

Research Article

Spines and surplus: existing inducible defenses and abundant resources may reduce the impacts of *Cercopagis pengoi* on a likely prey speciesStephanie E. Figary^{1,*} and Kimberly L. Schulz²¹Cornell University, Department of Natural Resources and the Environment, Ithaca, NY 14850, USA²State University of New York College of Environmental Science and Forestry, Department of Environmental Forestry and Biology, Syracuse, NY 13210, USAAuthor e-mails: sef92@cornell.edu (SEF), kschulz@sy.edu (KLS)

*Corresponding author

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Received: 7 October 2020**Accepted:** 22 January 2021**Published:** 17 May 2021**Thematic editor:** Elena Tricarico**Copyright:** © Figary and SchulzThis is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).**OPEN ACCESS****Abstract**

A lack of co-evolved defensive mechanisms can make organisms especially vulnerable to invasive predators. *Bosmina longirostris* is an herbivorous zooplankton known to change morphology as an inducible defense mechanism against the native predatory invertebrate *Leptodora kindtii*. In 1999, *Cercopagis pengoi*, another predatory zooplankton, invaded six of the eleven New York Finger Lakes in which both *L. kindtii* and *B. longirostris* co-occur. This created a natural experiment for studying *C. pengoi*'s (1) influence on the presence of *B. longirostris*' long morphological form, a known inducible defense against predation by native *L. kindtii*, (2) consumption rates of *B. longirostris* using mass-balance equations for several prey preference scenarios, and (3) overlap with the native predatory cladoceran *L. kindtii*. *Bosmina longirostris* densities were lower in the invaded Finger Lakes and exhibited more long form morphology, with longer percent relative mucro lengths, than in non-invaded lakes (Mann Whitney, $p = 0.006$). The percent relative mucro length was positively correlated with predator densities, particularly those of *C. pengoi* (Spearman, $r = 0.812$, $p < 0.001$), consistent with *C. pengoi* predation on *B. longirostris* as a potential driver of this inducible defense expression. Mass balance calculations estimated predation by *C. pengoi* could reduce *B. longirostris* densities by 10–100% during peak *C. pengoi* densities if the latter only consumed the former or preferentially selected large zooplankton from the available prey assemblage. Additionally, *C. pengoi* and *L. kindtii* populations overlapped temporally in the invaded lakes, suggesting that their prey species were abundant enough to support both populations. This study indicates that (1) *B. longirostris* likely produce an inducible defense protective against native predators in response to invasive *C. pengoi*, and (2) *C. pengoi* distribution overlaps with *L. kindtii* in invaded lakes.

Key words: invasive species, *Bosmina longirostris*, *Leptodora kindtii*, predatory invertebrates

Introduction

Invasive species are second only to land use changes as threats to biodiversity in aquatic systems (Sala et al. 2000) and are known to impact biodiversity at the global scale (Doherty et al. 2016). Invasive species reduce biodiversity by altering food web dynamics, including increasing predation pressure or competition (Clasen et al. 2010). These processes can

cause local extinctions of prey species or replacement by invasive species of native species that occupy similar niches. Native prey can be particularly vulnerable to predation from invasive predators that do not share a coevolutionary history (Fritts and Rodda 1998; Carthey and Banks 2014), known as prey naiveté, and evidence suggests some invasive predators cause more harm to prey than native predators (Salo et al. 2007; Ros et al. 2019). However, there is also evidence of native prey using pre-adapted inducible defense mechanisms to protect against predation from non-native predators (Whitlow 2010; Bible et al. 2017).

Bosmina longirostris (O.F. Müller, 1776), a herbivorous cladoceran, is known to use morphological plasticity as an inducible defense mechanism by producing a “long form” with lengthened mucrones and antennules at times of high predation by invertebrates (Kerfoot 1975a). This long form is more difficult for these native predators, specifically *Leptodora kindtii* and predatory copepods, to handle, increasing the chances of escape by *B. longirostris* (Kerfoot 1977a; Chang and Hanazato 2004); however, the long form morph has reduced fecundity due to additional energy requirements for growing and maintaining the long-form and having less space for eggs (Kerfoot 1977b). Density declines of *B. longirostris* have been attributed to predation by *L. kindtii* and the invasive predatory zooplankton, *Cercopagis pengoi* (Branstrator and Lehman 1991; Benoît et al. 2002). A paleolimnological study of two invaded New York Finger Lakes demonstrated that the mucro length of *B. longirostris* increased after *C. pengoi* invasion, suggesting that the defense mechanism may be effective against *C. pengoi* predation (Brown et al. 2012).

Cercopagis pengoi (Ostroumov, 1891) is a predatory cladoceran native to the Ponto Caspian region that invaded the Baltic Sea in 1992 and Lake Ontario in 1998 through ballast water from cargo ships (MacIsaac et al. 1999). Since the invasion to Lake Ontario, *C. pengoi* established in several more Laurentian Great Lakes and inland lakes of New York and Michigan (Makarewicz et al. 2001). The average dry weight of *C. pengoi* is 6.2 µg (Snyder 2004) and the average body length is 1.5 mm, not including the long caudal appendage, which can be over 8 mm in length (Grigorovich et al. 2000). In the Baltic Sea, a stable isotope study confirmed that *C. pengoi* is zooplanktivorous (Gorokhova et al. 2005; Holliland et al. 2012). Field studies on the Great Lakes suggest that *C. pengoi* preys on *B. longirostris*, copepod nauplii, rotifers, and potentially *Daphnia retrocurva* (Forbes, 1882) (Benoît et al. 2002; Laxson et al. 2003; Warner et al. 2006; Barbiero and Warren 2011). There is evidence that *C. pengoi* can have large negative impacts on prey populations, such as rotifers in Lake Ontario (Makarewicz and Lewis 2015), because the invader reaches higher summer densities compared to the native predatory cladoceran *L. kindtii* (Focke, 1844). *Leptodora kindtii* has an average dry weight of 8.5 µg (Hawkins and Evans 1979) and an average length of 7.4 mm (Balcer et al. 1984) in Lake

Michigan. In 2007, the peak density of *C. pengoi* in Owasco Lake in New York was nearly four times greater than *L. kindtii* peak density (Brown and Balk 2008).

Overall, the impacts of *C. pengoi* are not fully understood due to its frequent co-occurrence with another predatory invasive species, *Bythotrephes longimanus* (Lange and Cap 1986). *Bythotrephes longimanus* is known to have high consumptive demand (Yurista and Schulz 1995) and strong negative impacts on herbivorous zooplankton populations (Schulz and Yurista 1999; Barbiero and Tuchman 2004). Additionally, experimental studies on *C. pengoi* are limited because *C. pengoi* suffers high mortality during handling (Snyder 2004). The difficulty of maintaining *C. pengoi* in culture suggests that many feeding experiments were conducted on stressed organisms and likely were not fully representative of field interactions.

Cercopagis pengoi invaded six of the eleven New York Finger Lakes (USA) in 1999, creating a natural experiment for studying its effects on *B. longirostris* and the zooplankton assemblages without potential complicating effects from presence of *Bythotrephes longimanus*, which is not present in these lakes. This study included three objectives. First, compare *B. longirostris* density and morphology in the invaded and non-invaded lakes to assess differences in the presence of the “long form” inducible defense mechanism in lakes with only native predators compared with those also containing *C. pengoi*. Second, estimate the reduction of *B. longirostris* after one day of *C. pengoi* consumption, using field population size changes and mass balance equations for three possible prey-preference scenarios. Lastly, investigate the effects of *C. pengoi* on the total predatory Cladocera densities and the densities of its potential native competitor, *L. kindtii*.

