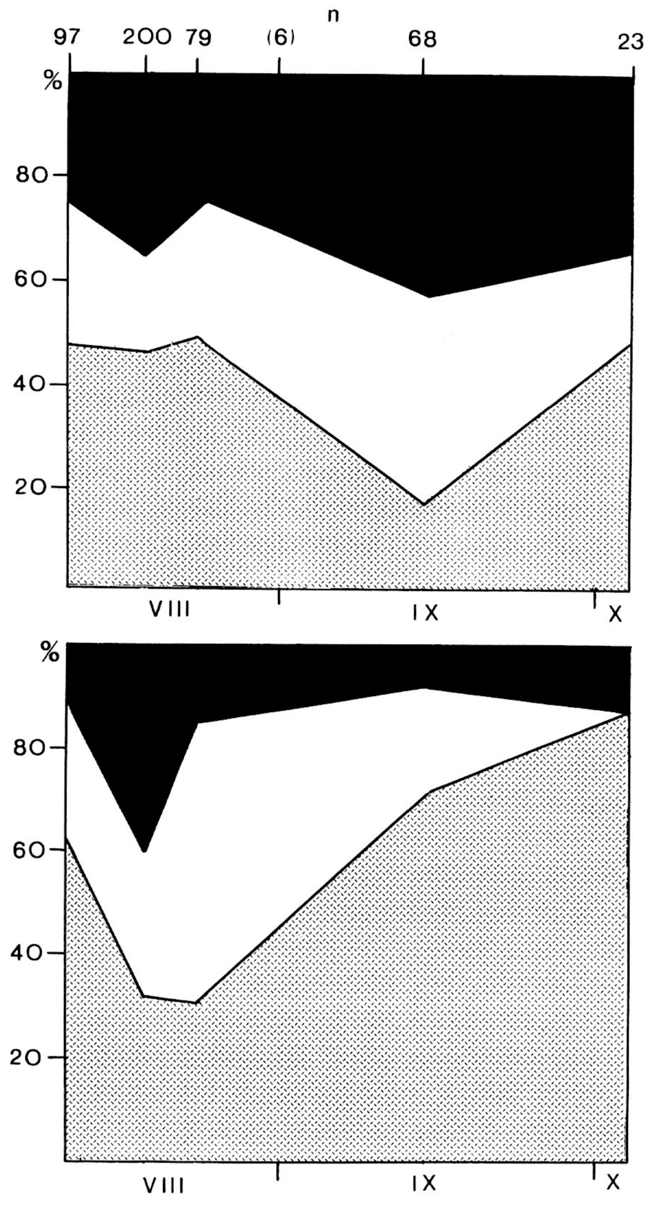

Fig. 4. Relative abundance of instars (upper panel) and reproductive stages (lower panel) in the population of *Cercopagis pengoi* in the eastern Gulf of Finland. Upper panel: percentage of barb stage 1 (black area), barb stage 2 (white area) and barb stage 3 (dotted area) in the population of *C. pengoi*. Lower panel: percentage of males (black area), females with resting eggs (white area) and parthenogenetic females (dotted area) in the population of *C. pengoi*. The number of specimens used in analysis (n) is shown on the upper horizontal axis.

One of the most remarkable life history characteristics of *C. pengoi* in the eastern Gulf of Finland in 1996 was its ability to produce a large number of resting eggs during most of the season. The first peak in population density coincided with the appearance of males and females with resting eggs (Fig.4, lower panel). The maximum density of females with resting eggs (36.5 ind./m^3) was recorded on 18 August. In mid-August the average percentage of females bearing resting eggs (for all stations sampled) reached 43%

of the total number of adults. In some samples, the percentage of gamogenetic females constituted 67 % of the total number of adults. The density of males was also high, up to 107 ind./m^3. Later in the season, when water temperature decreased, the number of sexual females and males declined. No females with resting eggs were found on the last sampling date (15 October); however, some males were still present in plankton. In August, 94% of the gamogenetic females from the Gulf of Finland were bearing two resting eggs; one female with three resting eggs was found in one of the 18 August samples.

