# Further expansion of the genus *Cercopagis* (Crustacea, Branchiopoda, Onychopoda) in the Baltic Sea, with notes on the taxa present and their ecology

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## Abstract

The onychopod cladoceran *Cercopagis* that recently invaded the Baltic Sea is reported from new zones of the northern Baltic proper. Because of successful survival and an expanding distribution range, the addition of *Cercopagis* to the Baltic fauna is considered to be permanent. What has previously been cited as *Cercopagis pengoi* encompasses the morphology of several other species, subspecies and forms. Either a number of morphologically similar species is present, or there is a number of spurious species in *Cercopagis*. The last hypothesis is favoured. The spatial distribution pattern of *Cercopagis*, as well as that of total zooplankton, was correlated with depth. Deep ($>100$ m) and shallow ($<10$ m) stations had significantly lower abundance than stations of intermediate depth ($<100$ m). An overview of the distribution of *C. pengoi* group in fresh and brackish waters suggests a high tolerance to environmental factors, but with differences among taxa. Due to this ecological flexibility, the colonization of the Baltic is not unexpected. Increasing salinity may restrict dispersal of cercopagids to the southern areas of the Baltic and to the North Sea, but inland lakes (e.g. in Sweden) present an ecological profile suitable for colonization.

## Introduction

The genus *Cercopagis*, with the presumed species *Cercopagis pengoi* (Ostroumov, 1891), invaded the Baltic Sea during the late 1980s–early 1990s (Ojaveer & Lumberg, 1995; Panov et al., 1996). Since the mid-1990s, it established permanent populations in the Gulfs of Finland and of Riga (Avinski, 1997; Krylov et al., 1999; Uitto et al., 1999). Furthermore, in the wake of notorious invasions by Ponto-Caspian taxa that dramatically altered North America Great Lakes, *Cercopagis pengoi* recently appeared in Lake Ontario (MacIsaac et al., 1999). The appearance and rapid expansion of this species have attracted attention to its natural history, ecology, reproductive biology and genetics. Whether and how *Cercopagis* may alter zooplankton tropho-dynamics, phytoplankton development, fish nutrition and community structure is a subject of ongoing research (Ojaveer et al., 1998; Gorokhova, 1998; Uitto et al., 1999). To predict the consequences of the invasion, one must know how far and how fast the invader will increase its range and which areas the species can potentially occupy (Grosholz & Ruiz, 1996). In order to study colonization and to predict the potential dispersal of *Cercopagis* around the Baltic and other regions, it is essential to have information on the biotic and abiotic factors governing its distribution. Here, we report

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four additional records on *Cercopagis* occurrence in the northern Baltic Proper, emphasize its morphological variability, and analyze spatial distribution along a depth gradient in the open sea and its seasonal dynamics in coastal areas. We also review studies on temperature and salinity ranges of *Cercopagis* from both native and colonized areas, and discuss its further dispersal on the basis of its environmental tolerance.

## Taxonomy and zoogeography

The family Cercopagidae (Crustacea, Branchiopoda, Onychopoda) recently corrected to Cercopagididae (Martin & Cash-Clark, 1995), is currently believed to be comprised of 14 species, belonging to the genera *Bythotrephes* (1 or 2 freshwater species, see Rivier & Grigorovich, 1999) and *Cercopagis* (13 brackish water species). The genus *Cercopagis* is further subdivided in the subgenera *Cercopagis* (9 species) and *Apagis* (4 species) (Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). The distinction between the subgenera is weak, and based only on the shape of the long caudal appendage, with terminal loop and associated spinulation in *Cercopagis* and without loop and spinulation in *Apagis* (Mordukhai-Boltovskoi, 1968; Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). The taxonomy of the genus as a whole, compared to that of the anomopods, appears unsettled, with an unusually high degree of polymorphism within species (Mordukhai-Boltovskoi, 1968, Martin, 1992). Moreover, some of these 'species' have only been recorded at their type localities, described on the basis of a several parthenogenic females (e.g. *C.(C.) longiventris*, *C.(C.) robusta*, most of the *Apagis* species) while males and gametogenic females were described for only 4 species of 13 (Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). Consequently, physiological and ecological data are often entirely lacking.

All species of *Cercopagis* were originally restricted to the Ponto-Aralo-Caspian basin, i.e. the Caspian, Black, Aral and Azov seas/lakes. The ranges of the different species are variable in extent, but much overlap occurs. The Caspian Sea is home to the largest number of *Cercopagis* species and its middle-south basin is the only place where *Apagis* is believed to occur naturally (Rivier & Mordukhai-Boltovskoi, 1966; Mordukhai-Boltovskoi, 1968; Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). There are, however, some reports about finding of *Apagis* species beyond the Caspian region: in Danube and Dniester estuaries (NE part of the Black Sea; Meliyan, 1972, 1973) and in brackish Lake Chany (Western Siberia, 55° N, 78° E; Ivanova & Makartseva, 1982; Vizer, 1986). Moreover, a form of *Cercopagis* closely resembling *C. (Apagis) ossiani* was recently found in the Gulf of Riga, Baltic Sea (Simm & Ojaveer, 1999).

