Potential Predator-prey Relationships between *Bythotrephes longimanus* and *Cercopagis pengoi* in Southwestern Lake Michigan

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ABSTRACT. *The introduction of multiple non-native predators to a lake may influence food-web dynamics in unpredictable ways, but in large lakes it is often difficult to conduct field experiments to test directly the impact of each new exotic species. Instead, a combination of field data, mathematical modeling, and laboratory experiments is often employed. In this study, we use this combination to address potential interactions between two exotic predators (*Bythotrephes longimanus *(formerly* B. cederstroemi) and Cercopagis pengoi) in southwestern Lake Michigan. Specifically, we conducted laboratory experiments in which we varied the size of enclosure (10 mL, 100 mL, 1,000 mL, 10,000 mL) to determine how container size affects the outcome of predator-prey interactions. We also recorded the occurrence of both species in 2002–2003 and used a mathematical model to estimate potential encounter rates between these two species. Densities of *C. pengoi *ranged from 5 to 717 individuals/m³ at our sampling stations while *B. longimanus *was rare. The results from the laboratory experiments indicated that *B. longimanus *will eat* C. pengoi. *However, the predicted number of daily encounters between these two species in southwestern Lake Michigan was relatively small under most model scenarios. Moreover, our results also indicated that the size of the container and the species involved can significantly affect experimental outcomes. Hence, our results demonstrate that although the findings of laboratory experiments can provide insight into possible interactive dynamics, great care should be taken when extrapolating laboratory results to the field.*

INDEX WORDS: *Invasive species, encounter model, container effect.*

INTRODUCTION

It is now well understood that the effects of multiple predators on a prey assemblage can not be predicted by simply adding the effects of each individual predator-prey interaction in isolation (Soluk and Collins 1988, Wilbur and Fauth 1990, Lohrer and Whitlach 2002). As a result, when more than one non-native predator invades a new system, the combined effects of this exotic assemblage may be difficult to estimate. If both invasive predators share the same prey items or if one predator facilitates the feeding of another, native prey assemblages may be reduced with the addition of each new non-native predator (Sih *et al.* 1998). Alternatively, intraguild predation among the exotic predators may reduce the predatory impact on the native prey species (Polis *et al.* 1989). Determining potential non-linearities in predator-prey interactions is key to understanding how multiple exotic species may impact native prey assemblages.

Numerous exotic species have invaded the Laurentian Great Lakes and threaten the quality of these economically important ecosystems (Mills *et al.* 1993). In particular, two predatory cladocerans have invaded the Great Lakes from the Palearctic and Ponto-Caspian regions (Ricciardi and Rasmussen 1998, Rivier 1998). *Bythotrephes longimanus* initially invaded Lake Huron in 1984 (Bur *et al.* 1986) and spread to all of the Great Lakes by 1987 (Lange and Cap 1986, Lehman 1987, Cullis and Johnson 1988). *Bythotrephes longimanus* is an effective predator and includes both large-bodied and small-bodied prey items in its diet (Schulz and Yurista 1999). Thus, predation by *B. longimanus* has been implicated in altering the zooplankton assemblage in Lake Michigan (Lehman and Cáceres 1993). A more

recent invader, *Cercopagis pengoi* is closely related to, but considerably smaller than, *B. longimanus* (Rivier 1998). *Cercopagis pengoi* was first documented in Lake Ontario in 1998 (MacIsaac *et al.* 1999), in Lake Michigan in 1999 (Charlebois *et al.* 2001), and has since invaded several other North American lakes (Makarewicz *et al.* 2001). *C. pengoi* also eats other zooplankton, but at present its exact diet and predation rates on native species can only be inferred from temporal changes in native species since its introduction (e.g., Benoît *et al.* 2002, Laxson *et al.* 2003).