Materials and methods

Lake district and site selection

The Finger Lakes District has eleven lakes with similar land use and climate (Halfman and O'Neill 2009), including six lakes invaded by *Cercopagis pengoi* and five non-invaded lakes. To avoid large potential confounding factors of comparing zooplankton in lakes with and without planktivorous fish, the eight lakes with alewife (*Alosa pseudoharengus* (Wilson, 1811)) populations, known to have strong size-selective effects on zooplankton assemblages (Brooks and Dodson 1965; Wells 1970), were selected for study, and lakes without alewife were excluded. In order to maintain a large number of lakes in the study, no other selection factor was used.

Five lakes invaded by *C. pengoi* (Otisco, Owasco, Seneca, Cayuga, and Canandaigua) and three non-invaded lakes (Canadice, Hemlock, and Conesus) were sampled. Each lake had one nearshore site (depths ranged from 11 to 20 m) and one or two offshore sites (depths ranged from 16 to 122 m) because density of *C. pengoi* is known to vary between nearshore and offshore

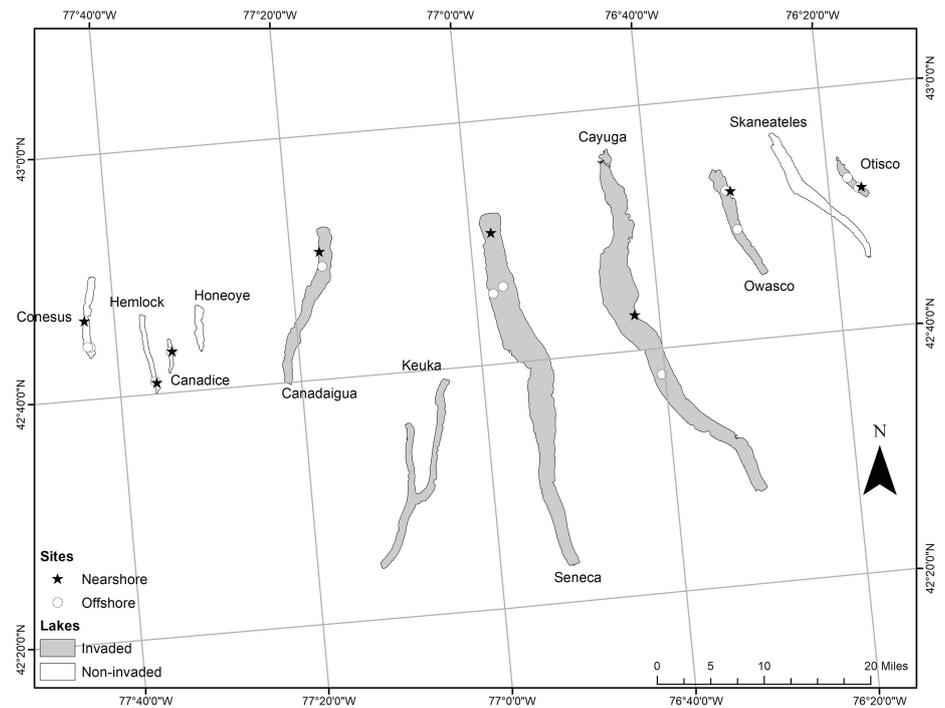


Figure 1. The Finger Lakes District of New York, United States. Invaded lakes are grey and non-invaded lakes are unshaded. Nearshore sites are marked with black stars and offshore sites with hollow circles.

locations in the Great Lakes (Makarewicz et al. 2001, Figure 1, coordinates and site depths in Appendix 1). *Cercopagis pengoi* densities were not significantly different between the nearshore or offshore sites in this study (Appendix 2).

Of the eight lakes, five were chosen as survey lakes and three as focal lakes. The five survey lakes included three invaded lakes (Otisco, Cayuga, and Canandaigua) and two non-invaded lakes (Canadice and Hemlock) and were used to compare the zooplankton assemblages (*C. pengoi*, *L. kindtii*, and *B. longirostris* densities) during times of high *C. pengoi* densities in July and August 2010. Three focal lakes were sampled more intensively; these included two invaded lakes, Owasco and Seneca Lakes, and one non-invaded lake, Conesus Lake. The invaded lakes, Owasco (surface area = 26.7 km², volume = 0.78 km³, maximum depth = 54.0 m) and Seneca (surface area = 175.4 km², volume = 15.54 km³, maximum depth = 198.4 m; Schaffner and Oglesby 1978) were chosen because they were sampled in previous studies investigating *C. pengoi* in the Finger Lakes (Brown and Balk 2008; Brown et al. 2012). Conesus Lake (surface area = 13.7 km², volume = 0.16 km³, maximum depth = 20.2 m; Forest et al. 1978) was chosen as the focal non-invaded lake because it is the largest lake not invaded by *C. pengoi* with an alewife population. Though using one non-invaded lake raises concerns of pseudoreplication, we choose this approach because Conesus Lake is the only non-invaded lake close in size to the invaded lakes, due to the unique morphology of the New York Finger Lakes, and Conesus Lake is likely to have the most similar predation pressures from alewife, based on alewife

condition measurements (Figary 2013). The authors are not aware of any biological, chemical or physical factors or history in Conesus Lake that would make it a poor representative of a non-invaded Finger Lake.

Field methods

Zooplankton were collected with vertical net tows pulled by hand at a rate of 1 m sec⁻¹, from the bottom to the surface. Predatory cladocerans (*C. pengoi* and *L. kindtii*) were collected using a 500- μ m mesh, high efficiency net (collared; Aquatic Ecosystems) with a diameter of 30 cm. Herbivorous zooplankton, including rotifers, were collected using a 50- μ m mesh, high efficiency net (collared; Aquatic Ecosystems) with a diameter of 20 cm. Samples were narcotized using a quarter tablet of Alka Seltzer[®] and preserved in 4% sugar formalin. In the focal lakes, zooplankton sampling was conducted during daylight hours, twice monthly from June to October 2010. Three to seven days separated each lake's two monthly samplings and the first sampling dates of each month were approximately 30 days apart. Survey lakes were sampled once in July and once in August, during the expected peak density of *C. pengoi* (Makarewicz et al. 2001; Brown and Balk 2008).

Laboratory methods:

Cladocera and rotifers were identified using taxonomic keys (Balcer et al. 1984; Thorp and Covich 1991). Adult copepods were not identified to further taxonomic detail in this study because they were considered unlikely prey for *C. pengoi*. Adult predatory copepods were assumed to be at low densities in the Finger Lakes because a previous study on invaded Owasco Lake found low predatory copepod densities (Brown and Balk 2008). Additionally, July 2010 samples from the survey and focal lakes had no occurrences of the predatory copepod *Epischura* spp. and August 2010 samples only had low occurrences (< 2 individuals/m³) in Owasco and Conesus lakes (Figary 2013).

In the survey lakes, only *C. pengoi*, *L. kindtii*, and *B. longirostris* densities were enumerated. In the focal lakes, predatory and herbivorous cladocerans, and rotifers also were counted. The predatory cladocerans, *C. pengoi* and *L. kindtii*, were identified and counted on a dissecting microscope (Leica MZ12.5, Leica Microsystems). Entire samples were counted because *C. pengoi*'s tendency to clump together prevents accurate subsampling. The first 100 *C. pengoi* encountered were staged to instar by counting the number of barbs on the caudal appendage. At least two subsamples of herbivorous cladocerans were counted from each sample, each containing at least 200 individuals of any dominant species (> 10% of sample; coefficient of variation between subsamples < 10%). From the first sampling date of each month, only abundant cladocerans (> 10% of the sample) were counted.

