Cercopagis pengoi in Southwestern Lake Michigan in Four Years Following Invasion

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ABSTRACT. *In 1999, a long-term monitoring program in southwestern Lake Michigan captured the invasion of* Cercopagis pengoi *(fish hook flea), a predatory zooplankton native to the Ponto-Caspian region. This invasion provided an opportunity to examine both the responses of a population following establishment in a new area and the immediate response of the native community. We compared seasonal dynamics and several morphological and life history traits of* C. pengoi *both among and within the 4 years following its invasion into Lake Michigan. Samples collected from five nearshore sites in southwestern Lake Michigan from 1999–2002 indicated that the average density doubled from 75 individuals/m³ in 1999 to 150 individuals/m³ in 2002. We found no evidence for rapid changes in body size or average clutch size as the population established. We did, however observe a shift in seasonal phenology, with the population occurring in the water column earlier each year. By 2002,* Cercopagis pengoi *appeared in the water column by July and persisted until early fall. We also compared the average monthly densities of several potential prey items in August in the years before (1998–1999) and after (2000–2003) establishment. Although we found a significant reduction in the average number of rotifers, the general trend was a decline in all zooplankton species. Given the number of previously established exotic species in this system, it may prove difficult to quantify the impact of this most recent addition on what is left of the native community.*

INDEX WORDS: Lake Michigan, Cercopagis pengoi, *zooplankton, phenology.*

INTRODUCTION

In the United States, biological invasions currently are second only to habitat destruction in causing biodiversity loss, and the cost of invasive species has been estimated to run into the hundreds of billions of dollars (Enserink 1999, Pimental *et al.* 2000). It remains difficult, however, to predict why certain species are successful invaders, or which invader will become a nuisance. In many cases, an absence of natural history information precludes the development of precise predictions for a particular invader (Simberloff 1989). This lack of information can be further complicated by rapid changes in morphology, behavior, or life-history as the invader becomes established in the new system (Lambrinos 2004). Finally, detailed sampling of the invaded system often does not begin until well after the invader has become established, making it impossible

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to assess change in either the community or in the invading population. Ideally, data should be available for both the pre-invasion community and initial stages of establishment to follow the dynamics of both the native and invasive species as the new population establishes.

Long-term monitoring of southwestern Lake Michigan provides just such an opportunity. Zooplankton samples have been collected at least monthly since 1998, and samples were collected less frequently in 1988–1990 and 1996–1997. This regular monitoring captured the arrival of the predatory zooplankton *Cercopagis pengoi* (fish hook flea) (Crustacea: Cladocera) in 1999 (Charlebois *et al.* 2001). Native to the Ponto-Caspian region, *C. pengoi* was first documented in North America in Lake Ontario in 1998 (MacIsaac *et al.* 1999, Makarewicz *et al.* 2001), and has since invaded several other North American lakes (K. L. Schulz, pers. comm. SUNY—ESF). *Cercopagis pengoi* had previously invaded the Baltic Sea and this population may have been the source of the North American invasion (Ojaveer and Lumberg 1995, Cristescu *et al.* 2001).

As a predator, *C. pengoi* has the potential to directly impact the population dynamics of native species. However, the community-level effects of this non-indigenous species in Lake Michigan remain unknown. A decrease in average densities of zooplankton has coincided with a high abundance of *C. pengoi* in Lake Ontario (MacIsaac *et al.* 1999, Laxson *et al.* 2003), and evidence also suggests the invasion of *C. pengoi* may have been responsible for the declines of zooplankton in the Baltic Sea (Ojaveer *et al.* 2004). However, limited experimental information on the basic natural history of this organism and whether or not populations can show rapid local adaptation to their new environment hamper making quantitative predictions regarding its impact on native species in new environments. In this study we document the seasonal dynamics of *C. pengoi* over the first 4 years of establishment in southwestern Lake Michigan (1999–2002). The specific questions addressed are (1) Has the seasonal phenology of *C. pengoi* changed during the first 4 years of its establishment in Lake Michigan? (2) Is there evidence for rapid local adaptation to the new environment? (3) Is there evidence for dramatic shifts in the prey community as the result of the establishment of this new predator?

