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LARGE NONLETHAL EFFECTS OF AN INVASIVE INVERTEBRATE PREDATOR ON ZOOPLANKTON POPULATION GROWTH RATE

Kevin L. Pangle,[1,4] Scott D. Peacor,[1,2] and Ora E. Johannsson[3]

[1]*Michigan State University, Department of Fisheries and Wildlife, 13 Natural Resources Building,*
East Lansing, Michigan 48824-1222 USA
[2]*National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory,*
2205 Commonwealth Boulevard, Ann Arbor, Michigan 48105-2945 USA
[3]*Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road,*
Burlington, Ontario L7R 4A6 Canada

Abstract. We conducted a study to determine the contribution of lethal and nonlethal effects to a predator's net effect on a prey's population growth rate in a natural setting. We focused on the effects of an invasive invertebrate predator, *Bythotrephes longimanus*, on zooplankton prey populations in Lakes Michigan and Erie. Field data taken at multiple dates and locations in both systems indicated that the prey species *Daphnia mendotae*, *Daphnia retrocurva*, and *Bosmina longirostris* inhabited deeper portions of the water column as *Bythotrephes* biomass increased, possibly as an avoidance response to predation. This induced migration reduces predation risk but also can reduce birth rate due to exposure to cooler temperatures. We estimated the nonlethal (i.e., resulting from reduced birth rate) and lethal (i.e., consumptive) effects of *Bythotrephes* on *D. mendotae* and *Bosmina longirostris*. These estimates used diel field survey data of the vertical gradient of zooplankton prey density, *Bythotrephes* density, light intensity, and temperature with growth and predation rate models derived from laboratory studies. Results indicate that nonlethal effects played a substantial role in the net effect of *Bythotrephes* on several prey population growth rates in the field, with nonlethal effects on the same order of magnitude as or greater (up to 10-fold) than lethal effects. Our results further indicate that invasive species can have strong nonlethal, behaviorally based effects, despite short evolutionary coexistence with prey species.

Key words: Bosmina longirostris; Bythotrephes; Daphnia; *Great Lakes; invasive species; nonlethal effects; predation; predator–prey interactions; trait-mediated indirect interaction; vertical migration.*

Introduction

Predators can have large effects on prey distribution and dynamics. However, what has recently become clearer is that predation itself is only one of a suite of effects that a predator has on its prey. Predators induce changes in prey phenotype, including behavioral, morphological, and life history traits, in taxa as disparate as bacteria and ungulates (reviewed in Lima 1998, Tollrian and Harvell 1999). Whereas such phenotypic responses of prey can reduce predation risk, they are typically associated with a cost of reduced growth rate (Werner et al. 1983, Peckarsky et al. 1993, Diehl and Eklov 1995, reviewed in Peacor and Werner 2004), which can affect prey and predator abundance and dynamics (e.g., Abrams 1995, Luttbeg and Schmitz 2000, Bolker et al. 2003). Further, these induced effects on prey phenotype can ripple through a community in the form of trait-mediated indirect interactions (Turner and Mittlebach 1990, Werner and Peacor 2003, Schmitz et al. 2004; also termed "interaction modifications," Wootton 1994). Therefore, "nonlethal" predator effects may play a large role in ecological systems, and improved understanding of their role may be critical to building predictive ecological theory.

Empirical studies on nonlethal effects of predators on prey have focused almost exclusively on responses to individual prey growth rate and fecundity (Peacor and Werner 2004). Recently, researchers have used mesocosms to demonstrate nonlethal effects of a predator on population-level responses in a damsel bug–pea aphid system (Nelson et al. 2004) and in a *Chaoborus*–*Daphnia* system (Boeing et al. 2005). These analyses provide evidence that nonlethal effects contribute to the net effect of a predator on prey populations. Nevertheless, little is known of either population-level nonlethal effects or the relative importance of lethal and nonlethal effects in natural (uncontrolled) field environments.

We quantified both the lethal and nonlethal effects of an invasive invertebrate predator, *Bythotrephes longimanus* Leydig (see Plate 1), on native zooplankton populations in the Laurentian Great Lakes. Prior studies suggest that *Bythotrephes* has impacted the pelagic ecosystem of the Laurentian Great Lakes (Lehman and Caceres 1993, Barbiero and Tuchman 2004) and smaller surrounding lakes (Hoffman et al. 2001,

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[4] E-mail: pangleke@msu.edu