This uncertainty about the diet of *C. pengoi* and the lack of information regarding how it will interact with other members of the Lake Michigan community make it difficult to predict the direction and magnitude of food-web changes that may accompany its invasion. One possibility is that predation by *C. pengoi* will decrease abundances of native species, which may further exacerbate the problems of declining yellow perch recruitment (Dettmers *et al.* 2003). Alternatively, *C. pengoi* may serve as a preferred prey item for *B. longimanus* or a native predator, which could lessen the predation pressure on native species (Sih *et al.* 1998). Impacts of both *B. longimanus* (Lehman and Cáceres 1993, Schulz and Yurista 1999, Yan *et al.* 2002) and *C. pengoi* (Benoît *et al.* 2002, Bushnoe *et al.* 2003, Laxson *et al.* 2003) have been documented, but to date no study has directly examined the interaction between these two exotic predators.

Field studies can record food-web responses that are correlated with the establishment of each new invader, but manipulative experiments are also needed to determine processes driving the observed patterns. Because it is difficult to conduct manipulative field experiments in the Great Lakes, the potential impacts of predatory zooplankton are often investigated in the laboratory. In the past, laboratory experiments involving predatory cladocera have been conducted in as little as 10 mL of water (Branstrator 1995) and it is well known that most container experiments introduce several factors that are not found in nature including elevated densities, edge effects, spatial confinement, and the presence of a homogeneous environment (Gerritsen and Strickler 1977, O'Brien 1988). O'Brien (1988) examined the effect of a range of container sizes (0.114–200 L) on the feeding rate of copepods and determined a consistent hyperbolic nature to the relationship between feeding rate and container size. Feeding rate increased rapidly in containers smaller than 2 L, but began to level off in the larger containers. However,

O'Brien's study included a collection of existing experimental data with differing methods. Applying an identical experimental procedure over a gradient of container sizes for the particular predator in question seems necessary to determine how container size may impact the outcome of laboratory experiments.

The arrival of *C. pengoi* into the Great Lakes has raised questions regarding the food-web impacts of this new invader (MacIsaac *et al.* 1999, Charlebois *et al.* 2001). However, basic information regarding its natural history and interactions with other species in its new habitats remains rare (but see Benoît *et al.* 2002, Bushnoe *et al.* 2003, Laxson *et al.* 2003). Moreover, it remains unclear how well laboratory experiments capture the natural dynamics of this exotic species. We integrate field samples, laboratory experiments and an encounter rate model to (1) quantify the spatial overlap of *B. longimanus* and *C. pengoi* in southwestern Lake Michigan, (2) estimate the potential encounter rates between *B. longimanus* and *C. pengoi*, and (3) determine if container size affects the outcome of the interaction between these two species. Our results suggest that *B. longimanus* will consume *C. pengoi*, but the food-web effects of this interaction in southwestern Lake Michigan may be minimal due to spatial segregation of these two exotic predators.

METHODS

Spatial Distribution

In 2002 and 2003, we collected replicate monthly samples May through September at two sites: inshore (2.5 km from shore, 10 m depth) and offshore (12 km from shore, 50 m depth). In 2003, we included a third sampling site half-way between our two regular sites (7 km offshore, 27 m depth) and sampled all three stations in the transect biweekly mid-August through September while both exotics were present. All three sites were located near Waukegan Harbor, IL (42°21′ N, 87°48′ W). We also examined the potential for vertical segregation of the two exotics at the furthest offshore site. All samples at stations at the nearshore and half-way station were replicate bottom to surface tows, and replicate epilimnion, metalimnion, and hypolimnion samples were collected at the offshore station, except on 2 September when the thickness of the metalimnion was too small to sample effectively with our closing net (Table 1). Samples were collected with a 0.5 m diameter, 500 μm closing net and were immediately preserved in a sucrose-formalin solution and later transferred to ethanol in the laboratory. All *C. pengoi*

	19 August 2003	2 September 2003	16 September 2003
Epilimnion	0–7	0–15	0–11
Metalimnion	7–17	not sampled	11–13
Hypolimnion	17–45	15–45	13–45

and *B. longimanus* were counted using a dissecting microscope.