METHODS

We sampled five sites in southwestern Lake Michigan, all which are approximately 2.5 km offshore in ~10 m of water. We choose to compare samples from three sites north of Chicago near Waukegan Harbor, IL (42° N, 87° W) ("North") with two sites south of Chicago, IL (41° N, 87° W) ("South"). From 1998–2002, one or two samples were collected at each site with the goal of sampling all sites weekly May through October. However, poor weather often precluded sample collection, especially at the southern sites. Samples were collected at night with a 73 μm mesh, 0.5 m diameter zooplankton net via a vertical tow from 0.5 m above the lake bottom to the water surface and were preserved in a 5% sucrose-formalin solution immediately following collection. In the laboratory, each sample was re-suspended in water and replicate subsamples were taken with a 5 mL Hensen-Stempel pipette until at least 100 individuals of the common taxa had been counted. Zooplankton were classified into the following groups: rotifers, zebra mussel veligers, nauplii, calanoid copepods, cyclopoid copepods, and all cladocera were identified to at least genus. All *C. pengoi* were removed from each sample for further analysis. We used a dissecting microscope and ocular micrometer to take the following measurements on each individual: tailspine length, body length, sex, and instar (number of barb pairs). Body length, from the tip of the head to the base of the tailspine, was measured to the nearest 0.01 mm. Individuals with damaged bodies or tailspines were excluded from the analysis of these traits. A compound microscope was used to determine the number of the embryos/eggs if present. If replicate samples were collected, each sample was counted individually and the two counts were averaged.

Statistical Analysis

To assess changes in population size over time and space, we used a repeated measures split-plot ANOVA with year as the main effect and location (north versus south) as the subplot (Maceina *et al.* 1994). Sampling stations (three in the north, two in the south) served as the replicates for each week (see Table 1). We used a spit-plot design with Type IV Sums of Squares because not all five stations were sampled every week. We used all data in our analysis of density, but we excluded the 2001 data from all other analyses due to relatively small sample size (881 *C. pengoi* in 1999, 3,903 in 2000, 14

TABLE 1. *Results from repeated-measures, spilt-plot analysis of variance models on abundance, clutch size, or body size of* C. pengoi *in southwestern Lake Michigan.*

A) Abundance

Source	df	Sum of Squares	Mean Square	F-value	P
Location	1	1,377.3	1,377.3	1.24	0.2682
Year	3	12,134.1	4,044.7	1.98	0.2942
Location*Year	3	6,121.3	2,040.4	1.84	0.1463
Week	16	89,574.6	5,598.4	5.05	0.0001
Year*Week	18	41,458.6	2,303.3	2.08	0.0141
Location*Week	9	41,412.2	4,601.4	4.15	0.0002
Location*Year*Week	4	12,786.1	3,196.5	2.88	0.0276
Error	80	88,641.1	1,108		
Corrected Total	135	326,261.9			

B) Clutch size

Source	df	Sum of Squares	Mean Square	F-value	P
Location	1	7.14	7.14	14.4	0.0007
Year	1	8.60	8.60	1.83	0.4
Location*Year	1	4.71	4.71	9.5	0.004
Week	11	116.3	10.6	21.3	0.0001
Year*Week	4	21.1	5.26	10.6	0.0001
Location*Week	6	43.8	7.3	14.7	0.0001
Location*Year*Week	1	0.25	0.25	0.5	0.484
Error	29	14.4	0.5		
Corrected Total	54	259.6			

