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Research Article

The potential link between lake productivity and the invasive zooplankter *Cercopagis pengoi* in Owasco Lake (New York, USA)[♣]

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Abstract

The fishhook water flea (*Cercopagis pengoi* Ostroumov, 1891) is an invasive zooplankter that can decrease the abundance and diversity of cladocerans and rotifers, which theoretically could release phytoplankton from grazing pressure and increase algal primary productivity. In the last decade, *C. pengoi* established and primary productivity increased concurrently in Owasco Lake (New York, USA). We studied plankton density, primary productivity, and standard limnological conditions in Owasco Lake during summer 2007 (1) to document summer densities of invertebrate predators, (2) to investigate correlations between *C. pengoi* and the abiotic environment, and (3) to examine the relationships among *C. pengoi*, native zooplankton, and productivity. Although the maximum abundance of *C. pengoi* observed (245 ind./m^3) far exceeded that of any native invertebrate predator, at most locations and dates unimodal density peaks between 35-60 ind./m^3 were typical and comparable to *Leptodora kindtii* (Focke, 1844), the most common native planktivore. Abiotic conditions were suitable for growth and reproduction throughout the sampling period, but were not linearly correlated with *C. pengoi* abundance. We observed reciprocal trends between predacious cladoceran density (both *C. pengoi* and *L. kindtii*) and herbivorous cladoceran density, and between herbivorous cladoceran density and Chlorophyll *a* concentration. Although these trends are only corollary, they support the possibility that *C. pengoi* may affect the trophy of Owasco Lake by reducing grazing zooplankton beyond the level of the native planktivores. Further study is needed to quantify the relative contributions of *C. pengoi* and *L. kindtii* to seasonal changes in the herbivorous cladoceran assemblage.

Key words: *Cercopagis pengoi*, Finger Lakes, invasive species, *Leptodora kindtii*, top-down control, trophic cascade

Introduction

The fishhook water flea (*Cercopagis pengoi* Ostroumov, 1891) is a zooplankter native to the Caspian cradle of Eurasia, but invasions during the 1990s were noted by fisherman who found *C. pengoi* ensnared on their angling equipment in and around the Baltic Sea (Ojaveer and Lumberg 1995) and in North America (MacIsaac et al. 1999; Panov et al. 2004). Their range expansion to North America is thought to have resulted from the transport of sexual diapausing eggs in ballast water of ocean-going vessels traveling from the Baltic Sea to Lake Ontario (Cristescu et al. 2001; Makarewicz et al. 2001). In North America, *C. pengoi* is now established in two additional Laurentian Great Lakes (Lakes Michigan and Erie) and inland lakes in Michigan and New York, USA (Charlebois et al. 2001; Makarewicz et al. 2001; Ojaveer et al. 2001; Therriault et al. 2002). Invasions by this carnivore have been associated with declines in

[♣] This paper was presented at the special session "Ecology and Ecotoxicology of Invasive Species in Inland Waters" of the 30th Congress of the International Association of the Theoretical and Applied Limnology (SIL), August 12-18, 2007, Montreal, Canada native plankton density and economic losses for fisheries (Makarewicz et al. 2001; Benoit et al. 2002; Laxson et al. 2003).

The Finger Lakes of western New York have been particularly impacted by *C. pengoi*, which has invaded 6 of the 11 lake basins that comprise this region. These lakes occupy deep, narrow, elongate, glacially scoured valleys, and collectively occupy a surface area near 5,000 km^2 and a water volume over 30 km^3 (Schaffner and Oglesby 1978). The lakes serve as the major drinking water source for 1.5 million people, support the agricultural and viniculture economy, and provide recreation opportunities for residents and tourists. The introduction of exotic species such as *C. pengoi* to the Finger Lakes, in addition to non-point source pollutants and shoreline development, have led to their listing as threatened water bodies.