We used a paired t-test to compare the water-column densities of *B. longimanus* and *C. pengoi* across both years and all three sampling stations. For the 2003 transect data, we used a repeated measures ANOVA to compare the densities of *C. pengoi* from nearshore to offshore over time. Because we could not collect a metalimnetic sample on 2 September, the vertical distribution of *C. pengoi* was analyzed separately for each of the three sampling dates using either ANOVA (19 Aug., 16 Sept.) or t-test (2 Sept.). Data for ANOVA were log(x+1) transformed prior to analysis to normalize residuals and equalize variances. *B. longimanus* was excluded from these analyses due to small sample sizes in 2003. All statistical analyses were conducted using SYSTAT 8.0 (Wilkinson 2000).

Laboratory Experiments

In 2002 and 2003, we conducted laboratory experiments with *C. pengoi* and *B. longimanus*. We had three main objectives: first to investigate if one exotic species would eat the other, second to determine if container size affected the outcome of this interaction, and third to address how container effects may vary with each pair-wise interaction. Three sets of trials were conducted: *B. longimanus* versus *B. longimanus* (BB), *C. pengoi* versus *C. pengoi* (CC), and *B. longimanus* versus *C. pengoi* (BC). All three experiments were identical with the exception of the combination of species involved. *Bythotrephes longimanus* and *C. pengoi* were collected from southwestern Lake Michigan with a 500 μm zooplankton net. After a minimum 6 hour acclimation period, two adult individuals were placed in four different sized containers (10 mL, 100 mL, 1,000 mL, 10,000 mL). Although all but the largest container

size resulted in densities that were elevated well above our ambient densities, we chose these volumes because many previous experiments have been conduced in enclosures that span this size range (e.g., O'Brien 1988, Branstrator 1995, Schulz and Yurista 1999). We also established containers of each size with only one individual to assess recovery rates of both live and dead animals after 24 hours. All individuals of both species were recovered from these containers.

All containers were filled with filtered (75 μm) Lake Michigan water and kept at 21–23°C and a 12:12 photoperiod. After 24 hours, each individual was scored as alive, killed (severely damaged body/only tailspine remaining), or dead (no longer alive, but no evidence of body damage/attack). At least 30 successful replicates were conducted for each container size for each species combination. A trial was only considered to be successful if both animals remained alive after 24 hours or if an individual animal was identified as having been eaten. Trials where one individual simply died during the 24 hours were excluded from the final analysis. The effects of container size (10 mL–10,000 mL) and treatment (BB, BC, CC) were analyzed with the two-way logistic ANOVA available in PROC GENMOD, SAS 8.0 (Littell *et al.* 2002).

Encounter Rates

All else being equal, the encounter rate between one predator and one prey should decrease as the volume (container size) that the predator has to search increases. To interpret the outcome of the laboratory experiments and to extrapolate laboratory results to the field, the frequency of predator-prey encounters must be assessed. Encounter rates between *B. longimanus* and *C. pengoi* were calculated with a model developed by Gerritsen and Strickler (1977):

$$E = \frac{\pi R_b^2 N_c}{3} \left(\frac{\bar{S}_c^2 + 3S_b^2}{S_b} \right) \qquad (1)$$

where the encounter radius (maximum distance of detection of other animals) of *B. longimanus* is represented by R_b, N_c refers to the density of *C. pengoi*, and S_b and $\bar{S}_c$ represent the swimming speed of an individual *B. longimanus* and the mean swimming speed of the *C. pengoi* population respectively. Five encounter radii from 2 mm to 10 mm were used based on the encounter radii measured by Muirhead and Sprules (2003) under different lighting intensi-

ties. We used 18 mm/s as the mean swimming speed of *B. longimanus* based on values for the different instars reported in Muirhead and Sprules (2003). Because the swimming speed of *C. pengoi* is unknown, we tested the sensitivity of the model to a range of values (5–30 mm/s). However, since the model is relatively insensitive to changes in swimming speed (Gerritsen and Strickler 1977, Muirhead and Sprules 2003), and the swimming speed of *C. pengoi* did not appear to influence the magnitude of the encounter estimates, we used a speed of 15 mm/s.