C) Body size

Source	df	Sum of Squares	Mean Square	F-value	P
Location	1	0.02	0.02	4.63	0.04
Year	1	0.14	0.14	3.13	0.33
Location*Year	1	0.05	0.05	8.81	0.006
Week	11	0.18	0.02	3.16	0.03
Year*Week	4	0.06	0.02	3.03	0.03
Location*Week	6	0.09	0.01	2.99	0.02
Location*Year*Week	1	0.003	0.003	0.65	0.42
Error	29	0.15	0.005		
Corrected Total	54	0.57			

in 2001, and 5,817 in 2002). Clutch size and body size were analyzed as described above, but only for 2000 and 2002 since *C. pengoi* was not found in the south in 1999. To further explore potential differences in population phenology among years, we tested for differences in the annual timing of first appearance of *C. pengoi* in the water column, onset of male production, and initial occurrence of females with diapausing eggs. Because we often found no within-year variation in the timing of these events among our sampling stations, we investigated differences over time with a randomization test (MRPP) available in BLOSSOM (Cade and Richards 2001). The relationship between body size and tail-spine length was investigated with re-gression. To examine variation in body size across all stations and dates, we used a two-way ANOVA with gender and instar (1, 2, or 3 barb).

To address impacts that *C. pengoi* might have on community structure, we restricted our analyses to two northern sites for which we had both pre- and post-invasion data. We also focused only on the community structure during August, when *C. pengoi* was most abundant. We calculated average monthly densities for each zooplankton taxon and contrasted each average in the years pre-establishment (1998–1999) and post-establishment (2000–2003). We include 1999 in the "pre-establishment" years because no *C. pengoi* were found in that year until late August. Although zooplankton
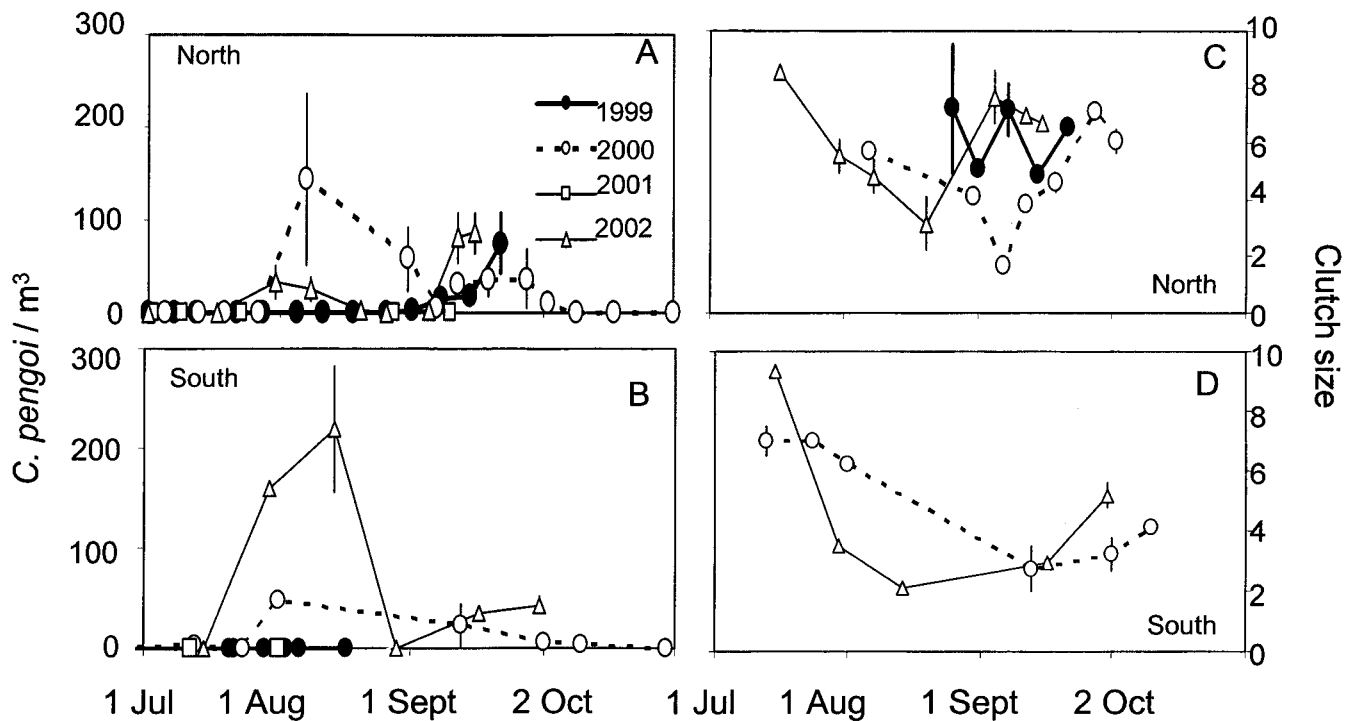
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FIG. 1. *Water column densities (individuals/m³) and clutch size (eggs/reproducing female) at both the northern (A, C) and southern (B, D) sampling stations. No* **C.** **pengoi** *were found in the south in 1999 or 2001. Error bars are ± 1 S.E.*