From the second sampling date, all herbivorous cladocerans were counted, including *B. longirostris*, *Eubosmina coregoni* (Baird, 1857), *Ceriodaphnia* spp., *Diaphanosoma birgei* (Korinek, 1981), *Eurycercus* spp., *Daphnia retrocurva*, *Daphnia mendotae* and *Sida crystallina* (O.F. Müller, 1776). Rotifers were identified and counted on a compound microscope (Leica DMLB, Leica Microsystems) using a Sedgewick-Rafter counting cell with the subsampling technique detailed above for the larger herbivorous zooplankton. Five genera were counted, including (1) *Keratella* spp., (2) *Polyarthra* spp., (3) *Trichocerca* spp., (4) *Conochilus* spp., and (5) *Synchaeta* spp., because they were the most abundant rotifer genera and their different body types and defense strategies (hard/loricated, rapid jumping motion, spiny, colonial and soft-bodied) offer varying degrees and forms of protection from predation (Thorp and Covich 1991). As with the larger herbivorous Cladocera, only the rotifer genera that were abundant (> 10% of the sample) were counted from the first sampling date of each month, and from the second sampling date, all five genera were counted.

Density and morphology of B. longirostris:

The densities of *B. longirostris*, a likely prey item of *C. pengoi*, were compared in July and August between the invaded and non-invaded lakes (including both survey and focal lakes), using a Mann-Whitney U-test with both volumetric and areal densities. Both volumetric and areal densities were used because the zooplankton were collected with whole water column tows, so the maximum depth of *B. longirostris* presence on each sampling date was not known. The morphology of *B. longirostris* was determined for the first 30 individuals encountered in samples from the first offshore site on the first sampling date of each month in the focal lakes. *B. longirostris* was photographed using a CoolPix 4500 Nikon camera fitted to the compound microscope under 400x magnification. Measurements were made from the photos using ImageJ (version 1.46r) calibrated with images of a stage micrometer at the sample magnification. Morphological measurements of *B. longirostris* were taken (on the side that faced up during photographing) including length of carapace (total length; TL), mucro length (ML), and antennule length (AL) (Figure 2). The percent relative mucro length (ML/TL), and percent relative antennule length (AL/TL) were calculated for each *B. longirostris*. Relative lengths account for the organism's TL, making them better indicators of long or short form, as mucro and antennule length alone are functions of both body size and the overall shape. Using the ML:TL values, we calculated monthly variance in ML:TL and the monthly percent long-forms. Though research documented *B. longirostris* increases ML:TL in the presence of invertebrate predators (Kerfoot 1975a), no definition of what constitutes a short-form compared to long-form *B. longirostris* exists. In this study, ML:TL values

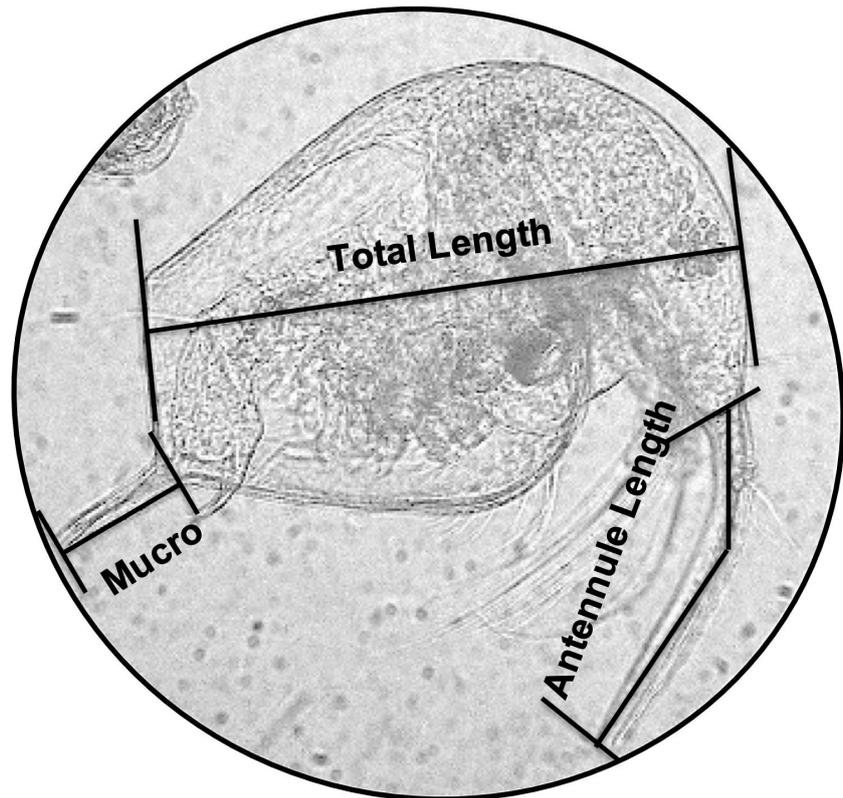


Figure 2. Measurements of total length (TL), mucro length (ML), and antennule length (AL); made for *Bosmina longirostris* using ImageJ software.

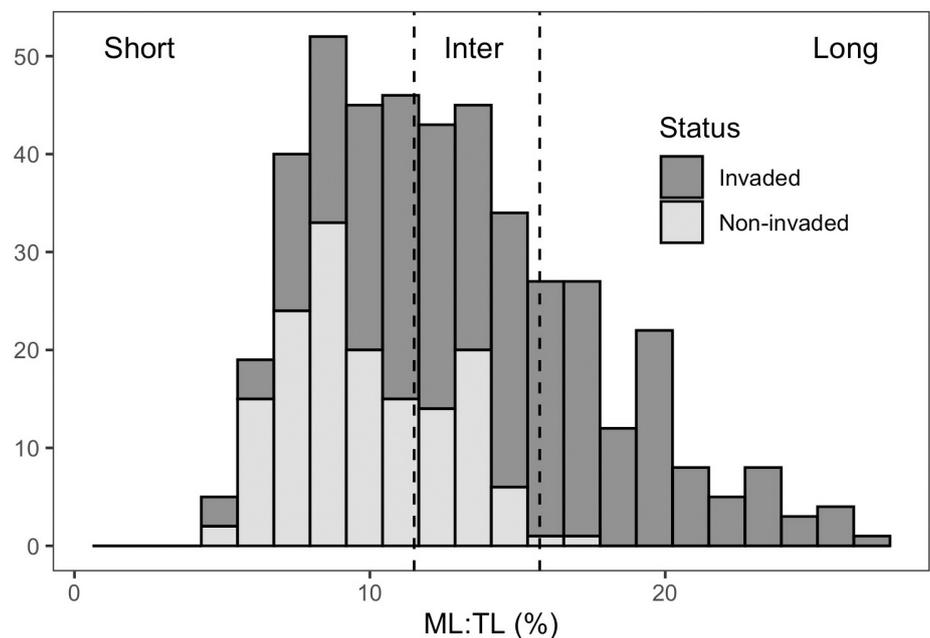


Figure 3. Relative mucro length (ML/TLx100) of *Bosmina longirostris* from all three focal lakes (June to October 2010). The invaded lakes' data (Owasco and Seneca lakes) bars are dark grey, while the non-invaded lake's data (Conesus Lake) bars are light grey. Long-form was defined as having a ML/TLx100 > 15.75%, the mid-point of the range of ML:TL. The short- and intermediate-forms were defined by the natural break in the distribution of ML:TL (near 11.5%).

were used to define the long-form *B. longirostris* by determining the ML:TL midpoint (ML:TL midpoint = 15.75%) from the range of ML:TL throughout the season for all focal lakes (Figure 3). The mid-point was

used as a cut-off between long form (ML:TL > 15.75%) and short- or intermediate-forms (ML:TL < 15.75%). There was also a small natural gap in the distribution of ML:TL near 11.5%, which we used as the cut-off between short- (ML:TL < 11.5%) and intermediate- forms (11.5% < ML:TL < 15.75%). The percent long-form *B. longirostris* in the population was calculated for each month.

