Leptodora kindtii population dynamics in the island region of western Lake Erie before and after the invasion of the predacious cladoceran *Bythotrephes longimanus*

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ABSTRACT. Competition among native and non-native species can cause decreases in population size and production of both species. The native predaceous crustacean zooplankter *Leptodora kindtii* shares a similar niche with the invasive *Bythotrephes longimanus* in Lake Erie. This niche overlap may contribute to the decline in abundance, and production of *L. kindtii* in the Western Basin of Lake Erie. Historical (1946) and recent (2006) data were used to determine if the decline in *L. kindtii* abundance and production was associated with the effects of *B. longimanus*, which invaded Lake Erie in the mid-1980's. Pre-invasion abundances and lengths of *L. kindtii* were compared with current data (2006). A change in prey community abundance, composition and dynamics were observed, relative to pre-invasion, with a marked decline in abundance and size of *L. kindtii* after the invasion of *B. longimanus*. Competition for food and direct predation are two explanations, among others, for the declines observed in *L. kindtii* size, abundance and production that have occurred since *B. longimanus* invasion.

INTRODUCTION

The structure and population dynamics of aquatic communities may by altered by the introduction of non-native, invasive species. Native populations suffer effects including extinction, habitat alteration, and food web disruption, often via changes in energy flow and nutrient availability (Ricciardi and MacIsaac 2000). One disruptive mechanism is interspecific competition between native species and one or more invaders occupying similar niches. However, these interactions are often more complex and the effects are distributed more widely in the food web than simple competition (Strecker and Arnott 2008).

In aquatic ecosystems, zooplankton are functionally important, occupying a mid-trophic level (i.e. primary and secondary consumers) and changes in the ecosystem must propagate through these taxa (Richardson and Schoeman 2004). Changes in phytoplankton composition (i.e. bottom-up effects) are transferred via zooplankton interactions to the fish community (Hampton et al. 2006), while fish community changes, such as loss of predator diversity (i.e. top-down effects), likewise cascade through the secondary producers (Worm et al. 2006). Introduced zooplankton predators act both directly and indirectly on the structure of zooplankton communities and other trophic levels thus, the structure is strongly influenced by predator-prey interactions among trophic levels (Hanazato and Yasuno 1989; Wellborn et al. 1996; Chang and Hanazato 2004; Weis 2011; Weisz and Yan 2011).

Bythotrephes longimanus (Leydig 1860) is a predacious zooplankter native to the Ponto-Caspian region that invaded the Great Lakes during the mid-1980s (Lehman 1987). This predator has affected freshwater ecosystems through direct predation and competition with native zooplankton species and through indirect food web alteration (Lehman and Branstrator 1995; Johannsson et al. 1999; Shuter and Mason 2001;, Barbiero and Tuchman 2004; Barbiero and Rockwell 2008; Strecker et al. 2011; Yan et al. 2011). Because of similarities in life history, the zooplankter most threatened by *B. longimanus* in the Laurentian Great Lakes is the native predacious cladoceran, *Leptodora kindtii* (Focke 1844) (Lehman

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and Cáceres 1993). *B. longimanus* uses similar habitat and is in many ways a superior competitor to *L. kindtii* (e.g. body size, defense mechanisms, and efficiency of prey consumption) (Berg and Garton 1988; Garton et al. 1990; Branstrator 2005). Other studies have shown the abundance and biomass of *L. kindtii* decreases when the competitor *B. longimanus* is introduced (Yan et al. 2002). For example, after the initial discovery of *B. longimanus* in Lake Michigan in 1986, *L. kindtii* decreased dramatically, along with concurrent decreases and changes in species composition in the *Daphnia* community (Lehman and Cáceres 1993). These changes in the community remained through 2000, though attributing this solely to *B. longimanus* is difficult given the wide range of changes in the Lake Michigan ecosystem (Madenjian et al. 2002). Similar declines in *L. kindtii* and changes in prey composition were observed in Harp Lake, ON (Yan and Pawson 1997) and in Lake Huron (Lehman and Cáceres 1993), where zooplanktivory by *B. longimanus* outpaces *Mysis* and fish predation (Bunnell et al. 2011).