*C. (C.) pengoi* is among the most widely distributed species of the genus and the only 'species' believed to date to be invasive (Figure 1). It is common in the Caspian and Azov seas, in brackish estuaries of the Black Sea, and in the lower reaches of the Danube, Dniester, Bug, Dnieper and Volga Rivers (Mordukhai-Boltovskoi, 1968; Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998). It has also been recorded from coastal lakes fringing the Black (Lake Gebedzhinsko, Bulgaria: Valkanov, 1951) and Aral Seas (Lake Sudoche, Kazakstan: N. Aladin, pers. obs.), from man-made reservoirs on the Don and Dnieper Rivers (Mordukhai-Boltovskoi, 1968; Glamazda, 1971; Mordukhai-Boltovskoi & Galinsky, 1974; Gusinskaya & Zhdanova, 1978; Volvich, 1978) and connecting canals (Bazilevich, 1972).

*C. pengoi* also is the taxon that is believed to occur in the Baltic Sea. However, due to considerable morphological variation in specimens from different geographic locations, Mordukhai-Boltovskoi & Rivier (1987) had to create a '*C. pengoi* group', composed of three forms, in addition to the typical form. All share a pointed dorsal brood pouch, and include (listed in a neutral, non-taxonomic notation): (1) *neonilae*, which is characterized by a prosoma:metasoma ratio <1, a comparatively short pointed apex of the brood pouch and relatively small lateral claws on the caudal appendage (Sars, 1902). By Mordukhai-Boltovskoi and Rivier (1987) this phenotype is considered as a species; it inhabits the Caspian and Azov seas and estuaries of the Black Sea; (2) '*gracillima*' with an extremely thin and sharp brood pouch and long lateral claws, known from the North Caspian. All transitions between typical *C. (C.) pengoi* and form *gracillima* exist and co-exist (Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1998); it shows so much variation that it cannot be considered as more than a variety; (3) '*aralensis*', a subspecies described from the Aral Sea (Mordukhai-Boltovskoi, 1974), has a shorter caudal appendage than the typical form, a reduced or no loop, and a shorter distance between the lateral claws.

*Figure 1. C. pengoi*: zoogeographic distribution in Eurasia (/// - native range, ▲ - regions of introduction).

## Sampling sites and methods

There were considerable differences in sampling methods and gears used, because these surveys were not specifically designed to collect *Cercopagis*. Generally, nets with smaller opening and/or filtering of the known volume of the surface water through the net were used in the shallow coastal areas, and larger nets or water bottles were used in the open sea. As it turned out, samples collected in northern Baltic Proper by several independent surveys during summer–autumn 1997 contained *Cercopagis*.

### Gotland basin

Horizontal distribution of zooplankton was investigated during a cruise with R/V 'Baltica' to the eastern Gotland basin July 29 to August 10, 1997. During the cruise, we sampled 15 stations in a grid covering about 90 NM with sampling depth varying from 56 to 233 m (Table 1). Each station was sampled four times. Zooplankton samples were collected using bottom to surface hauls with a 90-$\mu$m WP-2 net (mouth opening 0.125 m$^2$), equipped with a flow meter according to the recommendations of HELCOM (1988).

### Himmerfjärden

This area is an embayment of the southern part of the Stockholm archipelago. It receives the effluents of a municipal sewage treatment plant and is included in the monitoring program carrying out by the Department of Systems Ecology, Stockholm University (http://www.ecology.su.se/dbhfj/hfjsmall2.shtml/). Regular sampling at station H4 was performed fortnightly during summer and monthly during winter, using a 23-l water bottle. Vertically stratified plankton samples were obtained from the surface, 5, 10, 15, 20 and 25 m depth, filtered through 35-$\mu$m net, and pooled for further analysis.

### Askö area

Several locations situated at the vicinity of Askö Laboratory of Stockholm Marine Research Center (Table 1; Trosa archipelago, northern Baltic Sea proper, Sweden), were surveyed in August 1997. Plankton was collected at the nearshore station with bottom depth 10 m using a 55-$\mu$m plankton net (mouth opening 0.11 m$^2$). Two sampling methods were used: bottom to surface hauls and filtering of a known volume of surface water through the net.

### Brunnsviken

This small bay in the Stockholm archipelago with low salinity (Table 1) was sampled on a few occasions in June–September 1997. A small zooplankton net (mouth opening area 0.03 m$^2$, mesh size 20-$\mu$m) was used to collect integrated samples from bottom to surface (bottom depth 4 m). To obtain sufficient amounts of zooplankton, 3–7 hauls were taken.