samples were collected in several years prior to 1998, no samples were collected in August of those years. All repeated measures analyses were conducted in PROC GLM available in SAS Version 8.2 (SAS Institute Inc. 1999). All other analyses with the exception of the MRPP were performed in Systat 10.0 (Wilkinson 2000).

RESULTS

We found no effect of either year or location on the average abundance of *C. pengoi* (Fig. 1, Table 1a). Water-column densities were, however, significantly influenced by week as well as all higher-order interactions that included week (Table 1a). During 1999 and 2001 *C. pengoi* was only found at the northern sites. In the other 2 years (2000 and 2002), the population appeared in the water column in July or early August and persisted until October (Fig 1). The significant higher-order interactions indicate that the population dynamics were variable, especially within a season, but did not demonstrate a predictable inter-annual pattern in space. However, we could partially explain this variation in overall dynamics by examining when *C. pengoi*

first appeared in the water. In the north, we found a significant difference in the timing of first appearance as the population became established (MRPP standardized test statistic = −1.93, p = 0.04). In 1999, *C. pengoi* was only found at two stations and it appeared at both of them on 26 August. In the years that followed, the average date of first detection was 15 August 2000 (± 14 days (S.E.)) and 20 July 2002 (± 4 days (S.E.)). In the south, *C. pengoi* appeared at both stations on 13 July 2000, more than a month before they were found at the northern sites that year. In 2002, we recorded them at low densities at one southern station on 15 July but did not find them at the other southern station until our next sampling trip on 30 July. This shift in annual phenology contributes to the significant year*week interaction in the abundance model.

In addition, we also found that the initial occurrence of males differed among years (MRPP Standardized Test Statistic = −2.79, p = 0.02). Males were not found until the middle of September in 1999, but were first recorded in the end of August in 2000, and the end of July in 2002. Males likely had little impact on overall population growth rate, however, as they comprised at most 30% of the
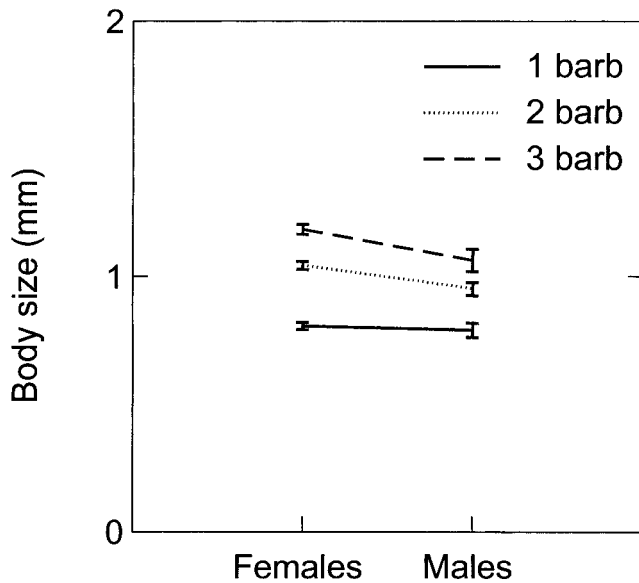
FIG. 2. *Body size (mm) of both males and females with 1, 2, or 3 sets of lateral barbs. Error bars are ± 1 S.E.*

population at both the northern and southern sites. Despite the earlier onset of males, the initial occurrence of diapausing eggs did not differ significantly among years (MRPP Standardized Test Statistic = –0.92, p = 0.16). Across all five sites, the average date of initial diapausing eggs occurrence was 15 September 1999, 18 September 2000, and 29 August 2002. Females with diapausing eggs constituted at most 25% of the population. Most often, the population was dominated (> 50%) by females carrying parthenogenetic eggs (70% of the samples). The second largest category was most often nonovigerous females (up to 77% of the population). Many nonovigerous females were likely juveniles that had not yet reached the age of first reproduction. We could not separate accurately adult female *C. pengoi* from juvenile females because reproductive females were found with 1, 2, and 3 sets of lateral barb pairs.