In this study we investigate the effects of the introduced predator *B. longimanus*, on the abundance, biomass, and secondary production of the native predator, *L. kindtii*. We focus on the effects of *B. longimanus* on food web dynamics in the western basin of Lake Erie. We compare historical (pre-invasion, 1946) and recent (post-invasion, 2006) abundance and biomass of *L. kindtii* and compare contemporary estimates of abundance and production of *L. kindtii* and *B. longimanus*. In contrast to other studies, we also assess indirect foodweb effects by comparing seasonal abundance of prey species on a weekly basis. Due to similar niches and the declines in *L. kindtii* attributed to *B. longimanus* in other lakes, we predicted that *L. kindtii* abundance, biomass, and secondary productivity would decline in the presence of *B. longimanus* in western Lake Erie.

METHODS

Zooplankton samples were collected off Peach Point between South Bass Island and Gibraltar Island, in the Western Basin of Lake Erie (Fig. 1). Samples were collected weekly from 22 June to 15 August 2006 one hour after sunset. Predator samples were collected using a horizontal surface (0-1 m) tow with a 1m-diameter, 153μm-mesh ichthyoplankton net equipped with a flow meter (General Oceanics 2030R), hauled from a motorboat moving at low speed. Surface tows were conducted for predators in order to assure that a large

enough volume of water was sampled to collect enough predators to perform necessary length measurements. Prey samples were collected by a vertical tow (surface to near bottom (approximately 8 m) and then back to surface) using a 0.5-meter diameter, 64μm-mesh net, equipped with a flow meter (General Oceanics 2030R) until the flow meters indicated approximately 100 m³ of water was sampled. The samples were preserved in sugar formalin (Haney and Hall 1973).

Each prey sample was diluted and enumerated until the most abundant taxa of zooplankton present reached 100 individuals; a minimum of two subsamples were counted for all collections. Cladocerans were identified to species, while copepod copepodites and nauplii were identified to suborder; The densities of each taxon were calculated using flow meter readings. A YSI multiprobe (Yellow Springs Instruments, Yellow Springs, Ohio) was used to measure surface temperature. These samples were representative of Peach Point, where the historical samples of *L. kindtii* were taken. For a comprehensive overview of the changing zooplankton community in Lake Erie and for more details on the general zooplankton sampling and enumeration methods we employed (Conroy et al. 2005, 2008).

Predator samples were diluted and enumerated for abundance and length. We measured the first 20 *L. kindtii* and *B. longimanus* individual lengths using an ocular micrometer, with the body length of *L. kindtii* from the top of the head to the base of the posterior spine and the body length of *B. longimanus* from the top of the head to the base of the caudal spine (Manca and Comoli 2000). Shrinkage corrections were not applied, as measurements of live individuals were not
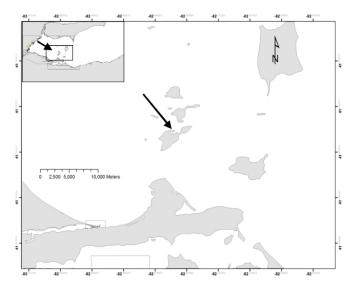

Figure 1. Sampling sites for zooplankton in the Western Basin of Lake Erie during the summer of 2006.

possible in our sampling regime, which may mean an underestimate of *Bythotrephes* size in some cases. Individual lengths (mm) were used in a length (L)-weight (W) regressions (W= aLb) and coefficients for *L. kindtii* (a= 0.44, and b= 2.67) and *B. longimanus* (a= 11.13 and b= 2.77) were obtained from Rosen (1981) and Yan (OMEE, Dorset, personal communication 2000) respectively (Johannsson et al. 2000 Appendix 1a) to estimate biomass (B, g/m³) for each predatory species. The average biomass of each species for each sampling date was calculated and used in conjunction with known production to biomass ratios (P/B) in water above 10 °C (Johannsson et al. 2000) to calculate daily production (P) for each species.