*Table 1.* Sampling localities, depth, temperature and salinity in the mixing layer, and *Cercopagis* abundance

| Area | Location | Depth (m) | Temperature (°C) | Salinity (%) | Abundance ind. m$^{-3}$ |
|---|---|---|---|---|---|
| Gotland basin | 58° 18′ N, 20° 05′ E - 57° 33′ N, 19° 36′ E | 50–250 | 18–20 | 7.0–7.5 | 5–65 |
| Himmerfjärden | 58° 59′ N, 17° 43′ E | 25–30 | 12–22 | 5.7–5.8 | 15–420 |
| Askö | 58° 50′ N, 17° 33′ E | 3–10 | 24–26 | 7.0–7.5 | 18–60 |
| Brunnsviken | 59° 20′ N, 18° 10′ E | 4–5 | 17–20 | 3.0–4.0 | 2–3 |

Surface temperature was measured at each sampling occasion. Simultaneously, data on salinity (measured using the Practical Salinity Scale, PSU), water transparency, oxygen content, chlorophyll *a*, primary production, and phytoplankton composition were collected during the cruise to the Gotland basin and in the course of the regular monitoring sampling program in Himmerfjärden bay. These data are available elsewhere (Olesen et al. (1999) and http: // www.ecology.su.se/dbhfj/hfjsmall2.shtml for Gotland basin and Himmerfjärden bay, respectively). Zooplankton samples were immediately fixed in 4% sugar-formaldehyde solution. Species and stages were analyzed under an inverted microscope according to the protocols of HELCOM (1988). All *Cercopagis* individuals in the samples were counted under dissecting microscope. Population analysis involved the determination of gender, age and reproductive stage of the animals. The following groups, typical for Cercopagidae (Rivier, 1971; Mordukhai-Boltovskoi & Rivier, 1987), were distinguished: 1. neonates, newly released individuals, sex was not determined; 2. males, typically a second or a third instar; 3. parthenogenic females (any instar) with embryos at different stages of embryogenesis; 4. gametogenic females (any instar) with resting eggs. Age-specific morphological stages (or barb stages) were distinguished by the number of lateral claws (paired barbs) at the base of the chitinous caudal appendage. One pair of barbs occurs in neonates (first instars), then a pair is added at each subsequent molt, so that second and third instars have two and three pairs, respectively.

## Results

*Cercopagis* was found in about 30 samples collected during August–September 1997 in Swedish coastal waters and open Baltic Proper. Typical *C. (C.) pengoi* together with *C. (C.) pengoi gracillima* (Figure 2A,B) constituted a majority in all the samples. However, there were specimens that could be identified as *C. (C.) aralensis*, (shorter caudal appendage with reduced loop and closely apposed caudal claws; Figure 2D) and as *C. (C.) neonilae* (metasoma shorter than the rest of the body and rounded brood pouch with a pointed apex; Figure 2C). Thereafter, individuals with these morphological features are referred as *aralensis* and *neonilae*, respectively.