One of the Finger Lakes where *C. pengoi* has established is Owasco Lake (surface area = 26.7 km^2, volume = 0.78 km^3, Z_{max} = 54 m), which has concurrently experienced changes in productivity and water quality. Chlorophyll *a* (Chl. *a*), dissolved nutrient concentrations (soluble phosphates, nitrates and silica), water transparency, and bacterial counts indicate that Owasco Lake has impaired water quality (J. Halfman, unpublished data). The lake's watershed, which is dominated by agricultural land (52%), is large compared to its volume (17:1, Bloomfield 1978), and nutrient enrichment from agricultural runoff and wastewater treatment are thought to have contributed to the lake's maximum productivity in the 1970s, when Chl. *a* concentration exceeded 5 µg/L. Reductions in nutrient loading in the intervening decades have decreased Chl. *a* to near 2 µg/L. However, periodic blooms of diatoms and cyanobacteria and dense macrophyte stands have recently become a nuisance during the summer (B. Gilman, T. Sellers, and B. Zhu, unpublished). Changes in the lake's trophy in the last decade have been attributed to increased phosphorus load from agriculture and human wastewater treatment (J. Halfman, unpublished). However, an alternative top-down explanation is that the concurrent invasion of *C. pengoi* has increased predation on herbivorous zooplankton and cascaded to release phytoplankton from grazing pressure.

Since the Finger Lakes are dominated by small-bodied zooplankton (Birge and Juday 1914; Chamberlain 1975; Schaffner and Oglesby 1978), *C. pengoi* may be able to alter the native plankton assemblages in these lakes. Invasions by *C. pengoi* have been associated with declines in herbivorous zooplankton density (Makarewicz et al. 2001; Laxson et al. 2003; Panov et al. 2004), with significant affects concentrated on taxa with biomass less than 0.13 µg (Benoit et al. 2002). Laboratory and field experiments demonstrate that *C. pengoi* feeds on small-bodied cladocerans such as daphnids and bosminids and field reports indicate that the zooplankter also feeds on copepods, both nauplius and copepodid stages, and rotifers (Rivier 1998; Benoit et al. 2002; Laxon et al. 2003). A decrease in planktonic filter feeders theoretically should cascade to the base of the food web and alter the lake's primary productivity.

During the summer of 2007, we examined the seasonal dynamics of *C. pengoi* in Owasco Lake to determine if this invasive species could in part be responsible for the observed changes to the lake's trophy. Our goals were (1) to document summer density dynamics of *C. pengoi* and native invertebrate predators, (2) to investigate correlations between *C. pengoi* and abiotic conditions in Owasco Lake, and (3) to examine the relationships among *C. pengoi*, native invertebrate predators, herbivorous zooplankton, and algal productivity. We specifically aimed to investigate if *C. pengoi* in part could be contributing to changes in the lake's productivity.

Methods

From May to August 2007, Owasco Lake was sampled at three locations (Figure 1): station 1 (42°52.4'N, 76°31.35'W, Z=34m), station 2 (42°49.2'N, 76°30.45'W Z=50m), and station 3 (42°47.1'N, 76°29.0'W, Z=45m). These stations were selected (1) to provide broad spatial coverage from the northern to the southern end of the lake in the pelagic region, (2) to sample at the same locations as other investigators during 2007, and (3) to replicate the site locations of a water quality study in 2006 (J. Halfman, unpublished).

Zooplankton were collected by triplicate vertical hauls of Puget Sound nets, which included an 80 µm aperture mesh net (0.25 m diameter opening) for collection of the smaller herbivorous zooplankton and a 500 µm aperture mesh net (0.5 m diameter opening) for collection of the larger invertebrate predators. Nets were lowered to a depth one meter from the bottom