In order to estimate *B. longimanus* consumption of *L. kindtii* (direct predation upon *L. kindtii*) and other crustacean zooplankton (competition with *L. kindtii*), we obtained growth efficiency (production/consumption) estimates for *Bythotrephes* (Dumitru et al. 2001) and then calculated the consumption rates of *L. kindtii* required to support the observed production of *B. longimanus*. Growth efficiency of *B. longimanus* has previously been estimated at 27 percent (Dumitru et al. 2001). Thus the consumption rate must equal 3.7 times the production rate (100 percent/27 percent) to maintain 100 percent production.

Estimates of non-predatory crustacean zooplankton production were made using P/B values obtained for non-predatory cladocerans (0.162) at temperatures >10°C (Stockwell and Johannsson 1997 (as cited in Johannsson et al. 2000)) and for cyclopoids (0.169) and calanoids (0.060) using a median water temperature of 24.7°C [Shuter and Ing 1997 (as cited in Johannsson et al. 2000)]. Because we could not have actual production values for our non-predatory crustacean zooplankton (due to lack of length measurements taken), we obtained a range of 50-250 ug/L (mg/m³) for the crustacean biomass of in western Lake Erie during June-August (1995-2003) from the literature (Conroy et al. 2008). We then calculated an average biomass value for non-predatory cladocerans, cyclopoids, and calanoids and then multiplied this value by the P/B ratio to obtain a range of production values for non-predatory crustacean zooplankton.

RESULTS

Herbivorous zooplankton abundance (cladocerans and copepods) declined from 29 June 2006 to 15 August 2006 at our sample site (Fig. 2). Cladoceran abundances exhibited two peaks with the first of the two

consisting of primarily *Daphnia retrocurva* and *Bosmina* and the second *Eubosmina* and *Diaphanasoma* (Fig. 2a). The peak abundance in copepods occurred from 22 June to 28 June and was composed primarily of cyclopoid copepodites. From 28 June to 7 July abundance declined sharply, with cyclopoid copepodites remaining the most abundant taxa (Fig. 2b). From 3 August until 9 August, calanoid copepodites continued to increase while the other three groups declined, causing a shift to calanoid copepods as the most abundant taxon by the end of the sampling period.

L. kindtii densities reached a seasonal peak on 19 July followed by a steady decline until 9 August. There was a slight increase on the last sample date, perhaps corresponding to the beginning of a seasonal increase (Fig. 3). The average density of *L. kindtii* throughout the summer was 234.9 individuals/m³, ranging from 39.9 individuals/m³ on 7 July to 560.1 on 19 July. *B. longimanus* was not present in samples before 26 July.
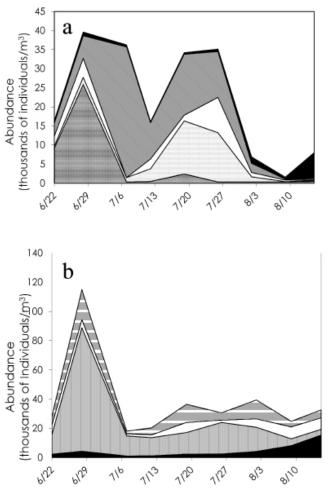

Figure 2. a.) Cladoceran seasonal abundances in the western basin of Lake Erie during the summer of 2006: ■ *Daphnia galeata mendotae* ▨ *Daphnia retrocurva* ☐ *Diaphanasoma* ▦ *Eubosmina* ▦ *Bosmina* b.) Copepod seasonal abundances: ▤ Cyclopoid nauplii, ☐ Calanoid nauplii, ▥ Cyclopoid copepodites, and ■ Calanoid copepodites.

From this date, *B. longimanus* abundance increased throughout the remainder of the sampling period (Fig. 3). The density of *B. longimanus* ranged from 3.27 individuals/m^3 on 26 July to 34.1 individuals/m^3 on 15 August. There was a concomitant decline in *L. kindtii* density and this pattern continued for the next three sampling events (Fig. 3). However, on the final sample date (15 August) there was an increase in *L. kindtii* though *B. longimanus* was at relative peak abundance. Water temperatures varied slightly with a lower initial temperature of 23° C and peak water temperature of 27° C on 21 July.