### Gotland basin

The weather during the cruise was mostly calm with a clear sky and high air and surface temperatures. The thermocline was usually distinct and situated around 15-m with epilimnetic temperature being uniform around 19–20 °C. Chlorophyll *a* fluorescence (mean value 2.2 mg Chl m$^{-3}$), primary production (1.0–1.5 gC m$^{-2}$ d$^{-1}$), and phytoplankton abundance and composition in the mixed layer were stable across the grid, with minor horizontal variability (Olesen et al., 1999; U. Larsson, Stockholm Univ., pers. comm., 1998). The mesozooplankton consisted of copepods (seven species), cladocerans (six), rotifers (four), tintinnids (two), and meroplanktonic larvae (mainly Lamellibranchiata). Total zooplankton abundance and density ranged from 1.3 to 13.9.10$^6$ ind. m$^{-2}$ and from 6.5 to 205.0 10$^3$ ind. m$^{-3}$, respectively, with calanoid copepods accounting for 75–97% of total zooplankton abundance.
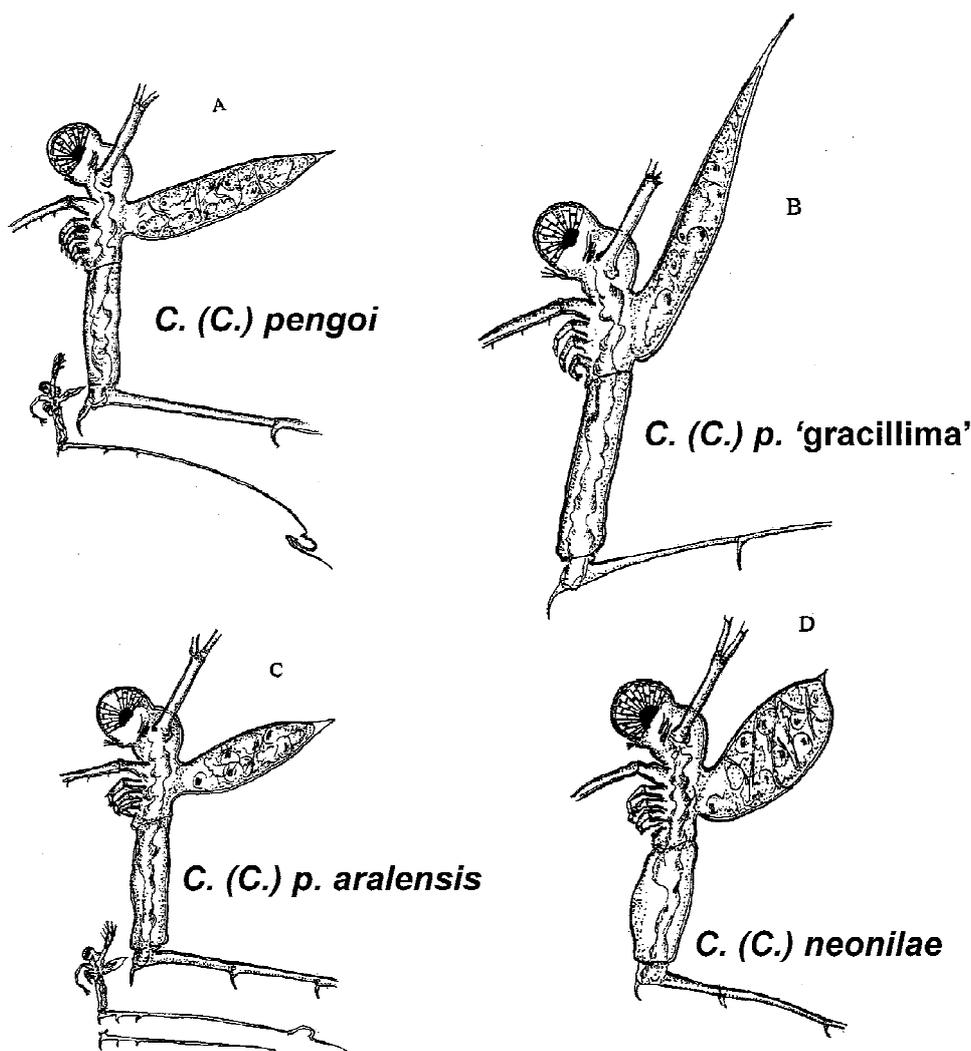
*Figure 2.* Species and forms found in the northern Baltic Proper in 1997: **A** – *C. (C.) pengoi*; **B** – *C. (C.) pengoi gracillima*; **C** – *C. (C.) aralensis*; and **D** – *C. (C.) neonilae*.

*C. (C.) pengoi* was found in about 20% of the samples. Typical *pengoi* together with *gracillima* constituted a majority in all the samples. However, 10–15% were *aralensis*, and 2% were parthenogenic females of *neonilae*. About half of the population consisted of maturing parthenogenic females and neonates. The frequency of gametogenic females with resting eggs was about 35%, with males comprising less than 15% of the population. The highest demographic variability among sampling sites was due to males (CV=84%) while the distribution of parthenogenic and gametogenic females was more uniform (CV=22% and 34%, respectively). Age struc-

ture showed a slight prevalence of first (mean value 40%) over second instars and adults (33 and 27%, respectively). Average densities were 5–15 ind. $m^{-3}$, being lowest (less than 12 ind. $m^{-3}$) at the deeper stations (bottom depth >100 m) and highest (5–65 ind. $m^{-3}$) in shallow (<100 m) areas (Figure 3). The maximum (65 ind. $m^{-3}$) was recorded at a shallow (60 m) station, which also had the highest overall zooplankton abundance.

*Himmerfjärden*

*Cercopagis* was present at an abundance of 15–420 ind. $m^{-3}$ from the end of July to the beginning of
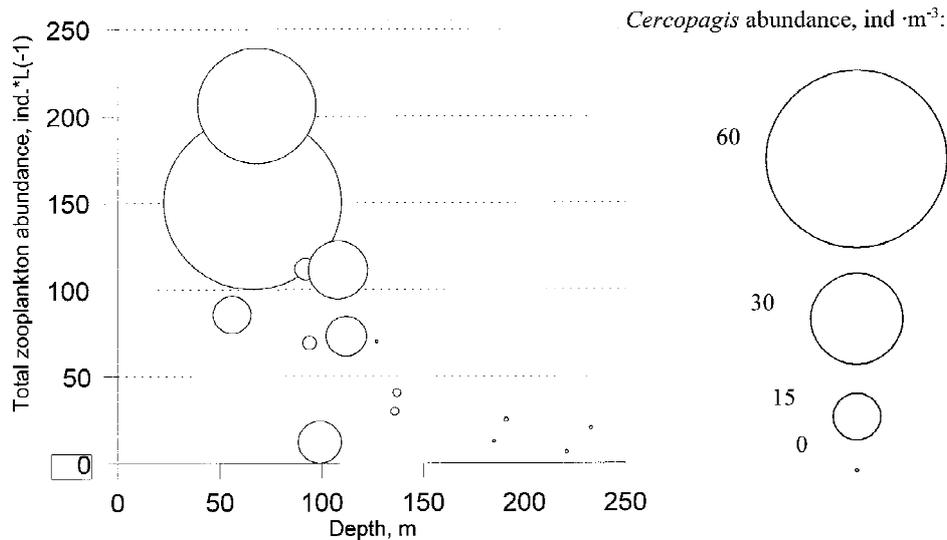
*Figure 3.* Abundance of *Cercopagis* (ind. m$^{-3}$) in relation to the depth and total zooplankton abundance in the Gotland basin.