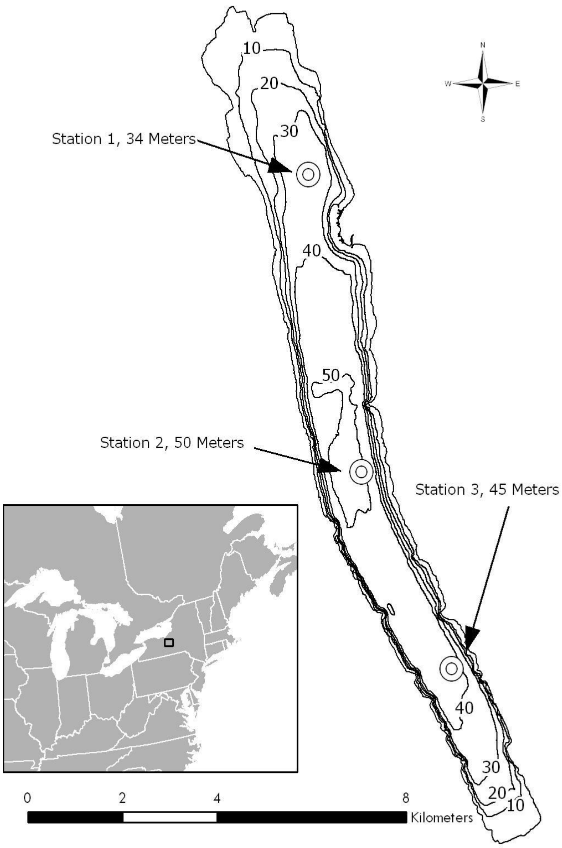

Figure 1. Bathymetric map of Owasco Lake (New York, USA) with 10 m depth contours. Locations marked within the lake are station 1 (42°52.4'N, 76°31.35'W), station 2 (42°49.2'N, 76°30.45'W), and station 3 (42°47.1'N, 76°29.0'W). Insert in the lower left corner shows the approximate location of Owasco Lake in eastern North America.

and towed to the surface at approximately 0.5 m/s using a mechanical winch during daylight hours. Triplicates were stored separately, with a few exceptions when they were combined as a composite. All samples were preserved in 70% ethanol (final volume). In the laboratory, the zooplankton collections from the 80 µm net were split in half using a Folsom-style plankton splitter. One split was diluted to a known volume and counted by subsample (Leica MZ 12.5 50X) until 100 organisms of each genus present were identified. The collections from the 500 µm net were searched in entirety for all large invertebrate predator species. For all taxonomic groups, densities were estimated as ind./m^3. Total herbivorous cladoceran abundance was calculated by summing the individual densities for all appropriate taxa from the 80 µm net volumetric estimates.

Phytoplankton biomass was estimated from an in-situ fluorometer (WET Labs Eco-FL-NTU) mounted on a Seabird 25 CTD (Sea-Bird, Inc. Bellevue, WA USA), which measured Chl. *a* fluorescence during a down-cast to within a meter of the sediment surface. To verify the accuracy of the in-situ method, water samples were collected every 15 m and filtered to concentrate phytoplankton. Chl. *a* was eluded from the filters with acetone and agitation, and the absorbance of the supernatant was measured with a spectrophotometer as detailed in Wetzel and Likens (2000). Mean epilimnetic Chl. *a* was calculated from the average Chl. *a* concentration above the thermocline. Water temperature (SBE 3F), dissolved oxygen (SBE 34 DO Sensor), photosynthetically active radiation (LI-COR LI-193 spherical PAR sensor), specific conductivity (SBE 4C), turbidity (WET Labs Eco-FL-NTU), and pH (SBE 18 pH sensor) were also recorded during the CTD down-cast. Mean temperature was estimated by averaging the epilimnetic values.

Results

At all three sampling stations, the most abundant invertebrate predators were *C. pengoi* (0-245 ind./m^3) and *Leptodora kindtii* (Focke, 1844) (0-62 ind./m^3). Both species were first detected in the water column in June, were most abundant in July, and then declined in density during August (Figure 2 A-C). At station 1, *C. pengoi* and *L. kindtii* abundances were similar and peaked during the same week in late July (Figure 2 A), but at station 2 the *C. pengoi* peak abundance preceded that of *L. kindtii* and was much greater (Figure 2 B). At station 3 abundances were similar to station 1 (Figure 2 C), but patterns in the density dynamics cannot be detailed since this station was only sampled on two dates. Most samples contained carnivorous *Cyclops* spp. and also omnivorous calanoids, such as *Epischura lacustris* Forbes (1882) and *Limnocalanus macrurus* Sars (1863) at very low abundance. *Polyphemus pediculus* Linné (1761) was present in a few samples but at low abundances. No *Chaoborus* spp. or *Mysis relicta* Lovén (1861) were detected.

Abiotic conditions were typical of an oligotrophic-mesotrophic lake (Figure 3, only 18 June 2007 profile shown for station 2). The