The monthly average (July to October 2010) morphological characteristics of *B. longirostris*, including TL, ML, AL, ML:TL, long-forms, ML:TL variance, and AL:TL were compared between the two invaded lakes and one non-invaded focal lake using a Mann-Whitney U-test (five months per lake, two invaded lakes n = 10, one non-invaded lake n = 5). Additionally, the monthly ML:TL distributions from each lake were compared among the two invaded lakes and the non-invaded lake using a Mann-Whitney U-test.

Correlations between the average monthly morphology of *B. longirostris* (ML:TL, percent long-form, and ML:TL variance) and predatory Cladocera densities (*C. pengoi*, *L. kindtii*, and *C. pengoi* plus *L. kindtii* combined), referred to as “standard correlations”, were determined using a Spearman rank order test. A post-hoc analysis using “lagged correlations” was added to account for potential lagged responses in *B. longirostris* morphology to the presence of their predators. In this analysis, the characteristics of *B. longirostris* were correlated with the predatory Cladocera densities from the prior month (e.g., morphological forms of *B. longirostris* in July are correlated with *C. pengoi* densities in June). This one month lagged response analysis allowed for multiple *B. longirostris* generations after initial predator density measurements, providing time for induction of the long morphological form of *B. longirostris* in response to the handling by predatory invertebrates (Sakamoto et al. 2007).

Potential impact of C. pengoi on prey

To estimate impacts of *C. pengoi* on potential prey species, Spearman rank order correlations were calculated between *C. pengoi* and densities of zooplankton in the two invaded focal lakes. Additionally, the potential effect of *C. pengoi* predation on *B. longirostris* population size was estimated in the invaded focal lakes using (a) bioenergetic equations for *C. pengoi* (Schulz 2005) to predict predatory demands, (b) the measured *C. pengoi* densities, and (c) available *B. longirostris* densities from each sampling date. These calculations were done for three predation scenarios: (1) *C. pengoi* only consumed *B. longirostris*, to bound the maximum predatory impacts, (2) *C. pengoi* consumed *B. longirostris* in proportion to their relative density (e.g., if *B. longirostris* were 50% of the zooplankton assemblage, *B. longirostris* would be 50% of the diet by number), to illustrate effects if *C. pengoi* had no preference for prey species, and (3) *C. pengoi* selected prey species by their mass with a preference for larger species.

All scenarios assumed that *C. pengoi* consumes prey items smaller than itself and was not consuming *Daphnia retrocurva*. Though *C. pengoi* consumed *D. retrocurva* in laboratory feeding settings (Laxson et al. 2003; Pichlová-Ptácníková and Vanderploeg 2009), it is not expected to consume *D. retrocurva* in field settings (Benoît et al. 2002). Scenario two assumes that all prey are equal in terms of nutrient and energy content, digestibility, capturability, and *C. pengoi*'s ability to detect them. The last scenario acknowledges that larger prey species likely are higher in calories and assumes that *C. pengoi* has a preference for prey that provide the highest energy relative to predation effort, consistent with an energy maximizing optimal foraging strategy (MacArthur and Pianka 1966).

For all scenarios, the daily energetic demand (in μg) of the *C. pengoi* population on each sampling date was estimated using the proportion of each instar of *C. pengoi* in the population and assuming daily consumption by *C. pengoi* is 80% of the its dry mass to meet energetic needs (Schulz 2005). Zooplankton dry mass was calculated using *B. longirostris* lengths from this study and published length-weight regressions for rotifers (Bottrell et al. 1976) and other Cladocera (Watkins et al. 2011). *Cercopagis pengoi* masses were from previous Finger Lake studies (Snyder 2004). The predatory impact of *C. pengoi* for each sampling date and scenario was estimated as the percent reduction in prey density from one day of *C. pengoi* consumption, as estimated by the energetic requirements, divided among prey according to each scenario's predation rules.

Predatory cladoceran densities and overlaps

Patterns in predatory Cladocera densities were compared between the invaded and non-invaded lakes (including both survey and focal lakes) to determine if the invaded lakes had higher predatory Cladocera densities. Mann-Whitney U-tests were used to compare the densities of *L. kindtii* between the invaded and non-invaded lakes, as well as the combined density of *L. kindtii* plus *C. pengoi*. Lastly, the densities of *C. pengoi* and *L. kindtii* at the first offshore site of the invaded focal lakes (Owasco and Seneca Lakes) were used to determine if there was any correlation between the density of two predators using a Spearman rank order test from June to October. Nonparametric tests were used in all analyses for all objectives due to low sample sizes. R Studio and R version 3.6.1 were used for all statistical analyses ($\alpha = 0.05$) and figures, unless stated otherwise.

Results

Density and morphology of B. longirostris

Bosmina longirostris densities were significantly higher in the non-invaded than invaded lakes in July (Mann Whitney, $n = 8$, $p = 0.036$, Figure 4) for both volumetric (m^{-3}) and aerial (m^{-2}) densities. In August, the non-invaded

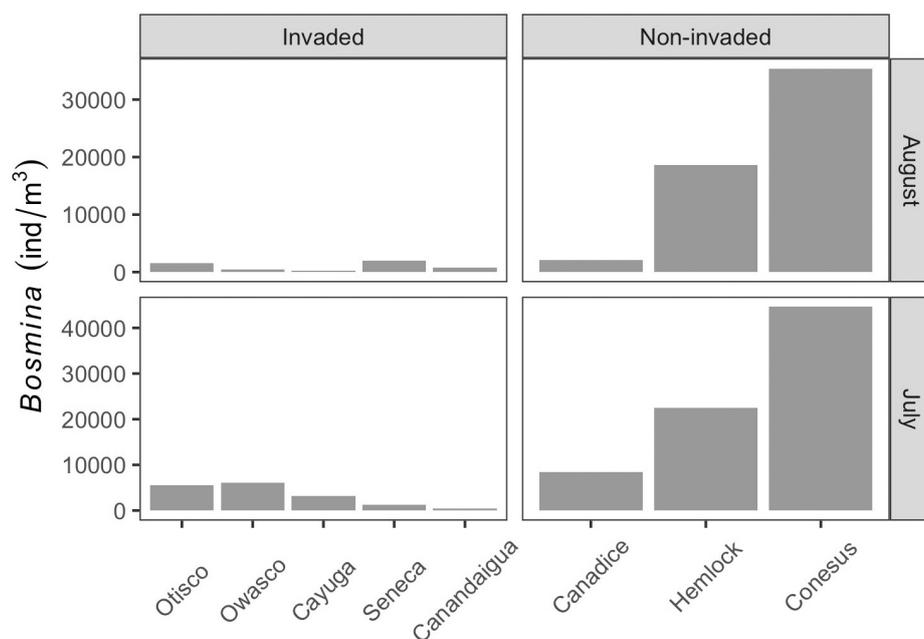


Figure 4. Volumetric densities of *Bosmina longirostris* in the invaded and non-invaded survey and focal lakes in July and August. *B. longirostris* volumetric densities were significantly higher in the non-invaded lakes in both July and August (Mann Whitney, $p = 0.036$ for both months).

Table 1. Morphology of *Bosmina longirostris* in the focal lakes from five sampling events (monthly, June–October). Bolded p -values indicate invaded (Owasco and Seneca) and non-invaded (Conesus) lake were statistically different (Mann-Whitney U-test; $\alpha = 0.05$).