We calculated encounter rates for both the laboratory and field. Laboratory encounter rates were calculated using the densities present in each container size ($100,000/m^3$, $10,000/m^3$, $1,000/m^3$, and $100/m^3$). To assess number of interactions between *B. longimanus* and *C. pengoi* in the field, the encounter rate of a single *B. longimanus* (E) must be multiplied by the density of *B. longimanus* (N_b) to obtain the total encounter rate (T) between all individuals of both species:

$$T = EN_b \qquad (2)$$

Field encounter rates were calculated using the density range of *C. pengoi* in the offshore waters of Lake Michigan ($0–250/m^3$) and the maximum density of *B. longimanus* found at our sampling sites ($1.3/m^3$). *C. pengoi* densities were greater nearshore, but no *B. longimanus* were detected nearshore to allow an interaction to occur.
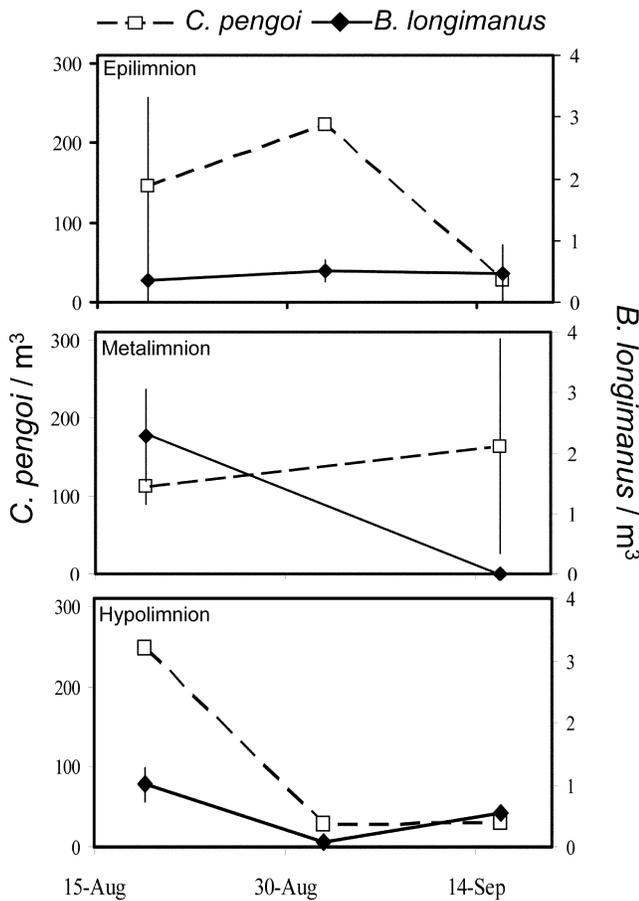
RESULTS

Spatial Distribution

Over both years, average densities of *B. longimanus* were lower than those of *C. pengoi* (Paired t-test, t = –2.05, df = 11, $P = 0.04$). Densities of *B. longimanus* were always < $2/m^3$ whereas the densities of *C. pengoi* ranged from < 1 to $717/m^3$. Moreover, *B. longimanus* was never detected at the two closest sites to shore. For the 2003 transect series, we found a significant effect of location ($F_{2,3}$ = 38.4, $P = 0.007$), time ($F_{2,6}$ = 371.8, $P < 0.0001$) and the location*time interaction ($F_{2,6}$ = 94.9, $P < 0.0001$) on the abundance of *C. pengoi* (Fig. 1). We found the highest numbers of *C. pengoi* in August, with densities at the nearshore station almost 4× higher than the other two sites. By September, overall densities were considerably lower and densities were comparable across the three sampling sites.