The average length of *L. kindtii* from 22 June to 12 July remained relatively constant and then became more variable (Fig. 4a). The average length of all *L. kindtii* measured was 3.67+/- 0.37 mm and these individuals ranged from 0.6 mm to 8.25 mm. *B. longimanus* length ranged from 0.98 mm to 2.7 mm, and the mean was 1.70 mm. The population biomass of *L. kindtii* remained constant through 7 July between 2 to 4 g/m^3. Peak population biomass was measured on 26 July corresponding to both peak abundance and peak measured lengths. A sharp decrease followed from 26 July to 9 August, and then a slight increase in biomass was observed from 9 August to 15 August (Fig. 4b). *B. longimanus* showed a sharp increase in biomass which corresponded with the *L. kindtii* decline (Fig. 4b). The maximum production found throughout the sampling period for *L. kindtii* was 6.92 g/m^3/day on 26 July, and the minimum was found to be 0.058 g/m^3/day on 9 August (Fig.4c). The production of *B. longimanus* ranged from 0.059 g/m^3/day on the date of initial appearance to 0.628 g/m^3/day on the last date

in the sample period (Fig.4c). A significant decline in production of *L. kindtii* occurred simultaneously with the appearance of *B. longimanus*.

Data from Andrews (1948) were compared with current data to determine if the abundance of *L. kindtii* has declined since the invasion of *B. longimanus*. Andrews published data including abundance and lengths of parthenogenetically produced females of *L. kindtii* from Hatchery Bay (near the same sample site as this study), starting on 16 June 1946 and ending on 25 October 1946. The nightly abundances of *L. kindtii* from mid-June 1946 to early to mid-July 1946 were high compared to the abundance from later dates within that same summer (Fig. 4d). The maximum abundance of *L. kindtii* during the summer of 1946 occurred on 2 July with a density of 8,274 individuals/m^3. The average density from 18 June to 12 July (the time of the highest abundance) was 2,808 individuals/m^3. During the latter part of the summer (15 July to 30 August) the average density decreased to 425 individuals/m^3. In contrast, the greatest numbers found in 2006 were <600 individuals/m^3. In addition, the average length of *L. kindtii* (n=830) found during the summer also declined by approximately half, from 7.69 mm (1946) to 3.67 mm (2006). There was also a broader distribution of individual lengths in 1946 than in 2006 (Fig. 5).

By applying consumption rates of 3.7 times production rate (see above) to the production levels of *B. longimanus* we obtained consumption values ranging 0.22 to 2.95 g/m^3/d (when *B. longimanus* was present). Comparing this with *L. kindtii* productivities ranging from 0.06 to 6.92 g/m^3/d (Fig. 4c) indicates that on the two later dates in 2006 (9 August and 15 August) that *B. longimanus* is present it could potentially prey on all *L. kindtii*, while on the other two dates (26 July and 2 August) it could not.