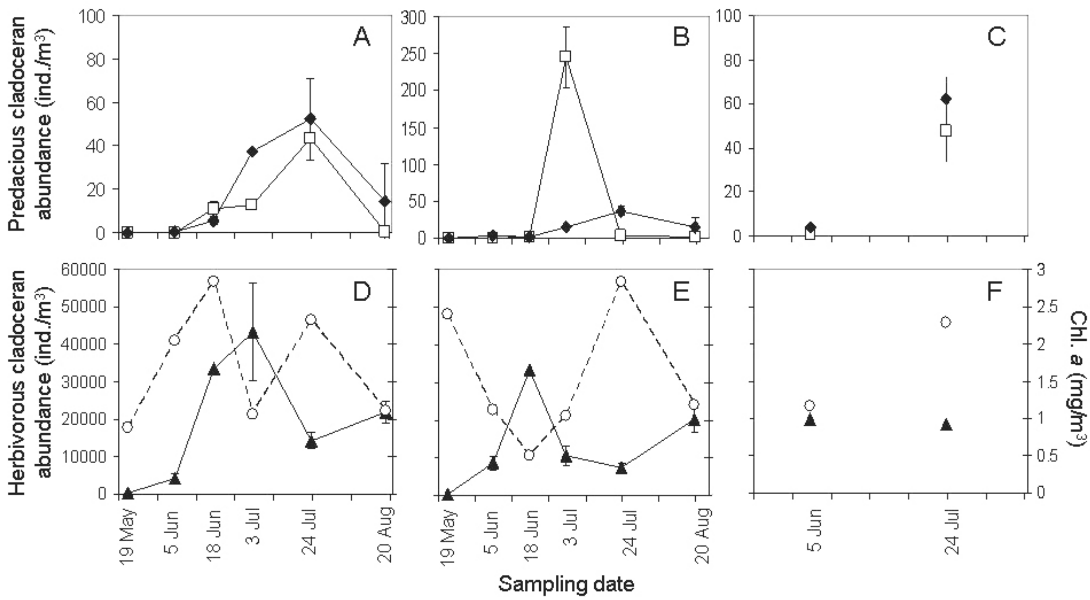

Figure 2. (A-C) Abundance of dominate invertebrate predators, the predacious cladocerans *Cercopagis pengoi* (open squares) and *Leptodora kindtii* (closed diamonds), at stations 1 (A), 2 (B) and 3 (C) during summer 2007. Note the change in scale between panel B and panels A and C. (D-F) Abundance of herbivorous cladocerans (closed triangles, primary y-axis) and mean epilimnetic concentration of Chl. *a* (open circles, secondary y-axis) at stations 1 (D), 2 (E), and 3 (F) during summer 2007. Station 3 (C, F) was only sampled on 5 June and 24 July. Error bars for predacious and herbivorous cladocerans show ± 1 standard deviation. Zooplankton samples collected on 19 May and 18 June at station 1 and 19 May at station 2 were combined as a composite and no error is reported. For all other dates without visible error bars, error is too small to be seen. The high variation in herbivorous cladoceran abundance on 3 July at station 1 resulted from a single replicate with roughly half the *Bosmina longirostris* (29,000 ind./m^3) as the other two replicates (49,000-56,000 ind./m^3).

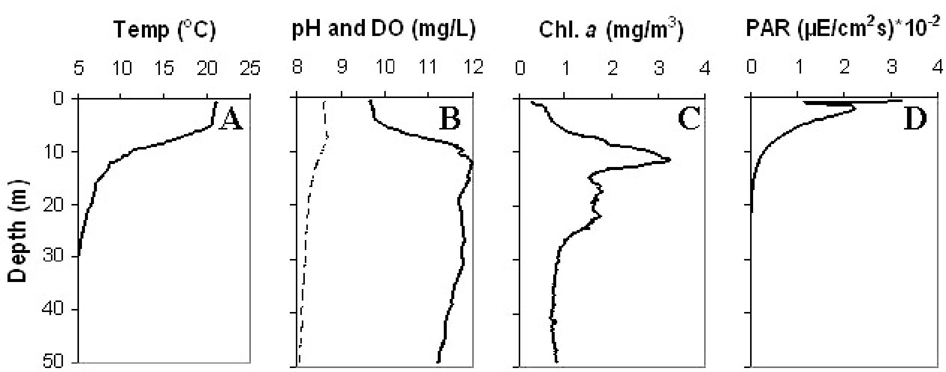

Figure 3. Vertical profiles of selected limnological parameters at station 2 on 18 June 2007: temperature (A), dissolved oxygen (DO: B, solid line), pH (B, dashed line), Chl. *a* (C), and photosynthetic active radiation (PAR: D). Conditions shown are typical of profiles during summer at all stations.

dimictic lake stratified by early June, with epilimnetic temperatures near or above 20^{o}C through the end of August at all sampled locations. *C. pengoi* was not detected in the water column until epilimnetic temperatures exceeded 17^{o}C and it became abundant when temperatures exceeded 20^{o}C, but there were no strong linear correlations between abundance and temperature (Figure 4). The entire water column remained oxygenated and slightly alkaline during the period of stratification (Figure 3). Photosynthetically active radiation (PAR) was high,