The *C. pengoi* population did not occupy a consis-
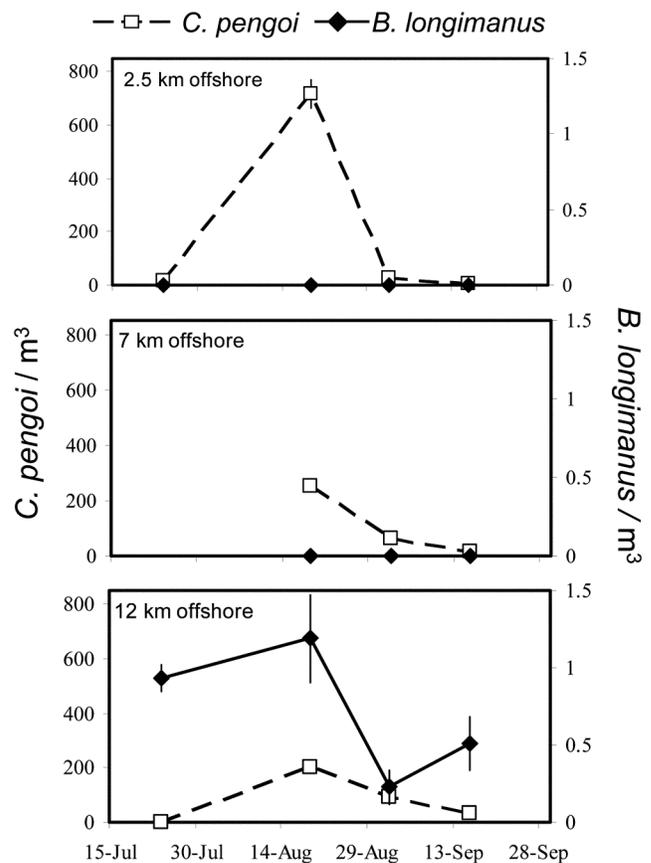
FIG. 1. *Density (± 1 S.E.) of* **C. pengoi** *and* **B. longimanus** *along a horizontal transect in south-western Lake Michigan in 2003. Top: 2.5 km off-shore. Middle: 7 km offshore. Bottom: 12 km off-shore. Note the differences in scales for the two predator species.*
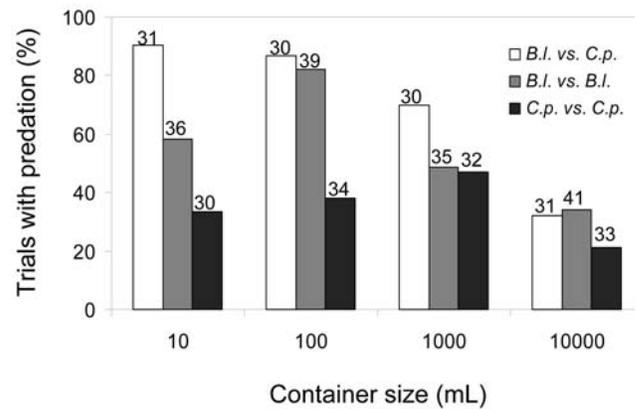
tent thermal habitat in the water column (Fig. 2). On 19 August, on average, 49% of the population was found in the hypolimnion, with the remaining members of the population fairly evenly split between the metalimnion and the epilimnion. However, because of the variance between epilimnetic replicates, we found no difference in the abundance among layers ($F_{2,3}$ = 0.77, $P = 0.54$). By 2 September, most individuals were found in the epilimnion (t = 34.9, df = 2, $P = 0.0008$) and the percentage of individuals in the hypolimnion had fallen to 11%. On our final sampling date (16 September) we found on average over 70% of the population in the metalimnion, but variance between those replicates resulted in no overall difference in the number of individuals in each layer ($F_{2,3}$ = 0.80, $P = 0.52$).