<i>Bosmina</i> characteristics	Invaded	Non-invaded	p -value
Total length (TL) (μm)	284.4	262.5	0.017
Mucro length (ML) (μm)	41.0	25.7	0.004
Antennule length (AL) (μm)	128.7	121.3	0.058
ML:TL (%)	14.9	9.6	0.006
AL:TL (%)	48.5	47.5	0.501
ML:TL (%) variance	3.7	2.3	0.006
Long-forms (%)	39.9	0.7	0.003

lakes had significantly higher *B. longirostris* volumetric densities (Mann Whitney, $n = 8$, $p = 0.036$) and higher, but not significant, areal densities (Mann Whitney, $n = 8$, $p = 0.071$).

In the focal lakes, *B. longirostris* from invaded lakes had more long-form characteristics than *B. longirostris* from the non-invaded lake (Table 1). In the invaded lakes, the TL (Mann Whitney, $n = 15$, $p = 0.017$), ML (Mann Whitney, $n = 15$, $p = 0.004$), ML:TL (Mann Whitney, $n = 15$, $p = 0.006$), ML:TL variance (Mann Whitney, $n = 15$, $p = 0.006$), and percent long-form (Mann Whitney, $n = 15$, $p = 0.003$) of *B. longirostris* all were significantly greater than in the non-invaded lake. Long-forms were rarely observed in the non-invaded lake ($0.7\% \pm 1.5$ of the *B. longirostris* population) compared to invaded lakes ($39.9\% \pm 15.1$). In each month, *B. longirostris* in invaded lakes had longer ML:TL compared to those in the non-invaded lake.

Morphometric parameters for *B. longirostris* (percent long-form, ML:TL, and ML:TL variance) from one sample month were correlated with

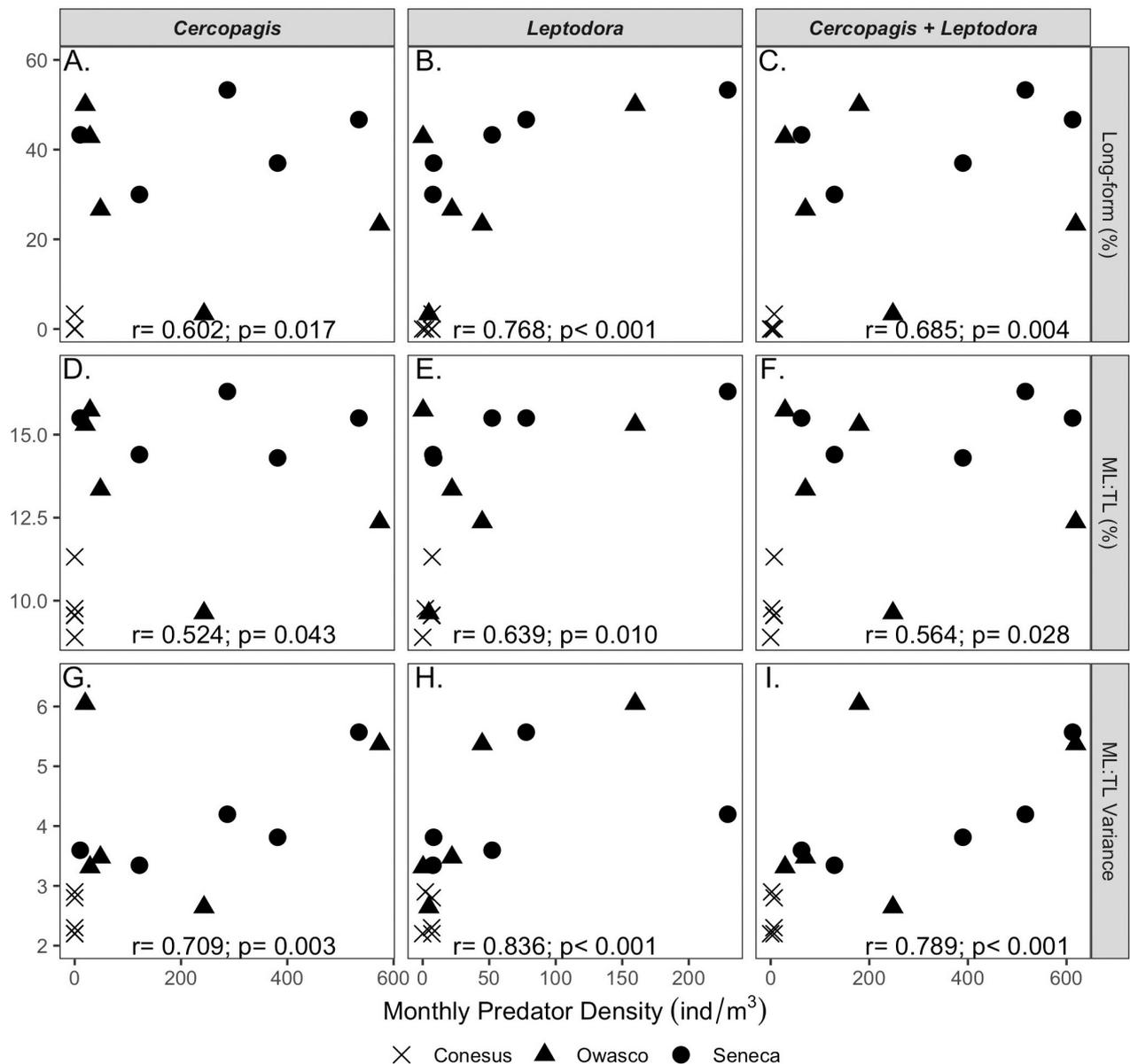


Figure 5. Standard correlations between the morphology of *Bosmina longirostris* (percent long-forms, relative micro length, and ML:TL variance) and densities of *Cercopagis pengoi*, *Leptodora kindtii*, and both predators combined from the same month. Relative micro length was calculated by dividing the micro length by the total length and multiplying by 100%. Invaded Owasco Lake is represented with a triangle, invaded Seneca Lake with a circle, and non-invaded Conesus Lake with an X. Each symbol represents a sampling date. All correlations (Spearman rank order) were statistically significant ($\alpha = 0.05$).

the densities of predatory cladocerans (*C. pengoi*, *L. kindtii*, and *L. kindtii* plus *C. pengoi* combined) from the same month (Figure 5). The long forms of *B. longirostris* significantly increased with increasing densities of *C. pengoi* (Figure 5A: Spearman, $n = 15$, $r = 0.602$, $p = 0.017$), *L. kindtii* (Figure 5B: Spearman, $n = 15$, $r = 0.768$, $p < 0.001$), and *C. pengoi* plus *L. kindtii* combined (Figure 5C: Spearman, $n = 15$, $r = 0.685$, $p = 0.004$). The ML:TL of *B. longirostris* also significantly increased with increasing densities of *C. pengoi* (Figure 5D: Spearman, $n = 15$, $r = 0.524$, $p = 0.043$), *L. kindtii* (Figure 5E: Spearman, $n = 15$, $r = 0.639$, $p = 0.010$), and *C. pengoi* plus *L. kindtii* combined (Figure 5F: Spearman, $n = 15$, $r = 0.564$, $p = 0.028$). The variance of ML:TL significantly increased with increasing *C. pengoi* as well (Figure 5G: Spearman, $n = 15$,