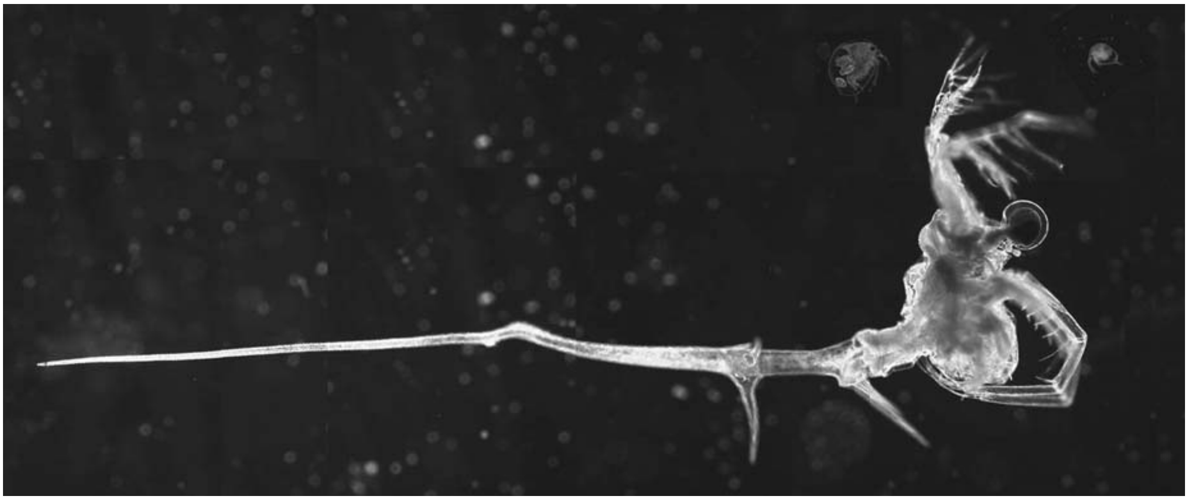

Plate 1. The invasive predator *Bythotrephes longimanus*, with its prey, *Bosmina longirostris*. Photo credit: K. Pangle.

Boudreau and Yan 2003). For example, the arrival of *Bythotrephes* coincided with loss and reduction in density of several zooplankton species in Lakes Michigan (Lehman and Caceres 1993) and Erie (O. E. Johannsson and D. M. Graham, *unpublished data*). Further, laboratory experiments show that some zooplankton prey modify their behavior in the presence of *Bythotrephes* by migrating to deeper, colder regions of experimental water columns (Pangle and Peacor 2006), whereas a field study indicates that *Daphnia mendotae* Birge vertical distribution deepened in Lake Michigan after the invasion of *Bythotrephes* (Lehman and Caceres 1993). These patterns are indicative of an anti-predation strategy commonly observed in zooplankton (Gliwicz 1986, Dodson 1988, reviewed in DeMeester et al. 1998). If indeed zooplankton prey typically respond to *Bythotrephes* in the field by inhabiting colder environments, such induced behavior may substantially reduce prey population growth rate (a nonlethal effect).

We focused our study on zooplankton species in Lakes Michigan and Erie that are common, preferred prey items for *Bythotrephes* (Vanderploeg et al. 1993, Schulz and Yurista 1999) in each lake. Our goals were to establish whether *Bythotrephes* induce changes in prey vertical distribution and then to estimate the consequences of these changes on population growth rate relative to lethal (consumptive) effects.

Methods

We performed two field surveys denoted the "extensive field survey" and the "intensive field survey." In the former, we sampled the vertical distribution of zooplankton during the day over a broad range of locations and dates to examine the potential influence of *Bythotrephes* on prey vertical position. The intensive field survey sampled fewer locations, but at more frequent depth and time intervals. The data from these latter surveys were used with growth and predation models to estimate the magnitude of *Bythotrephes*' lethal and nonlethal effects.

Influence of Bythotrephes *on zooplankton daytime vertical distribution*

Extensive surveys of Lakes Michigan and Erie were performed to evaluate the influence of *Bythotrephes* on the percentage of prey inhabiting either the surface epilimnion or the deeper, colder hypolimnion. Lake Michigan prey species included *Daphnia mendotae* and *Bosmina longirostris* Muller, whereas Lake Erie prey species were *Daphnia retrocurva* Forbes and *Bosmina longirostris*. We hypothesized that prey should be at lower risk in the hypolimnion, because *Bythotrephes* is a visually orienting predator that mainly inhabits the epi- and metalimnion (Muirhead and Sprules 2003; K. L. Pangle, S. D. Peacor, and H. A. Vanderploeg, *unpublished data*). Therefore, we predicted that the percentage of prey occupying the epilimnion would decrease and the percentage occupying the hypolimnion would increase as *Bythotrephes* biomass increased. We also examined whether abiotic environmental factors influenced prey vertical distribution and therefore predation by *Bythotrephes*. Specifically we evaluated the effects of epilimnion depth and secchi depth (water clarity), because both affect the light intensity of the epilimnion and predation of zooplankton.

Sampling was conducted during five different years and in multiple lake basins (Table 1). Prior to each sampling event, thermal stratification of the water column was determined using a submersible sensor. For Lake Michigan, sampling events consisted of collecting 1 m^3 of lake water from the center of the epilimnion, the center of the metalimnion, and from the hypolimnion 10 m below the bottom of the metalimnion. Water was collected using a diaphragm pump system and then filtered through a 64-μm mesh zooplankton net on the deck of the research vessel. Samples collected with

TABLE 1. Sampling locations and dates for Lake Michigan and Lake Erie field surveys.