FIG. 3. *Effects of container size and species pair on kill rate in the laboratory experiments. The numbers at the top of each column indicate the number of successful independent trials for each container*species-pair combination.*

FIG. 2. *Densities (± 1 S.E.) of* **C. pengoi** *and* **B. longimanus** *at the station 12 km offshore in the epilimnion (top panel), metalimnion (middle panel) and hypolimnion (bottom panel). Note both the difference in scales for the two predator species and the fact that the volume sampled in each layer changed through time (Table 1).*

Laboratory Experiment

Our experiments demonstrated predation by *B. longimanus* on *C. pengoi* and cannibalism in both *B. longimanus* and *C. pengoi* (Fig. 3). *Bythotrephes longimanus* killed and ate *C. pengoi* across all container sizes, but we found no evidence for the consumption of *B. longimanus* by *C. pengoi*. We found significant effects of container size ($\chi^2 = 41.35$, df = 3, $P < 0.0001$), species combination ($\chi^2 = 35.61$, df = 2, $P < 0.0001$), as well as the container*species interaction ($\chi^2 = 15.96$, df = 6, $P < 0.014$) on the percentage of experimental trials that ended in a predation event (Fig. 3). In general, the 10,000 mL containers had fewer kills ($\chi^2 = 37.04$, df = 1, $P < 0.0001$), but the relative decline in the kill rate

from the smallest containers depended on the particular interaction. Approximately 90% of the *C. pengoi* were consumed when placed in 10 mL of water, but only 32% of the *C. pengoi* placed in 10,000 mL of water were consumed. Percentages of consumption for the single-species interactions ranged from 34%–82% for *B. longimanus* but only 21%–48% for *C. pengoi*.

Encounter Rates

In the laboratory experiments, predicted encounter rates between *B. longimanus* and *C. pengoi* ranged from a low of 2.4 to a high of 6.0×10^4 potential encounters over the 24 hour experiment (Table 2). The number of predicted encounters was proportional to container size; the 10 mL container had the most predicted encounters, while the 10,000 mL had the fewest. In the field, predicted encounter rates between *B. longimanus* and *C. pengoi* were considerably lower. At ambient densities at the furthest (12 km) offshore site, the total number of predicted encounters between all members of both populations ranged from less than 2 to almost 200 encounters/m³/day (Fig. 4). In comparing the encounter rates predicted in the laboratory and the field, we found that the 10,000 mL containers were the only laboratory treatment to reflect predicted field encounter rates at all encounter radii because that was the only treatment that included natural densities of the *C. pengoi*. For the 1,000 mL containers, the encounter rates were within the range of the predicted field values for only the 2 mm and 4 mm

TABLE 2. Predicted encounters between one **B. longimanus** *and one* **C. pengoi** *in each of the four container sizes. Each number represents the total predicted encounters during the 24 hour experiment. These estimates are based on the volume of the container, swimming speeds of 18 mm/s and 15 mm/s for* **B. longimanus** *and* **C. pengoi** *respectively, and the particular encounter radius (R_b) used for* **Bythotrephes**.

	R_b (mm)				
	2	4	6	8	10
Container Size (mL)					
10	2,400	9,600	21,600	38,500	60,100
100	240	960	2,160	3,850	6,010
1,000	24	96	220	390	600
10,000	2.4	9.6	22	39	60

encounter radius estimates. All other laboratory encounters were much higher than what was predicted to occur in the field (Table 2, Fig. 4).