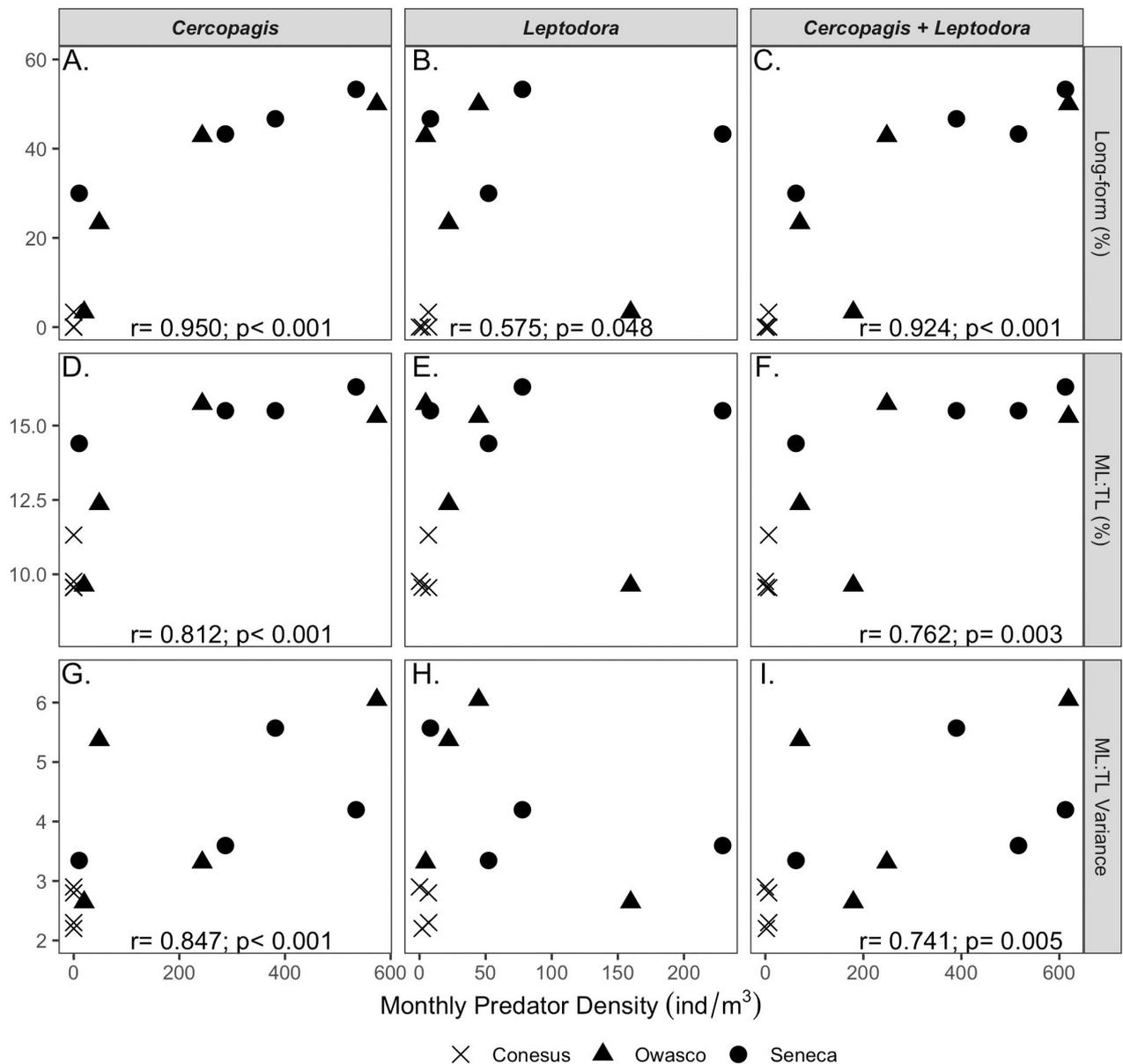


Figure 6. Lagged correlations between morphology of *Bosmina longirostris* and the predatory cladoceran densities from the previous month. See Figure 5 for further details. Panels without statistical information were not statistically significant ($\alpha = 0.05$, Spearman rank order).

$r = 0.709, p = 0.003$), *L. kindtii* (Figure 5H: Spearman, $n = 15, r = 0.836, p < 0.001$), and *C. pengoi* plus *L. kindtii* combined (Figure 5I: Spearman, $n = 15, r = 0.789, p < 0.001$). Figures of the morphometric parameters for *B. longirostris* and the predatory Cladocera densities over time can be found in Appendix 3.

In a post-hoc analysis using lagged correlations, in which morphometric parameters of *B. longirostris* were correlated with the previous month's predator densities (e.g., *B. longirostris* densities from July were correlated with *C. pengoi* densities in June), all morphological characteristics of *B. longirostris* (ML:TL, percent long form, and ML:TL variance) were significantly correlated with *C. pengoi* and total predatory Cladocera densities, but not always with *L. kindtii* densities (Figure 6). The percent

long-form *B. longirostris* significantly increased with increasing *C. pengoi* (Figure 6A: Spearman, $n = 15$, $r = 0.950$, $p < 0.001$), *L. kindtii* (Figure 6B: Spearman, $n = 15$, $r = 0.575$, $p = 0.046$), and *C. pengoi* plus *L. kindtii* densities combined (Figure 6C: Spearman, $n = 15$, $r = 0.924$, $p < 0.001$). The ML:TL significantly increased with increasing *C. pengoi* (Figure 6D: Spearman, $n = 15$, $r = 0.812$, $p < 0.001$) and *C. pengoi* plus *L. kindtii* densities combined (Figure 6F: Spearman, $n = 15$, $r = 0.762$, $p = 0.003$). The ML:TL variance significantly increased with increasing *C. pengoi* (Figure 6G: Spearman, $n = 15$, $r = 0.847$, $p < 0.001$) and *C. pengoi* plus *L. kindtii* densities combined (Figure 6I: Spearman, $n = 15$, $r = 0.741$, $p = 0.005$).

Bosmina longirostris morphology was more strongly correlated with *C. pengoi* and total predator densities in the previous month (lagged correlations; Figure 6) than with *C. pengoi* or *C. pengoi* plus *L. kindtii* combined densities in the same month (standard correlations; Figure 5). Morphology of *B. longirostris* was less correlated with *L. kindtii* density than with the density of *C. pengoi*. Overall, morphological characteristics of *B. longirostris* were most correlated with *C. pengoi* abundances the month before (Figure 6A, D, G).

Potential impact of C. pengoi on B. longirostris:

There were no significant correlations between *C. pengoi* and the density of its potential prey species collected on the same day in Seneca and Owasco lakes from June to October (Spearman rank order tests; for prey densities, figures, and p -values in Appendix 4). *Bosmina longirostris* was not significantly correlated with *C. pengoi* densities in Owasco (Spearman, $n = 9$, $r = -0.133$, $p = 0.709$) or in Seneca (Spearman, $n = 10$, $r = -0.417$, $p = 0.234$) lakes; however, high densities of *B. longirostris* were uncommon during high *C. pengoi* densities (Appendix 4, Figure S4).

Estimates of potential mortality of *B. longirostris* during one day of predation by *C. pengoi* consuming only *B. longirostris* (Scenario One) indicated that the prey population would be reduced more than 100% after one day of consumption during high densities of *C. pengoi* (July and September in Owasco Lake; July and October in Seneca Lake; Table 2). Scenario Two assumed that *C. pengoi* consume prey in proportion to their relative densities. Under this scenario, *C. pengoi* would reduce all prey species by a maximum of 29% (Owasco Lake, 15 July 2010) during times of high *C. pengoi* densities. But this high prey mortality only occurred on one sample date, with prey reductions of $< 5\%$ estimated for most other dates (16 of 20 sampling dates; Table 2). Scenario Three assumed that *C. pengoi* would select prey by their mass, with a preference for larger prey items. This excluded *D. retrocurva* that are unlikely to be consumed by *C. pengoi* in field settings (Benoît et al. 2002). This scenario resulted in mortality rates of *B. longirostris* lower than in Scenario One, but higher than in Scenario Two, with one day in each lake in which *C. pengoi* would consume 100% of

Table 2. Estimated percent reduction in densities of *Bosmina longirostris* after one day of *Cercopagis pengoi* predation if *C. pengoi* consumed: only *B. longirostris* (Scenario One), prey species in proportion to their densities (Scenario Two), prey with a preference for larger-bodied species by mass (Scenario Three). Bolded values indicate that *C. pengoi* could consume all available individuals on the given sample date (> 100%), and italicized values indicate that *C. pengoi* predation could reduce the species density by $\geq 10\%$ (from 10–99%). N/A indicates that the *B. longirostris* was not present in samples (below detection) on the given sample date.