September. Water temperatures in the upper 10 m during this period ranged between 22 °C (late August) and 12 °C (late September) being higher then monthly average calculated for 1978–1995, while salinity was rather stable and below average (Figure 4C,D; Table 1). High chlorophyll *a* (about 5 mg m$^{-3}$) and low water transparency (2.5–3 m) in the mixing layer during this period indicated substantial eutrophication. Most of *Cercopagis* had a *pengoi* phenotype, but 5–46% were *neonilae*, with highest proportion of *neonilae* found on September 11. The zooplankton community was comprised of copepods, cladocerans, including *Leptodora kindtii* in low numbers, and rotifers, mainly *Synchaeta* spp. (Figure 4E). The highest density of *Cercopagis* (420 ind. m$^{-3}$, mostly second instars) occurred in late August, coinciding with highest temperature and maximum total zooplankton abundance (Figure 4E). On all sampling occasions, the community was almost entirely composed of parthenogenic females; maximum frequencies of males (15%) and gametogenic females (12%) were observed on September 25, when water temperature in the upper 10 m had dropped to 12 °C (Figure 4C).

*Askö area*

Estimates of *Cercopagis* abundance by filtering of the surface water through the plankton net yielded values of 50–60 ind. m$^{-3}$ that was nearly three times higher than estimates from vertical hauls (18–20 ind. m$^{-3}$) indicating either patchiness in the vertical distribution or inadequate sampling method (high escape response and/or net clogging). The *gracillima* form was dominant, while *neonilae* accounted for only 4–5% of the total abundance. No males or gametogenic females were obtained.

*Brunnsviken*

A few specimens of the first and second instars of *C. (C.) pengoi* were collected at two occasions in August–early September, when water surface temperature was 20 and 17 °C, respectively. Cladocerans (*Bosmina coregoni maritima*) and juvenile stages of copepods (*Acartia bifilosa*) dominated the zooplankton.

**Discussion**

The onychopod cladoceran *Cercopagis* is reported here for the first time from new zones of the northern Baltic Proper, namely Swedish coastal waters and open sea areas (Figure 1; Table 1). *Cercopagis* has recently invaded the Baltic Sea, and previously its presence has been documented only for the relatively shallow bays of the Eastern Baltic (Gulf of Riga, Ojaveer & Lumberg, 1995 and Gulf of Finland, Panov et al., 1996). When analyzing the samples, individuals with a considerable different morphology were observed indicating possible taxonomical heterogeneity in *Cercopagis* populations. The variations were found
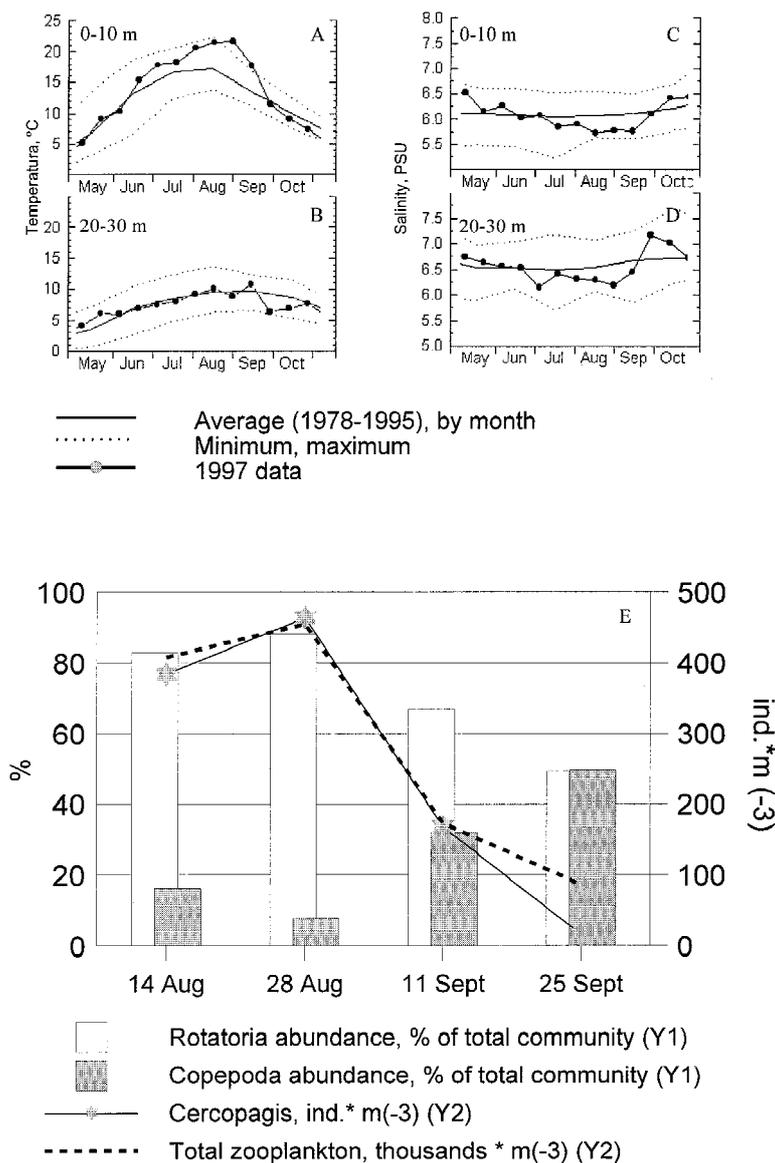
*Figure 4.* Variations in temperature (**A** – upper 10 m; **B** – 20–30 m), salinity (**C** – upper 10 m; **D** – 20–30 m), and zooplankton abundance and community structure in the Himmerfjärden Bay (monitoring station H4).