The diameter of the mature resting egg equalled 332 ± 19 µm (mean ±1 SD, n = 53, range 276-373 µm, females with two resting eggs from the mid-August samples). The eggs from the one-egg broods tended to be larger (428 µm), and the eggs from the three-egg broods tended to be smaller (310 µm) than the eggs from the two-egg broods. However, the number of measurements on eggs from both one- and three-egg broods was too small (n = 3 in both cases) for statistical assessment of the differences in size.

Discussion

In the Caspian Sea, its native area, *Cercopagis pengoi* switches to sexual reproduction in late autumn. Even then, however, the numbers of males and gamogenetic females are very low (RIVIER 1969, MORDUKHAI-BOLTOVSKOI & RlVTER 1971). Hence, the pattern observed in the Gulf of Finland seems to be quite unusual with respect to timing and duration of the period of resting egg production, the amount of energy invested in males and gamogenetic females and the size of sexual brood. No data are available on the reproduction biology of *C. pengoi* from the other water bodies that were invaded by this species, such as the reservoirs on the Don and Dnieper Rivers or the Gulf of Riga. VALKANOV (1950) reported that in the brackish-water Lake Gebedzhinsko (Bulgaria), males and gamogenetic females of *C. pengoi* sometimes could be found already at the end of June. However, quantitative data on their abundance were not provided. A mid-summer shift towards sexual reproduction was observed by MAKRUSHIN (1984) in populations of the marine cladocerans *Podon leuckarti* and *Evadne nordmanni.* In his analysis of long-term data sets (1961-1980) on the seasonal abundance of these species in the White Sea, he found that the number of gamogenetic females of both *Podon* and *Evadne* was strongly correlated with total population density. Peak numbers (19-year averages of 120 and 460 ind.m^{-3} for *Podon* and *Evadne,* respectively) were observed in the first ten days of August. At the same time, the number of females with resting eggs also reached a maximum (22 and 34 ind.m^{-3} for *Podon* and *Evadne,* respectively). MAKRUSHIN (1984) hypothesised that the ability to produce resting eggs throughout most of the summer season was an adaptation to the large-scale dispersal of *Podon* and *Evadne* by oceanic currents (e.g. from the Atlantic Ocean to the Barents Sea and even to the White Sea). At every latitude some fraction of the females would produce resting eggs at an appropriate time while another portion of the females would produce resting eggs early in the season or continue to reproduce parthenogenetically until late autumn. Although this hypothesis may be true for the wide-spread marine genera such as *Evadne* or *Podon,* it can not explain the relatively rapid (one to two year) changes in the reproductive biology of *C. pengoi,* a species with a limited distribution.

A comparison with another cercopagid invader, the freshwater genus *Bythotrephes,* reveals some similarities in reproductive behaviour. A summer switch to sexual reproduction was observed in the population of *Bythotrephes* in Harp Lake (Ontario, Canada), a lake which was invaded by this species in the early 1990's (YAN et al. 1992). In 1994-1995, resting eggs were produced starting in July; by the end of August, 50 to 80% of the females were bearing resting eggs (N.D.YAN & T.W. PAWSON, Dorset Env. Sci. Centre, Ontario, personal communication). In the western basin of Lake Erie, the earliest occurrence of males and ga-metogenetic females of *Bythotrephes* in some years was also recorded in mid-summer (GAR-TON et al. 1993). Females with resting eggs constituted 15% of the total *Bythotrephes* population on 15 September 1988 in Lake Superior (GARTON & BERG 1990). However, the establishment of permanent *Bythotrephes* populations in novel environments does not inevitably correspond with an early start of sexual reproduction. In the Biesbosch reservoirs (the Netherlands), where *Bythoterphes* was first recorded in 1987, and where by 1989 its density reached a maximum of 1800 ind.m^{-3} (KETELAARS & VAN BREEMEN 1993), females with resting eggs were detected only occasionally at the end of the growing season (KETELAARS et al. 1995). Since all these water bodies differ widely in latitude, light and temperature regimes, and in the productivity and abundance of prey items, it is difficult to relate the observed variability in the reproductive strategy to changes in key environmental factors.