We found no evidence of rapid changes in body size or clutch size as the population became established (Table 1b, 1c). Females carried clutches ranging from 1 to 17 embryos, and averaged 5.2 ± 0.3 (SE) eggs per parthenogenetically reproducing female (Fig. 1). Average clutch sizes were not different in 2000 and 2002, but clutch sizes were higher in the north by more than one embryo per clutch (Table 1b). We also found a decline in clutch size as the population crashed through late August,

suggesting food limitation as a potential contributor to the observed decline in water column abundance. Although average body size neither increased nor decreased as the population became established, (Table 1c) females were larger in the north (Table 1). Body sized averaged 1.04 ± 0.01 (S.E.) mm in the north, and 0.99 ± 0.01 (S.E.) mm in the south (range 0.69 and 1.25 mm). Tail-spine length was positively related to body size (r^2 = 0.32, p = 0.00001). In addition, we found significant effects of gender ($F_{1,214}$ = 13.2, p = 0.0003) and instar ($F_{2,214}$ = 83.2, p < 0.00001), but no effect of their interaction ($F_{2,214}$ = 2.3, p = 0.1) on the combined data set for body size at all stations and times (Fig. 2). Females were larger than males, and on average, individuals of each barb-class were larger than those in the previous instar.

In August of the years following establishment of *C. pengoi*, we found fewer rotifers (t = 10.96, df = 1, *P* = 0.01) than we did during the pre-establishment years. We also found a significant decline in the size of the cyclopoid copepod population (t = 4.73, df = 1, *P* = 0.05). It is not clear, however, that these changes should be attributed to the presence of *C. pengoi*, because all zooplankton taxa were less abundant in post-establishment years (Dettmers *et al.* 2003).

DISCUSSION

As is true for most introduced species, we do not know exactly when *C. pengoi* first invaded Lake Michigan. Nevertheless, long-term monitoring allowed us to record *C. pengoi* in southern Lake Michigan and follow its establishment. The population appeared earlier in the season each year following invasion, but we did not find any dramatic shifts in morophology, nor did we find any conclusive examples of predatory effects on the native zooplankton assemblage. Establishment of *C. pengoi* was correlated with declines in rotifer densities, but given the overall decline in zooplankton over the past decade (Dettmers *et al.* 2003), it is not clear how much of the rotifer decline can be attributed to this new exotic species. Unfortunately, manipulative experiments to determine potential interactions with native species have been hampered by the inability to culture *C. pengoi* in the laboratory. As a result, monitoring of several invaded systems may be the best way to assess the impacts of this new predator.

Cercopagis pengoi has become established along the entire Illinois coast, but its dynamics clearly

differ from site to site and year to year. For example, we found very few *C. pengoi* in 2001, a year when the densities of all nearshore zooplankton were low in 2001 (Dettmers *et al.*, unpublished data). By 2003, maximum population densities exceeded 700 individuals/m^3 (Witt and Cáceres 2004), which is still well below densities in Lake Ontario (2,500 individuals/m^3; Ojaveer *et al.* 2001). Despite these differences in maximum abundance, the seasonal timing of the population dynamics appears to be consistent among invaded habitats. For example, populations in Lake Ontario are also not found in the water column before July (Benoît *et al.* 2002) and peak abundances in the Baltic Sea are generally detected in August (Ojaveer *et al.* 2000). The presence of this species in the water column appears to be tied to temperature, with the majority of individuals being found in epilimentic waters when the water temperature exceeded 15°C (MacIsaac *et al.* 1999, Benoît *et al.* 2002). A preference for warmer temperatures would restrict both the seasonal timing and vertical distribution of this species. However, individuals have been found at colder temperatures (Ojaveer *et al.* 2000) and we found *C. pengoi* in the hypolimnion at deeper stations in Lake Michigan (Witt and Cáceres 2004).