in such features as relative length of abdomen, size of a brood pouch, and a length and a shape of the caudal appendage. Apparently, all species and forms of *C. (C.) pengoi* group were presented.

*Taxonomy*

Dumont (1994, 1998) argued that, while the pelagic zooplankton of ancient lakes is species-poor, the Caspian is exceptional because of its unique north–south salinity, temperature and depth gradient, which permits more niche diversification than elsewhere. Still, there is probably more 'taxa' of Onychopoda than niches present. One explanation is that a number of these 'species' in fact reflects only plastic morphology of one or a few 'core' species. Indeed, what has been called *C. pengoi* in the Baltic shows a mix of morphologies overlapping at least two 'species' and two subspecies or varieties. We suggest that these, in fact, represent only a single plastic species, charac-

terized by an apically pointed brood pouch, but with variable relative length of the metasome and of the caudal appendage. Similarly, Simm & Ojaveer (1999) observed two different morphological forms of *Cercopagis* in the Gulf of Riga. In their study, during the season, the form with morphological features of *C. (Apagis) ossiani* appeared first and was thereafter gradually substituted by the 'summer form' – typical *C. (C.) pengoi*. Despite the presence of the distinct morphological features of *C. (A.) ossiani*, the authors suggest that the two different forms belong to the same species – *C. (C.) pengoi* and represent different ontogenetic stages. Since characters like a pointed brood pouch, spinules on the caudal appendage, length and form of the caudal appendage, and even presence of a loop might be anti-predator and/or environment-related morphologies, it is quite possible that even fewer good species of *Cercopagis* and *Apagis* exist. Further genetic studies and laboratory observations are greatly needed to provide insights into cercopagid' taxonomy.

### Depth-related distribution pattern

The spatial distribution pattern of *Cercopagis* in the open sea was correlated with depth so that deep (>100 m) and shallow (<10 m) stations had significantly lower abundance than stations of intermediate depth (<100 m). Highest abundance among all sampling stations was observed at the Himmerfjärden Bay (approximately 1 km distance from the shore; bottom depth 30 m), and lowest abundance was found at the inshore shallow station in Brunnsviken (5 m from the shoreline; depth 4 m). It should be kept in mind, however, that the higher level of eutrophication in the Himmerfjärden, due to the sewage treatment plant effluents, may have enhanced *Cercopagis* spp. production and abundance. In the open sea of the Gotland basin, maximum abundances were at depths of 50–70 m and no individuals were collected at sites more than 180 m deep. However, as both a depth and a potential prey (total zooplankton abundance) gradients in the Gotland basin coincided, it is problematic to distinguish the primary factor in *Cercopagis* spatial distribution. In the Caspian Lake, *Cercopagis* spp. distinctly avoid nearshore shallow areas (0–14 m depth). Maximum abundance was usually observed in areas with a depth of 50–200 m (Mordukhai-Boltovskoi & Rivier, 1987), and decreased by a factor 2–12 at depths of 300–700 m (Rivier & Mordukhai-Boltovskoi, 1966). Yet, reverse pattern was suggested for the freshwater