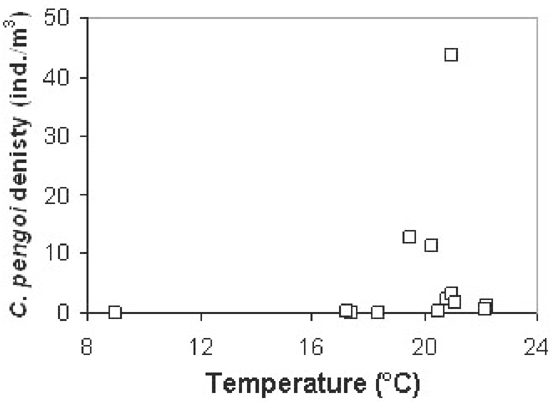

Figure 4. Relationship between mean epilimnetic temperature and *Cercopagis pengoi* density. Since density exceeded 200 ind./m^3 at station 2 on 3 July (see Figure 2), this data pair was excluded for improved scale. All other dates and stations are shown.

with 1% light levels reaching into the metalimnion throughout the summer (Figure 3). Specific conductance (320-340 µS/cm) and turbidity (<0.90 NTU) were also stable throughout the summer. No correlations were observed between these abiotic parameters (e.g., dissolved oxygen, pH, PAR) and *C. pengoi* density (data not shown).

There were strong relationships among Chl. *a*, herbivorous cladoceran abundance, and predacious cladoceran abundance (*C. pengoi* and *L. kindtii*) (Figure 2). At stations 1 and 2, maximum spring Chl. *a* concentrations (2.5-3 mg/m^3) declined following the establishment of herbivorous cladoceran, but returned to comparable concentrations during mid-summer when herbivorous cladoceran abundance declined (Figure 2 D-E). In late summer, Chl. *a* declined again when herbivorous cladoceran abundance rebounded (Figure 2 D-E). Although the dates of these peaks and crashes were not consistent between stations 1 and 2, they were concurrent at both stations with the seasonal density dynamics of invertebrate predators (*C. pengoi* and/or *L. kindtii*); peaks in *C. pengoi* and *L. kindtii* during mid-summer were followed by crashes in herbivorous cladoceran abundance and increased Chl. *a* (Figure 2). These reciprocal changes were consistent with conditions at station 3 (Figure 2 C, F), but no patterns were observable at this southern station since only two dates were sampled.

Discussion

C. pengoi and *L. kindtii* were common and widespread in Owasco Lake. Other invertebrate predators native to the Finger Lakes were rare or not detected, mostly likely a result of (1) their absence in the lake, (2) their predominately littoral distribution and our offshore sampling locations (e.g., *P. pediculus*), or (3) their extensive diel vertical migration and our daytime sampling regime (e.g., *M. relicta*). The maximum abundance of *C. pengoi* observed (245 ind./m^3) far exceeded that of any native invertebrate predator in the lake; however, this peak density was only observed once in the central pelagic region of the lake. At most locations and dates density trends were comparable between *C. pengoi* and *L. kindtii*. Nonetheless, the large population size and potential dominance of *C. pengoi* soon after its establishment in Owasco Lake are consistent with its invasion pattern in Lake Ontario and Lake Michigan, where *C. pengoi* peak density ranged between 200-3000 ind./m^3 soon after its initial detection (MacIsaac et al. 2001 ; Witt and Cáceres 2004).

The competitive and predatory interactions between *C. pengoi* and *L. kindtii* are not well studied, but the establishment of *C. pengoi* in Owasco Lake does not appear to have substantially decreased *L. kindtii* abundance, as the modern density of *L. kindtii* maybe similar or higher than abundances prior to the mid-1970s (Birge and Juday 1914; Hall and Waterman 1965; Chamberlain 1975; Schaffner and Oglesby 1978). If fact, surveys in the 1960s and 1970s did not detected *L. kindtii* in Owasco Lake (Hall and Waterman 1965; Chamberlain 1975; Schaffner and Oglesby 1978), but it is likely that these surveys failed to detect *L. kindtii* despite its presence given that *L. kindtii* is native and common in the study region. Whether its absence was due to much lower densities historically than at present or methodology (e.g., location, technique, time of day, period of the year) is not clear. The patchy distribution of *L. kindtii* and its ability to avoid plankton traps and small nets (Balcer et al. 1984) could account for its absence in samples during the mid-1900s. Nonetheless, from these limited comparisons, *L. kindtii* may be displaying resilience to invasion by *C. pengoi*, potentially exhibiting higher abundances than historically recorded. This is in contrast to previous studies that have attributed declines in *L. kindtii* to the establishment of a related cercopagid, *Bythotrephes longimanus* Leydig (1860) (e.g., Branstrator 1995; Makarewicz et al. 1995; Yan and Pawson 1997).