Date	Density (individuals. m ⁻³)			Scenario One	Scenario Two	Scenario Three
	<i>Cercopagis pengoi</i>	<i>Leptodora kindtii</i>	<i>Bosmina longirostris</i>	<i>Bosmina longirostris</i>	All prey	<i>Bosmina longirostris</i>
Owasco Lake						
6/18/10	5	3	62737	0	0	0
6/22/10	74	48	100564	0	0	0
7/15/10	599	25	376	> 100	29	> 100
7/20/10	409	85	3788	<i>64</i>	2	4
8/16/10	21	232	N/A	N/A	0	N/A
8/19/10	7	143	189	<i>21</i>	0	1
9/14/10	928	11	1271	> 100	<i>18</i>	38
9/20/10	212	3	531	> 100	2	<i>15</i>
10/19/10	36	0	805	<i>24</i>	1	2
10/22/10	18	0	1910	6	0	0
Seneca Lake						
6/21/10	42	0	2028	<i>11</i>	1	9
6/24/10	420	11	14540	<i>17</i>	1	1
7/19/10	204	42	N/A	N/A	4	45
7/22/10	426	39	3380	> 100	2	6
8/16/10	287	287	22178	<i>14</i>	<i>10</i>	<i>11</i>
8/19/10	194	158	8923	22	4	1
9/18/10	9	36	10979	0	0	0
9/20/10	15	41	23614	0	0	0
10/19/10	434	5	881	> 100	<i>13</i>	> 100
10/23/10	204	6	3885	<i>27</i>	3	2

Table 3. Median densities (individual/m³) of predatory Cladocera in survey and focal lakes. Five invaded and three non-invaded lakes were sampled. *Leptodora kindtii* plus *Cercopagis pengoi* densities were statistically different in invaded and non-invaded lakes in July (Mann-Whitney *U*-test; $\alpha = 0.05$).

Month	Predatory Cladocera	Invaded (<i>n</i> = 5)	Non-invaded (<i>n</i> = 3)	<i>p</i> -value
July	<i>Leptodora kindtii</i>	28.1	5.4	0.143
	<i>Leptodora kindtii</i> + <i>Cercopagis pengoi</i>	216.5	5.4	0.036
August	<i>Leptodora kindtii</i>	118.7	28.8	0.250
	<i>Leptodora kindtii</i> + <i>Cercopagis pengoi</i>	227.0	28.8	0.250

the *B. longirostris* population (Owasco Lake, 15 July 2010; Seneca Lake, 19 Oct 2010). Effects of predation Scenarios One and Three on *C. pengoi*-induced mortality for prey species other than *B. longirostris* can be found in Appendix 5, along with the estimated dry weight of prey species used for Scenario Three.

Predatory Cladocera densities and overlaps:

The non-invaded lakes tended to have lower densities of *L. kindtii* and *L. kindtii* plus *C. pengoi* combined than the invaded lakes in July and August 2010 (Table 3), with significantly lower *L. kindtii* plus *C. pengoi* densities combined in the non-invaded lakes in July (Mann Whitney, *n* = 8, *p* = 0.036). There were no significant correlations between *L. kindtii* plus *C. pengoi* densities combined from June to October 2010 in either Seneca or Owasco lakes (Appendix 6).

Discussion

In many systems the negative effects of invasive species on biodiversity are partially attributed to predation or competition (Clasen et al. 2010), and often it is assumed that native species will have few defenses against novel invaders; there is evidence this is particularly true in freshwater systems (Ricciardi and Macisaac 2010; Anton et al. 2020). Here, we used a natural experiment in the Finger Lakes of New York to estimate effects of the invasive predatory cladoceran, *Cercopagis pengoi*, on a prey species, *Bosmina longirostris*, known to use inducible defense mechanisms against predatory invertebrates (Kerfoot 1977a; Chang and Hanazato 2004). Though the number of lakes in this natural experiment is limited, this approach can provide new insight on the impacts of *C. pengoi*, because *Bythotrephes longimanus*, known to have strong negative impacts on herbivorous zooplankton, has not invaded the Finger Lake District, unlike other lakes in North America where both co-occur.

The first objective of this study was to investigate the effects of *C. pengoi* on the density and morphology of *B. longirostris* in invaded and non-invaded lakes. *B. longirostris* exhibits a “long-form” morphology under predation pressure from invertebrates (Kerfoot 1975b). Long-form *B. longirostris* are more difficult for some native predators, like *Epischura* and *L. kindtii*, to handle, which increases the prey's chances of escaping (Kerfoot 1977a; Chang and Hanazato 2004). In our study, the survey and focal non-invaded lakes had a higher density of *B. longirostris* (Figure 3) and *B. longirostris* in the focal non-invaded lake, Conesus, were predominantly short-form compared to the focal invaded lakes, which had a mixture of short- and long-form *B. longirostris* (Table 1). We cannot entirely attribute the lower *B. longirostris* densities in the invaded lakes to *C. pengoi* predation without knowing *B. longirostris* densities prior to the invasion. However, the longer morphological characteristics of *B. longirostris* from invaded lakes is consistent with predatory invertebrates, such as *C. pengoi*, preying on *B. longirostris*. Additionally, growing and maintaining the long-formed morphology requires increased energy expenditure, decreased the space available for eggs, and reduced fecundity of long-formed morphs compared to short-formed morphs (Kerfoot 1977b).

The strong correlations between morphology of *B. longirostris* and densities of predatory invertebrates, particularly the density of *C. pengoi* in the prior month (Figure 6A, D, G), provides evidence that *B. longirostris* responded to *C. pengoi* by altering its morphology. *B. longirostris* may have more pronounced morphological response to *C. pengoi* than to *L. kindtii* due to the higher densities that *C. pengoi* reaches in comparison to *L. kindtii* and the timing of these peaks. In Owasco and Seneca Lakes the *C. pengoi* densities ranged between 5–928 and 9–426 individuals/m³, respectively, while *L. kindtii* ranged between 0–232 and 0–287 individuals/m³, respectively

(Appendix 4). Additionally, the first *C. pengoi* peak occurred in July in Owasco Lake and late June in Seneca Lake, before the *L. kindtii* peak, which occurred in August in both lakes. The morphology of *B. longirostris* in a population may take time to reflect predation pressure for two reasons. First, *B. longirostris* takes time to alter morphology in response to cues from the presence of predatory invertebrates such as physical handling (Kappes and Sinsch 2002; Sakamoto et al. 2007). Second, time is required for the predators to reduce the presence of the short-form morph through selective predation. The lagged correlations were a post-hoc analysis that allowed for several generations of *B. longirostris* between the lagged dates. A future study could use weekly sampling to determine the number of generations that are needed for *B. longirostris* to respond to predatory invertebrate densities. The correlation results from this study are consistent with a previous paleolimnological study in the New York Finger Lakes that found the mucro length of *B. longirostris* increased in Owasco and Seneca Lakes following the invasion of *C. pengoi* (Brown et al. 2012).