reservoirs Veselovsk (Volvich, 1978) and Tsimlyansk (Glamazda, 1971), where *Cercopagis* occurred in the littoral zone, but was absent or nearly absent in the limnetic space and upper river-like parts. Unfortunately, due to the differences in the size of the nets used for sampling in the open sea (Gotland basin) and nearshore stations (Askö and Brunnsviken), our estimates of zooplankton densities, and especially actively moving species like *Cercopagis*, may not be fully comparable. Use of a 23-l water bottle and a WP-2 net was intercalibrated during the cruise in the Gotland basin and yielded close estimates (E. Gorokhova, unpubl. data), hence our estimates for Himmerfjärden and open sea are comparable. Moreover, use of small zooplankton nets with opening diameter of 20–28 cm appears to be common in the field studies on *Cercopagis* population dynamics and distribution (see sampling methods in Avinski, 1997; Krylov & Panov, 1998; Krylov et al., 1999; Uitto et al., 1999). Thus, we may compare our findings with densities of *Cercopagis* found in different localities in these studies. In the Eastern Gulf of Finland, Avinski (1997) studied horizontal distribution over a depth range of 7–60 m and found the lowest densities (<15 ind. m$^{-3}$) at stations with a depth of less than 15 m and the maximum densities (about 300 ind. m$^{-3}$) at 'deepwater' (30–60 m) stations. We also found lowest abundance (<20 ind. m$^{-3}$) at the stations with depth of less then 10 m situated near the shoreline, while highest densities (up to 420 ind. m$^{-3}$) were observed in the offshore stations having an intermediate bottom depth (<100 m). Considering results of other studies showing vertical heterogeneity of *Cercopagis* distribution, with main part of the population situated in the upper 30 m (Caspian Lake; Rivier & Mordukhai-Boltovskoi, 1966) or even upper 5 m (Kremenchug Reservoir; Gusinskaya & Zhdanova, 1978) and 10 m (Gulf of Finland; Avinski, 1997; Krylov et al., 1999; Uitto, et al., 1999), the maximal densities in thermally stratified waters of the deep stations may in fact be underestimated. Actual population density in the mixing layer off shore would be even higher then that in the shallow non-stratified waters. Thus, our observations and earlier published data (Rivier & Mordukhai-Boltovskoi, 1966; Avinski, 1997) suggest that depth is an important factor governing *Cercopagis* distribution.

### Environmental tolerance

Salinity and temperature are major environmental factors that limit the distribution of zooplankton spe-

*Table 2.* Comparative data on temperature (°C) and salinity (%) preferences of *C. pengoi* group

| Species | Locality | Temperature | | Salinity | | Source |
|---|---|---|---|---|---|---|
| | | range | optimal | range | optimal | |
| *C. (C.) pengoi, C. (C.) pengoi gracillima* | Caspian Sea | 13–30 | 20–25 | <13.5 | 3–10 | Mordukhai-Boltovskoi & Rivier, 1987 |
| *C.* spp | Caspian Sea | | | 2–13 | 9–10 | Kurashova & Kuzmicheva, 1991 |
| *C. (C.) pengoi* | Azov Sea | | | <10 | | Mordukhai-Boltovskoi, 1960 |
| *C. (C.) pengoi* | Black Sea | | | 1–4 | 1–3 | Markovski, 1954 |
| *C. (C.) pengoi, C. (C.) pengoi gracillima* | Caspian Sea | 3–32 | 8–24 | <15 | 4–10 | N. Aladin, laboratory observations, unpubl. |
| *C. (C.) pengoi, C. (C.) pengoi gracillima* | Black and Azov seas | 3–38 | 12–22 | <13 | 5–8 | N. Aladin, laboratory observations, unpubl. |
| *C. (C.) pengoi aralensis* | Aral Sea | 4–36 | 11–26 | <17 | 3–12 | N. Aladin, laboratory observations, unpubl. |
| *C. (C.) pengoi* | Baltic Sea | 8–20 | 16–20 | 0.5–6 | | Ojaver & Lumberg, 1995, Panov et al., 1996 |
| *C. (C.) pengoi* | Lake Ontario | 17–24 | | <0.25 | | MacIsaac, et al., 1999 |
| *C. (C.) pengoi* group | Baltic Sea | 12–26 | | 3–7.5 | | This study |

cies. A comparative analysis of temperature and salinity tolerances of *C. pengoi* reveals much flexibility (Table 2). Both typical *pengoi* and *gracillima* occupy aquatic habitats associated with relatively low salinity and warm water, with high population densities found at summer temperatures (16–26 °C) and at salinity of 1–10%, and the same is true of *neonilae* (Mordukhai-Boltovskoi & Rivier, 1987; Rivier, 1988). However, laboratory experiments designed as described by Aladin (1989) showed even higher tolerance to both temperature and salinity under controlled (food, light regime) conditions for all *Cercopagis* taxa tested (Aladin, unpubl. data). The highest salinity tolerance was found in *aralensis* that inhabited the Aral Sea until the beginning of 1980s (Mordukhai-Boltovskoi, 1974) and only disappeared when salinity reached 17% (Aladin & Andreev, 1984). At the lower end, *C. pengoi* readily adapts to freshwater, reaching even higher numbers in reservoirs and lakes than in the marine environment. Indeed, densities as high as 1400 ind. m$^{-3}$ (Kakhovka Reservoir; Tseeb, 1962), 600 ind. m$^{-3}$ (Tsimlyansk Reservoir; Glamazda, 1971), and 320 ind. m$^{-3}$ (Lake Ontario; MacIsaac et al., 1999) were reported.