DISCUSSION

Although *B. longimanus* will eat *C. pengoi* when confined in the laboratory and given no alternative food, the effect of this interaction on the food-web dynamics of southern Lake Michigan remains un-
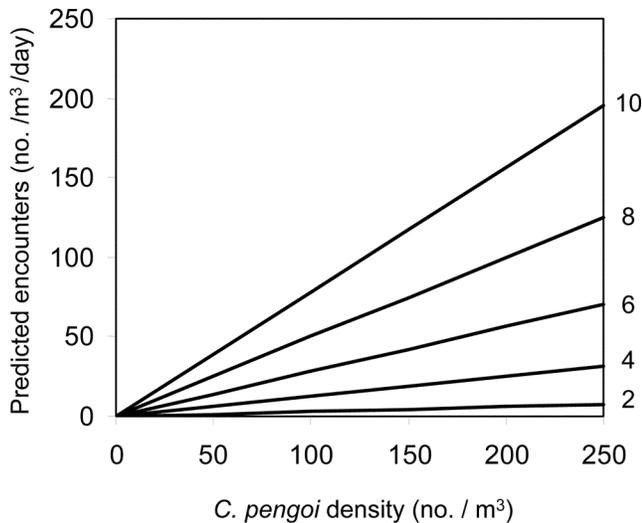
FIG. 4. Predicted encounter rates between **B. longimanus** *and* **C. pengoi** *at 12 km offshore in southwestern Lake Michigan under ambient densities with the encounter radius (R_b) of* **B. longimanus** *ranging from 2 to 10 mm*

clear. We found a significant effect of both the container size and the species combination on the outcome of our laboratory experiments, indicating that caution must be used when extrapolating these laboratory results to the field. Moreover, although *C. pengoi* can be quite abundant in southern Lake Michigan, we found consistently low densities of *B. longimanus*, and the encounter rate model often predicted few encounters at ambient densities. Hence, spatial segregation of the two species may limit their interaction in this part of the lake. Ultimately, lake-wide surveys that include vertical profiles will be needed to understand the potential for interaction between these two species, and how that interaction may influence food-web dynamics.

In Lake Michigan, maximum abundances of *B. longimanus* are most often found in offshore waters, and it has been suggested that predation by fish may exclude it from nearshore areas (Pothoven *et al.* 2001, 2003). In contrast, our data suggest densities of *C. pengoi* are highest nearshore, although we do not know if densities increase further offshore than we sampled. Although simultaneous reports on the spatial distribution of both species in North America remain rare, MacIssac *et al.* (1999) report unpublished data from the Baltic Sea suggesting that *B. longimanus* abundances are lower where *C. pengoi* is present (V. Panov, unpublished data). In Lake Ontario, where *B. longimanus* are rarely detected in the water column, (Mills *et al.* 2003; K.L. Schulz, pers. comm.) maximum densities of *C. pengoi* can exceed 2,500/m^3 (Ojaveer *et al.* 2001). At present, it is impossible to determine if this apparent spatial segregation results from the direct avoidance of one species by the other, or whether the two species rarely co-occur simply due to differences in preferred habitats or prey distribution within each lake.

At our deepest station, where the two species did co-occur, we often found *C. pengoi* throughout the water column. This is in contrast to the population of *C. pengoi* in Lake Ontario that has consistently been found only in epilimnion waters (Ojaveer *et al.* 2001, Benoît *et al.* 2002, Laxson *et al.* 2003) but similar to vertical distributions in the N.Y. Finger Lakes (Snyder and Schulz unpub. data). In zooplankton, position in the water-column is thought to be influenced by a balance among predation avoidance, food availability, avoidance of UV radiation and temperature optima (Lampert *et al.* 2003, Rhode *et al.* 2001). Bushnoe *et al.* (2003) found that alewife (*Alosa pseudoharengus*) larger than 66 mm consumed *C. pengoi* in Lake Ontario, and suggested that predation by alewife on *C. pengoi* may be wide-

spread due to the spatial overlap between predator and prey. In Lake Michigan, although alewife do consume *C. pengoi* (Charlebois *et al.* 2001), this exotic species is generally not a preferred item in the alewife diet (A. Storch, pers. comm.). Moreover, the deeper average depth of the *C. pengoi* population in Lake Michigan may reduce the encounters between this exotic species and its vertebrate predator. These differences in abundances and vertical and horizontal distribution between the *C. pengoi* populations in Lake Michigan versus Lake Ontario suggests different potential impacts for this species in the two lakes.