The ML:TL variance of *B. longirostris* increased with increasing *C. pengoi* densities; there are several potential explanations for the increased variance. First, even though the predation pressure was high enough to induce a morphological response, predation may not have been sufficient to remove all the short-formed *B. longirostris*. This assumes that if predation pressure were higher on the short-form *B. longirostris*, then ML:TL variance would eventually decrease, because the predators would preferentially eliminate the short-form prey, which are easier to capture and shift the entire population toward long-formed *B. longirostris*. Second, the ML:TL variance might not decrease, because long-form morphology might not actually be an effective defense mechanism against *C. pengoi* predation. Even though the long-form morphology helps to reduce capture of *B. longirostris* by *L. kindtii* and some predatory copepods (Kerfoot 1977a; Chang and Hanazato 2004), this study does not demonstrate directly that the long-form morphology is effective against the new predator, and such studies are not possible until this invasive can be maintained in experimental systems. The average mucro lengths and variability for *B. longirostris* found in this study were similar to those reported values from 2010 in Brown et al. (2012).

The non-invaded lake (Conesus) consistently had low percent long-formed morphs and lower relative mucro lengths compared to *B. longirostris* in Owasco and Seneca lakes, even early in the season before either *C. pengoi* or *L. kindtii* densities peaked. The prevalence of long forms early in the season may suggest that predation from previous years may influence long-form presence the next year, possibly from long-form morphs producing resting eggs that overwinter and hatch as new long-form morphs in the spring. An alternative explanation is that *B. longirostris* populations are more affected by alewife predation in the non-invaded lake. A previous

study in the region found that alewife from Conesus Lake (26.8% (\pm 3.3)) had a poorer condition, estimated by percent dry weight, compared to those from Owasco (34.8% (\pm 1.6)) and Seneca (29.0 (\pm 2.5)) lakes (Figary 2013). Ideally, our analysis would include another non-invaded lake, but there were no other non-invaded lakes similar in size, morphology, and alewife presence to the invaded lakes.

In the second objective, we estimated prey reductions from *C. pengoi* predation. In Scenario One, we estimated that *C. pengoi* would entirely consume *B. longirostris* if it were their sole prey or if the invader preferred larger mass prey (Scenario Three), by using the daily energetic demands of the *C. pengoi* populations in the invaded lakes and extrapolating these to predict potential predation effects (Table 2). However, the zooplankton abundance data show no correlations between *C. pengoi* and prey densities (Appendix 4), also suggesting that *C. pengoi* likely is not restricting its diet to *B. longirostris* or any other single prey. There are many other factors beyond *C. pengoi* predation that also impact *C. pengoi* prey abundances including, but not limited to, food availability, predation by other organisms, and other external factors such as temperature. Our results suggest that it is more likely that *C. pengoi* is an opportunistic predator that feeds on multiple prey species (Scenario Two), compared to just one prey species, and this is supported by some feeding experiments (Pichlova-Ptacnikova and Vanderploeg 2008).

Overall, the second objective results suggest that throughout the majority of the sampling season there were enough prey in the invaded lakes we surveyed to support both *C. pengoi* and *L. kindtii*, even if both zooplankton prey on the same species. This result is supported by the third objective finding that *C. pengoi* and *L. kindtii* overlapped from June to October in Owasco and Seneca lakes (Appendix 6) and finding no significant differences in the *L. kindtii* abundances in the survey lakes or focal invaded and non-invaded lakes in July and August (Table 3). These results might differ in less productive lakes with more limiting resources. Additionally, there are other factors beyond prey availability that likely impact both *C. pengoi* and *L. kindtii* abundances that were not accounted for here, such as predation from planktivorous fishes or *L. kindtii* preying on *C. pengoi*. While the body size of *C. pengoi* is within the range of *L. kindtii* prey, we do not expect *L. kindtii* to consume *C. pengoi* due to its long caudal appendage and *L. kindtii*'s feeding behavior. Previous studies suggest that *L. kindtii* favors smaller-bodied prey items than *C. pengoi*, due to studies documenting lower predation rates when *L. kindtii* was offered large compared to smaller prey items and had long handling times ($>$ 30 minutes) with large prey items (1.6 mm) (Havel 1985; Branstrator 1998), suggesting it is difficult for *L. kindtii* to handle prey that have a similar body size to *C. pengoi* even without its long caudal appendage.

The New York Finger Lakes District was selected for this study on *C. pengoi* because *Bythotrephes longimanus*, a predatory cladoceran closely related to *C. pengoi* (same Family), has not invaded the lakes and potential impacts from *C. pengoi* could be better assessed. This also enables us to compare the impacts of a *C. pengoi* invasion to that of *B. longimanus*. For instance, a hallmark of the invasion of *B. longimanus* is decreased *L. kindtii* densities (Barbiero and Tuchman 2004). However, this study found that *C. pengoi* and *L. kindtii* overlapped temporally in the *C. pengoi* invaded lakes, and the invaded lakes had higher overall predatory Cladocera densities than did the non-invaded lakes (Tables 3, 4). Additionally, our results support the suggestion that *C. pengoi* is not as voracious a predator as is *B. longimanus*. *Bythotrephes longimanus* is known to greatly reduce populations of prey species (e.g., large *Daphnia* spp.) (Barbiero and Tuchman 2004), perhaps not surprising given the larger size and energetic demands of *B. longimanus* (Yurista and Schulz 1995; Schulz 2005). For comparison, one Finger Lakes study measured *C. pengoi* as only 3.6% the mass of *B. longimanus* (Snyder 2004).

This study provides evidence that two predatory Cladocera, invasive *C. pengoi* and native *L. kindtii*, coexist in invaded New York Finger Lakes, likely because there is enough prey available to keep the competition between both of the predators low. Additionally, this study found that a likely prey item, *B. longirostris*, may utilize an inducible defense mechanism in the presence of *C. pengoi* to reduce predation from the invasive predator. This is counter to the prey naiveté hypothesis that suggests native species have few defenses against invasive species, particularly in freshwater systems (Ricciardi and Macisaac 2010; Anton et al. 2020). However, this supports that native prey are less likely to be vulnerable to invasive predators if they co-evolved with a similar predator (Ricciardi and Atkinson 2004; Cox and Lima 2006) or if the invasive predator has been established for a substantial period of time (Anton et al. 2020). In this case, *B. longirostris* had a pre-adapted inducible defense mechanism from historical predation by *L. kindtii*. These results are similar to common findings in marine environments, where invasive prey may use inducible defense mechanisms on native predators that use similar tactics as their native predators (Whitlow 2010; Bible et al. 2017; Pujol-Buxó et al. 2017), and provides additional evidence for this phenomenon in freshwater systems as well.

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Ethics and Permits

Research pertaining to this article did not require research collection permits. Research conducted in Hemlock and Canadice lakes was registered with the New York Department of Environmental Conservation (form: 81-20-3).

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Coordinates of nearshore and offshore sites used for zooplankton sampling at each lake.

Appendix 2. Comparison of nearshore and offshore *Cercopagis pengoi* densities from Owasco and Seneca lakes.

Appendix 3. *Bosmina longirostris* morphology and predatory Cladocera densities from June to October in the focal lakes.

Appendix 4. Predatory and herbivorous Cladocera and selected rotifers densities in the two focal lakes and Spearman rank order results.

Appendix 5. The potential impact of *Cercopagis pengoi* on all prey species for Scenario One and Three using mass balance equations.

Appendix 6. *Leptodora kindtii* and *Cercopagis pengoi* densities in the focal lakes from June to October 2010.

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