The co-existence of *C. pengoi* and *L. kindtii* in Owasco Lake may result from favorable abiotic and biotic conditions that allowed for rapid, parthenogenetic growth during summer for both predators. The abiotic conditions in Owasco Lake were within the tolerance range of *C. pengoi* and *L. kindtii* (Rivier 1998). Although there were no linear correlations between the abiotic conditions studied and density, warm summer temperatures were associated with high population densities, which likely reflects the temperature-based development of these invertebrates. Further, abundant, shared prey-resources likely contributed to the success of *C. pengoi* and *L. kindtii* that occupy similar dietary niches, preferring small cladoceran prey (e.g., Herzig and Auer 1990; Rivier 1998; Benoit et al. 2002).

There were strong top-down effects of *C. pengoi* and *L. kindtii* across multiple trophic levels as demonstrated by the negative relationship between the densities of these invertebrate predators and total herbivorous cladoceran density, and the negative relationship between herbivorous cladoceran density and Chl. *a* concentration. These cascading relationships are interpreted as a trophic rearrangement following the seasonal peak of invertebrate predators, which resulted in the decrease of planktonic filter feeders and increased the lake's primary productivity during mid-summer.

With the present data set, it is not possible to quantify the relative roles of *C. pengoi* and *L. kindtii* in the decline of herbivorous cladocerans, but other studies have pointed to the strong control of herbivorous plankton by *C. pengoi* following its establishment. In Lake Ontario, *C. pengoi* peak density is associated with declines in native herbivores and increases in Chl. *a* (Benoit et al. 2002; Laxon et al. 2003). Using bioenergetic models, Laxon et al. (2003) demon-strated that predation by the invasive could suppress herbivores to the levels observed in Lake Ontario. Additional work by Telesh et al. (2001) used a physiological method and found that *C. pengoi* (80-200 ind./m^3) is capable of modifying trophic webs by consuming upwards of 75% of the total production of herbivorous zooplankton in the Gulf of Finland. Given the comparable densities of *C. pengoi* and prey communities in Owasco Lake, it is possible that *C. pengoi* could sharply reduce herbivorous cladocerans within a few days of their peak density. This is particularly apparent at station 2 where *C. pengoi* abundance vastly exceeded and preceded the peak in abundance of *L. kindtii*, and it is also consistent with patterns at stations 1 and 3. However, although these mathematical predictions support a hypothesis of top-down control of phytoplankton in part by *C. pengoi*, *L. kindtii* is also an efficient invertebrate predator (Herzig and Auer 1990) and must contribute to declines in herbivores. Further study in Owasco Lake, including biomass estimates and predation models for both *C. pengoi* and *L. kindti*, is required to elucidate the influence of these two carnivores on lake productivity.

Certainly, other factors must influence the productivity of Owasco Lake, including nutrient contributions from streams and the surrounding landscape, and stocking and removal of fishes. However, invertebrate predation, specifically that of the exotic *C. pengoi*, is an important potential contributor to the lake's trophy that should be factored into management decisions and assessment of lake health. As demonstrated by this and other studies, *C. pengoi* may be able to alter the density and diversity of the native herbivores in lakes where it establishes. This could have significant impacts not only on the mid-summer phytoplankton biomass, but create food resource limitations for the native planktivores, both invertebrate and vertebrate. However, in Owasco Lake, despite their potential competitive interaction, there appears to be sufficient food resources to support two invertebrate predators with high dietary overlap. Nonetheless, high productivity resulting from a top-down cascade may also result in more dynamic phytoplankton communities with frequent blooms and crashes, influencing water quality through increased decomposition of organic matter and lower net uptake of nutrients. Given the importance of the Finger Lakes to the ecologic and economic health of New York, better understanding of the role of this and other invasive species in the limnology of these lakes is needed.

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