Clutch sizes observed in Lake Michigan were higher than those observed in other invaded lakes (e.g., Lake Ontario, mean = 3.7, maximum 13.1, Makarewicz *et al.* 2001; Baltic Sea mean = 4.7, Grigorovich *et al.* 2000). Average clutch size varied four-fold across seasons and years, and often decreased as population sizes increased. However, there appeared to be no relationship between water column abundances and clutch size. Clutch sizes above 8 eggs/female were only found when populations were small (< 10 individuals/m^3) but large clutches were not always found when densities were low, particularly at the end of the year at the southern stations. The late-August decline in average densities occurred at a time when clutch sizes were falling, suggesting food limitation as a potential contributor to this decline (Hall 1964). Declines in densities may also result from the switch to the production of males and diapausing eggs. This switch can slow overall population growth rate because males and gametogenic females do not produce offspring that contribute to the current population.

The average body size of *C. pengoi* in Lake Michigan was considerably smaller than *C. pengoi* in their native Caspian Sea (1.51 mm–1.73 mm; Grigorovich *et al.* 2000), Lake Ontario (1.36 mm;

MacIsaac *et al.* 1999) or the Baltic Sea (1.83 mm; MacIsaac *et al.* 1999). MacIsaac *et al.* (1999) suggested that animals might be smaller in Lake Ontario than in the Baltic Sea as a result of increased predation intensity in Lake Ontario. A similar explanation may also apply to Lake Michigan. Not only are the *C. pengoi* in Lake Michigan relatively small, but average water column densities are also lower than in other invaded habitats, despite the fact that clutch sizes in Lake Michigan were higher than has been reported from these other lakes. This suggests that predation may be an important regulator of the summer dynamics in Lake Michigan. Alternatively, Grigorovich *et al.* (2000) suggested that *C. pengoi* body size was positively related to latitude, and the North American data support this trend. The mechanisms underlying this latitudinal pattern in body size will be difficult to assess without more information on both the genetic structure of each new population and the specific selection pressures of that new environment. Cristescu *et al.* (2001) found limited variation in mitochondrial DNA sequence analysis in the Baltic Sea population. They also indicated that the Baltic may have provided the source population for North America, suggesting these more recently invaded populations may lack diversity as well. Low genetic diversity may also explain why we did not observe any rapid shifts in key traits.

It is clear that *C. pengoi* has the potential to invade a number of lakes in North America (Ricciardi and MacIsaac 2000, Therriault *et al.* 2002, Bushnoe *et al.* 2003, Kane *et al.* 2003). The important question then becomes, what impact will this species have on native communities? Recent studies of *C. pengoi* have suggested that their diet may be dominated by rotifers, cyclopoid copepodids, *Daphnia retrocurva* and *Bosmina* (Rivier 1998, Benoît *et al.* 2002, Laxson *et al.* 2003). We found a significant reduction in the densities of rotifers and cyclopoids following the introduction of the new predator, suggesting that the addition of this new species may have an impact on the Lake Michigan food web. However, we interpret our results with caution given the findings of Dettmers *et al.* (2003) that the densities of zooplankton in general appear to be declining. When *C. pengoi* became established in the Balitic Sea, Ojaveer *et al.* (2000) suggested that the impacts of this invasive species ranged from herbivores to fish. At this time, the long-term impacts on the Lake Michigan food web are less clear. Part of the difficulty in predicting the impact of *C. pengoi* in Lake Michigan is the number of other exotic

species already established in the lake. For example, *C. pengoi* is a prey item for non-native predators such as *Bythotrephes* (Witt and Cáceres 2004) and alewife (Charlebois *et al.* 2001) and will prey upon zebra mussel veligers (Cáceres, unpublished data). If *C. pengoi* interacts more strongly with non-native species than it does with natives, its impact on what is left of the native assemblage may be minor. Continued monitoring of this area of the lake is essential to understanding the role of this new species in the ever-changing food web.

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