When *B. longimanus* first invaded the Great Lakes in the mid 1980s, there was considerable controversy regarding the role of this exotic species in its new habitat (e.g., Sprules *et al.* 1990, Lehman 1991) and the arrival of *C. pengoi* has brought about a new round of speculation regarding the role of both exotics in the food-web (MacIsaac *et al.* 1999, Pothoven *et al.* 2003). It is clear from our container experiments that different enclosure sizes influence the outcome of predator-prey interactions with these species. This is especially true when small containers are used, resulting in artificially high densities of predators and prey. Hence, variation in experimental protocols among research groups may contribute to the differences in opinion regarding the impact of each new exotic species. For example, Vanderploeg *et al.* (1993) conducted a predation experiment in which they confined 60 *B. longimanus* with various prey items in 30 L containers and suggested that predation by *B. longimanus* likely had a minor impact on native species. Although the experiment of Vanderploeg *et al.* (1993) used much larger volumes of water (and reduced densities) they also included cannibalism in the total predation rate. In contrast, Schulz and Yurista (1999) only used one predator per 1.2 L container and concluded that *B. longimanus* had the potential to consume a significant portion of the cladoceran production, especially of large daphniids. Branstrator (1995) found differences in predation rates of *B. longimanus* on *Leptodora* depending on whether the interaction occurred in 10 mL versus 1,000 mL of water. Our study indicated that both container size and species combination had a significant influence on the results of our predator-prey experiments, suggesting that with these particular species, care must be taken in experimental design and especially the subsequent interpretation of the results.

In our experiments, the percentage of individuals consumed generally tended to decrease as container size increased, but the nature of the trend depended on the specific interaction. The trials with one *B. longimanus* and one *C. pengoi* showed almost a linear decline in kill rate with increasing container size. The reduced rate of predation in the larger containers may have been a result of declining encounter probabilities between *B. longimanus* and *C. pengoi* as container size increased. In contrast, when two *B. longimanus* were placed together, instead of showing a constant decline, there was an apparent increase from approximately 60% to 80% in 10 mL versus 100 mL of water. Reduced maneuverability of two large *B. longimanus* in the 10 mL container may have contributed to the lower kill rates in the smallest containers. Dodson *et al.* (1997) found that the swimming behavior of *Daphnia* was influenced by container size, with all species of *Daphnia* swimming slower and in more of a straight line in smaller containers. Because swimming behavior influences encounter rates, changes in the behavior of either the predator or the prey with container size will influence results. Finally, predation rates with two *C. pengoi* were lower and showed far less variation among container sizes as compared to the other two species combinations. There are at least two explanations for the reduced mortality rate when *C. pengoi* is acting as a predator. The first is that predation rates of *C. pengoi* are indeed lower than those of *B. longimanus*. If this is the case, an individual *C. pengoi* may have less of an impact on native species than does an individual *B. longimanus*. *Cercopagis pengoi* may also have less of an impact on native species as a result of the lower energetic demand of the much smaller predator (Snyder and Schulz pers. comm.). However, an alternative explanation that *C. pengoi* are simply less active in the laboratory than they are in the field. In fact, the mortality rate of *C. pengoi* once they are brought into the laboratory is extremely high. Hence, until this species can be successfully reared in the laboratory, great care should be taken when trying to extrapolate the results from container experiments to the field.

As these two species continue to invade new habitats in North America, their interaction may be predatory, competitive or a combination of these two processes. The direct and indirect effects of each species will influence how this exotic assemblage impacts each food web, and how these impacts may change as additional exotic species are introduced. An increased ability to rear *C. pengoi* in the laboratory, combined with appropriately designed experiments will facilitate our understanding of these effects. Although basic natural history about each

new species is important, a community approach that examines the interactions of introduced species with both native and other exotic species is necessary to quantify the influence of each new exotic that invades the Great Lakes.

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