These temperature and salinity tolerances help to explain the invasion patterns and current range extensions of *C. pengoi*. In 1960–1970, after the construction of a cascade of reservoirs on the Volga, Don and Dnieper rivers, *C. pengoi* was detected in six of them: Tsimlyansk (Glamazda, 1971), Veselovsk (Volvich,

1978), Kakhovka (Tseeb, 1962, 1964; Gusinskaya & Zhdanova, 1978), Zaporozhsk, Dneprodzerzhinsk (Mordukhai-Boltovskoi & Galinsky, 1974), and Kremenchug (Gusinskaya & Zhdanova, 1978). These habitats, located far upstream of the presumable source areas, were probably not colonized by active dispersal. However, once a reservoir far upstream had been colonized, *Cercopagis* could easily invade all the downstream space. This dispersal may have been a consequence of the intentional introduction of caspian mysids, amphipods, and polychaetes as a source of food for the fish stocked in these new reservoirs (Glamazda, 1971; Volvich, 1978). Accidental transfer of live cercopagids or their resting eggs along with the target species to these reservoirs seems likely, as might have happened in the Kaunas Reservoir on the Neman River, which opens to the Baltic Sea (Zhuravel, 1965). In 1963, after successful introduction and acclimatization of caspian mysids and amphipods in the Kaunas Reservoir, introduced species (e.g. *Mesomysis kowalewskyi*) was found in the Kuronian Bay and in the coastal Estonian waters. Moreover, according to Zhuravel (1965), further introduction of mysids from the Kaunas Reservoir to the Gulf of Riga and some Estonian and Latvian lakes and reservoirs was carried out in 1964.

The appearance of *Cercopagis* in the Baltic suggests a vector that could be (1) biological, like, fish or birds, provided resting eggs of cercopagids remain vital after passage through their digestive tracts (Flink-

man et al., 1994; Vranovsky 1994); (2) hydrological, individuals transported by currents or wind, or (3) anthropogenic (accidental introduction, ballast water, fishing nets, coupled to the junction of previously isolated river basins by man-made canals). Option (3), a man-aided invasion, seems by far the most probable, since options (1) and (2), operative in the past as today, did not give to range extensions in earlier times. It would be too much of a coincidence if these mechanisms were activated all of a sudden, coincident with a strong increase in the mechanisms of option (3). For option (3), three routes are available: (A) through the Volga, the canal linking the Volga to the Baltic, and lakes Onega and Ladoga. Since the plankton of Onega Lake has been well studied for a long time, and only *Bythotrephes* has been recorded here (Telesh, 1996 and pers. comm.), this pathway may be discounted, therefore. Pathway (B), down the Neman River from the Kaunas Reservoir, is a good probability, as well as accidental introduction to the Gulf of Riga via the Kaunas Reservoir, although to date no *Cercopagis* has been reported from the reservoir. It does not exclude, however, possibility of unsuccessful introduction in the past and downstream transition of introduced species to a new habitat. Long time series of samples from the river and reservoir are in existence, but no work on this material has been done or published so far (L. Nagorskaya, Institute of Zoology, Academy of Sciences, Minsk, Belarus; pers.com., 1999). In any case, downstream migration, from Kaunas Reservoir to the coastal lakes of the Baltic (Olenin & Leppäkoski, 1999), and from there onwards to western Europe, is one of the most likely sources of the recent invasion of *Hemimysis anomala* in Germany and The Netherlands (Ketelaars et al., 1999). (C) Ballast water exchange: shipping between the Caspian or the Sea of Azov and the Gulfs of Riga and Finland are definitely another possibility, since this is almost certainly the means by which *Cercopagis* crossed the Atlantic to reach Lake Ontario (MacIsaac et al., 1999).

The abundance and population analysis suggest that colonization by *Cercopagis* in the Baltic proper and in Swedish coastal areas is still at an early stage. Given its present distribution, the potential evidently exists for it to disperse into other coastal and open areas of the central and southern Baltic. Extension to the north (Bothnian Bay) may be limited by low temperatures and to the south and the North Sea, by rising salinity. But another kind of habitat, inland lakes, especially those with connections to the sea, like for example Lake Mälaren (Sweden), present an ecological profile suitable for colonization. An intense shipping traffic between the Baltic Sea and those lakes, and an active fishery activity make this colonization almost unavoidable.

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