Average P/B ratio for non-predatory crustaceans was calculated to be 0.345/d ((cladoceran = 0.145, cyclopoid = 0.654, calanoid = 0.231)). Multiplying this by 50-250 mg/m^3 yields an estimate of $0.0173 - 0.0865$ g/m^3/d of non-predatory crustacean zooplankton production. Based on consumption values of 0.22 to 2.95 g/m^3/d, *Bythotrephes* could theoretically consume all of this non-predatory crustacean production during the *Bythotrephes* one week production maximum at this sample site. However, given the relatively low abundance during the rest of the growing season, these impacts would be limited to the peak *B. longimanus* production.
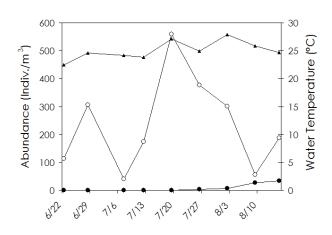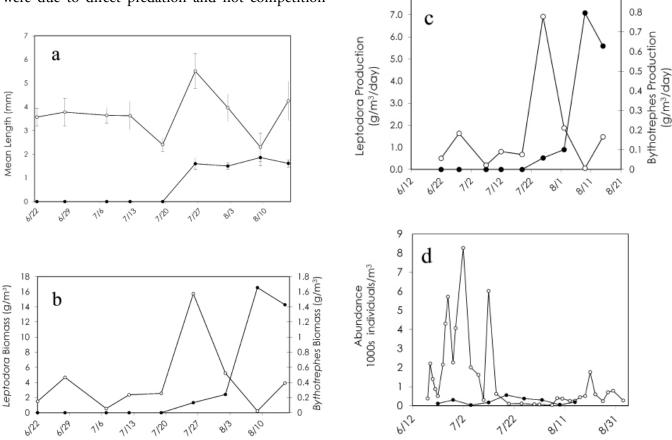

Figure 3. The abundance of *Bythotrephes longimanus* ⬤ and *Leptodora kindtii* ◯ in relation to temperature ▲ in the western basin of Lake Erie during the summer of 2006.

DISCUSSION

L. kindtii abundance was lower in 2006 than 1946, and corresponding differences in potential predator consumption rates and observed prey community structure suggest that *B. longimanus* influenced the change. When *L. kindtii* and *B. longimanus* co-exist, both competition for resources and direct predation of *L. kindtii* by *B. longimanus* may contribute to decreased abundance of the native *L. kindtii*. During the summer of 2006, we observed a decrease in *L. kindtii* abundance, biomass and productivity that inversely correlated with *B. longimanus*. By comparison in 1946, *L. kindtii* abundance increased through August. Yan and Pawson (1997) found similar effects on the *L. kindtii* population in the smaller Harp Lake (Ontario, Canada). They attribute this to direct predation by *B. longimanus* on *L. kindtii*. Further, Barbiero and Tuchman (2004) suggested that declines in *L. kindtii* in lakes Michigan, Huron, and Erie (Central and Eastern basins) after introduction of *B. longimanus* were due to direct predation and not competition owing to increases of *L. kindtii's* preferred rotifer prey in those lakes. However, we also saw concomitant changes in prey structure, which has been linked to *B. longimanus* introductions in other lakes (Hovius et al. 2006; Manca et al. 2008) as well as introductions of the similar *Cercopagis pengoi* (Warner et al. 2006).

Similar to these other studies, prey structure changes at our site were consistent with competition effects of *L. kindtii* and *B. longimanus*, but long-term environmental changes between 1946 and 2006 also may have restructured the prey community via bottom-up trophic and/or abiotic effects. For example, the combination of competition, predation, and temperature are important in structuring predaceous cladoceran dynamics in Lake Michigan (Cavaletto et al. 2010). *B. longimanus* has different life history strategies than its competitor as noted by Branstrator (2005). This comparative study in life histories noted that the caudal spine protection of *B. longimanus*

Figure 4. a.) The mean lengths (+/- SE) in millimeters of *Leptodora kindtii* (open circles —O—) and *B. longimanus* (closed circles —●—) throughout the summer of 2006 in the western basin of Lake Erie. b.) The mean population biomass (g/m³) in for each predator species found in the western basin of Lake Erie during the summer of 2006. *Leptodora kindtii* (open circles —O—) corresponds to the left y-axis and *B. longimanus* (closed circles —●—) corresponds to the right y-axis. c.) The daily production (g/m³/day) of *Leptodora kindtii* and *Bvthotrephes longimanus* in the western basin of Lake Erie during the summer of 2006. *L. kindtii* production is indicated by the open circles —O— and corresponds to the left y-axis values, and *B. longimanus* is in closed circles —●— corresponding to the right y-axis values. d.) A comparison of *L. kindtii* abundances during the summer of 1946 (open circles —O—) and the summer of 2006 (closed circles —●—) in the western basin of Lake Erie.

provides additional post-contact protection against predation, lacking in *L. kindtii*. Further, Yan and Pawson (1997) found that egg production in *L. kindtii* did not always decrease in response to increasing *B. longimanus* production, supporting a role for selective fish predation on *L. kindtii*.