In the Gulf of Finland, more than 90% of the gametogenetic females of *C. pengoi* were bearing two resting eggs. In addition, we observed few individuals with 3 eggs. Studies on reproduction of *C. pengoi* in the water bodies of the Ponto-Caspian basin have reported one (seldom two) resting eggs per female (VALKANOV 1950, RIVIER 1969, MORDUKHAI-BOL-TOVSKOI & RIVIER 1971). Thus, the sexual brood size of *C. pengoi* from the Gulf of Finland was higher than in its native area. However, a comparison with *Bythotrephes* shows that the dispersal to a new habitat may or may not result in an increase in the number of resting eggs per female. In the Rybinsk Reservoir (Russia), gamogenetic females *of Bythotrephes* usually carry two or three and a maximum of four resting eggs (RIVIER 1969, 1993). In the Lauren-tian Great Lakes, a mean sexual brood size of 3.4 (Lake Superior) and 4.0 (western Lake Erie) has been reported (GARTON & BERG 1990, GARTON et al. 1990). A gamogenetic female bearing seven resting eggs was collected from the central basin of Lake Erie (BERG & GAR-TON 1988), while in a European Arctic tundra lake, under extreme environmental conditions, females may bear up to eight resting eggs (VEKHOV 1981). However, in the Biesbosch reservoirs gamogenetic females carry typically from one to four resting eggs, like in the native area of this species (KETELAARS et al. 1995).

The mean diameter of the mature resting egg from the two-egg brood of *C. pengoi* in the Gulf of Finland equalled 332 µm. We do not know any published data on the size of resting eggs of *C. pengoi* or any other *Cercopagis* species. In *Bythotrephes,* resting egg size varied from 380-440 µm in the lakes of Belorussia (CHEREMISOVA 1960) to 488 ± 18 µm in Mond-see (HERZIG 1985) and 450-600 µm in the Rybinsk Reservoir (ZOZULYA 1977). These data show that there may be considerable inter-population differences in the resting egg size in Cercopagids; however, more research is needed to analyse resting egg variation in *C. pengoi.*

Several environmental factors are responsible for the induction of resting egg production in Cladocera. Light (photoperiod), temperature and food regimes are considered to be of major importance (STROSS & HILL 1965, STROSS 1966, KLEIVEN et al. 1992). Chemical cues, such as fish kairomones or chemical substances released by injured animals of the same species, may also be important for the initiation of resting egg production (SLUSARCZYCK 1995, PIJANOWSKA & STOLPE 1996). In novel environment all of these factors differ considerably from the native water bodies and may affect the population of the invader, resulting in a change in the timing of the switch to sexual reproduction. In addition, inter-clonal differences in reproductive characteristics in cladoceran populations have been reported (FERRARI & HEBERT 1982, LARSSON 1991). If the population of *C. pengoi* in the Gulf of Finland originated from only a few specimens belonging to one clone, the observed differences in the mode of reproduction of *C. pengoi* in this novel environment compared with its native habitat may reflect the life-history traits of this clone. Transport of ballast water by cargo vessels is a major mechanism of dispersal of marine organisms (CARLTON & GELLER 1993). The traffic route from the Caspian Sea to the Baltic Sea via the Gulf of Finland is very popular for at least three decades. Thus, it is very likely that there have been many introductions of *C. pengoi* in the past. However, it is possible that these introductions were not successful until by chance the animals of the "right" genotype (i.e. genotype with the proper sex-inducing response) were introduced. However, at present it is difficult to assess the relative importance of all possible causes of the observed changes in reproductive strategy of *C. pengoi;* this problem requires further studies.

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