The abundance of *L. kindtii* in western Lake Erie declined between 1946 and 2006. Abundances published by Andrews (1948) for the summer of 1946 showed only peaks occurred early in the season, followed by a decline in abundances. These peaks were not evident in data collected from the summer of 2006. For the remainder of both summers, *L. kindtii* showed little differences in abundance. In addition, data published soon after the invasion of *B. longimanus* by Berg and Garton (1988) did not show these historical peaks in *L. kindtii* abundance early in the summer of 1987.

Hubschman (1960) published daily population densities of cladocerans from the Bass Island region of Lake Erie for the summer of 1959. Several species of cladocerans showed a different trend in the summer of 1959 than in 2006. In 1959, total daily population densities of cladocerans (other than *L. kindtii*) showed several peaks though out the entire summer (30 June to 21 August) (Hubschman 1960) while in 2006, the only peak occurred early in the season, followed by a decline in total species. Barbiero and Tuchman (2004) provide evidence that alterations in zooplankton communities occurred in lakes Michigan, Huron, and Erie (Central and Eastern basins) after introduction of *B. longimanus*, including alteration of *Daphnia* and other cladoceran yearly abundances. Perhaps less food in the way of non-predatory cladocerans is now

available later in the summer and this may limit *L. kindtii* population size.

Previous studies suggest that *B. longimanus* invasion caused declines in *L. kindtii* abundance in North America (Foster and Sprules 2009, Weisz and Yan 2011), as well as a trend for smaller *L. kindtii* size with increased abundances of invasive *B. longimanus* (Foster et al. 2012). Foster et al. (2012) suggest size declines in *L kindtii* in central Ontario lakes invaded by *B. longimanus* could be due to direct consumption by *B. longimanus*, indirect effects of *B. longimanus* decreasing available zooplankton prey for *L. kindtii*, and other factors, such as fish predation. They concluded that decreased *L. kindtii* size was due to competitive effects of *B. longimanus* predation on small cladocerans. While our study shows a decline in *L. kindtii* abundance and size correlated with the invasion of *B. longimanus*, we cannot easily attribute the cause entirely to competitive or predatory interactions.

The Lake Erie ecosystem has undergone many changes since the 1940s, including fluctuations in nutrient loading, algal blooms, and regional climate change. Eutrophication, and the water quality issues associated with it including Central Basin hypoxia and harmful algal blooms (HABs), led to the implementation of the Great Lakes Water Quality Agreement. One result of the agreement is seen in reductions of total phosphorus (TP) in the water column and a subsequent reduction in hypolimnetic oxygen depletion rate the early 1970s until the early 1990s (Bertram 1993). By the mid-1990s there was an increase in mesotrophic plankton species (Munawar et al. 2002; Kane et al. 2004). However, recently, phytoplanktonic communities have shown a resurgence of eutrophic taxa and increased biomass of inedible/potentially toxic cyanobacterial taxa (Conroy et al. 2008; Kane et al. 2014) at the same time that SRP concentrations in the water column are rebounding (Baker et al. 2014, Kane et al. 2014)), though there has been no rebound in *L. kindtii*. These changes are concurrent with the introduction of *B. longimanus* and may also have contributed to the decline of *L. kindtii* size, abundance, and production.
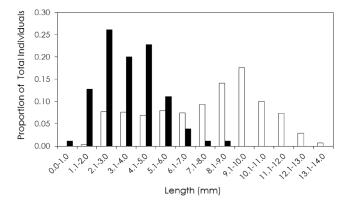

Figure 5. A histogram comparing *Leptodora kindtii* lengths from the summer of 1946 (Andrews, 1948) (white bars) and the summer of 2006 (black bars) within the Western Basin of Lake Erie. The proportions of individuals in each length (mm) size class are given.

ACKNOWLEDGMENTS

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