System (basin)	Latitude	Longitude	Depth (m)	Sampling months, year	No. sampling events
Lake Michigan (south)	43°11′29″ N	86°25′92″ W	45	June–August 2004	6
Lake Michigan (south)	43°11′15″ N	86°27′15″ W	60	August 2004	2
Lake Michigan (south)	43°11′29″ N	86°32′16″ W	110	June–October 2004	7
Lake Erie (east)	42°37′35″ N	80°03′16″ W	38	June–September 1993	6
				June–October 1994	16
				June–October 1998	8
Lake Erie (Long Point Bay)†	42°35′30″ N	79°28′02″ W	24–64	June–September 1997	10
Lake Erie (central)	42°24′00″ N	80°38′62″ W	22	July–August 1998	2
Lake Erie (central)	42°21′52″ N	81°26′57″ W	23	August–September 1998	2
Lake Erie (central)	42°04′36″ N	82°20′24″ W	16	July–September 1993	5
Lake Erie (central)	41°59′00″ N	82°08′24″ W	22	June–August 1993	5

† Sampling events in Long Point Bay occurred at five different locations, all of which were located close to the reported coordinates.

the diaphragm pump system were similar to those taken by typical net sampling (K. L. Pangle, *unpublished data*). Lake Erie samples were collected using a 110-μm mesh closing plankton net, 3 m long with a 0.5 m diameter opening. The net was towed through each stratum, cinched at the desired depth using a secondary line, and then retrieved. Secchi (20-cm black and white disc) depth was measured during each Lake Erie sampling event. Samples were preserved in a buffered sugar-formalin solution and were subdivided prior to enumeration with a Henson-Stempler pipette after gentle but thorough mixing. Adult and juvenile zooplankton were identified to species and genus, respectively. For each Lake Michigan sample, at least 600 individuals were counted, whereas for each Lake Erie sample, at least 400 individuals were counted, with at least 100 individuals of the major groups included, or if animals were scarce, 20% of the sample was counted. For all samples, *Bythotrephes* body lengths were measured using a drawing tube and digitizer (Roff and Hopcroft 1986), and *Bythotrephes* biomass was calculated using a length–mass relationship (Yan and Pawson 1998).

Percentage of prey in the epi- and hypolimnion and *Bythotrephes* biomass (in milligrams per square meter) were calculated using densities from each stratum weighted by the stratum thickness. Statistical analysis of the effect of *Bythotrephes* biomass on these percentage variables was performed for each zooplankton prey species using ordinary least squares regression. A further analysis was performed that included epilimnion depth, secchi depth, and *Bythotrephes* biomass as independent variables in a multiple linear regression model to evaluate their effects on the percentage of *Bosmina longirostris* and *D. retrocurva* occupying the Lake Erie epilimnion. Prior to analysis, percentages were arcsine transformed and *Bythotrephes* biomass was log-transformed to normalize distributions of dependent and independent variables (Zar 1999).

Estimates of lethal and nonlethal effects of Bythotrephes

We estimated the nonlethal and lethal effects of *Bythotrephes* on prey population growth rate using data from the intensive field survey and the following model of per capita prey population growth rate:

$$\frac{1}{N}\frac{dN}{dt} = b - \Delta b - d - m \tag{1}$$

where b is the per capita birth rate in the absence of a phenotypic response, Δ is the proportional reduction in per capita birth rate due to the phenotypic response to predation risk (sensu Peacor and Werner 2004), d is the per capita consumption of prey by *Bythotrephes*, and m is background per capita death rate due to other sources. This representation allowed us to express the nonlethal (Δb) and lethal (d) effect of *Bythotrephes* with a common currency. Data requirements limited our analysis to species that were most abundant, which included *Daphnia mendotae* from one survey in Lake Michigan and *Bosmina longirostris* from two surveys in Lake Erie. We next describe the intensive field surveys used to collect the necessary stage-specific data and the mathematical model used to estimate Δb and d.

Nonlethal effects of *Bythotrephes* were estimated using data from the Lake Michigan intensive survey conducted on 3 and 4 August 2004 at a 60 m deep site located ~10 km west of Muskegon, Michigan (Table 1). Four sampling profiles were carried out over a 24-h period, and profiles were initiated consecutively at 14:00, 21:00, 01:00, and 09:00. A sampling profile consisted of collecting 1 m^3 of lake water from five different depths ranging from 4 m to 40 m corresponding with the centers of the epilimnion, metalimnion, hypolimnion, and the transitions between them. Water was collected using the same methods described in the Lake Michigan extensive field survey. Nonlethal effects in Lake Erie were estimated from samplings collected on 30 July and 8 September 1997 in Long Point Bay (Table 1). On each date, *Bythotrephes* and zooplankton prey were collected at midday and midnight from 10 different depths that were distributed through the epi-, meta-, and hypolimnion. A propeller-style pump was used to collect 250 L of lake water from each depth, then water was filtered through a 64-μm mesh net. Samples were processed and counted in the same fashion as described for the extensive survey.

Field-derived estimates of *D. mendotae* and *Bosmina longirostris* fecundity were combined with known developmental rate–temperature relationship to estimate per capita birth rate (b) using the egg ratio method (Palheimo 1974) according to the equation

$$b = \frac{\ln(E/N + 1)}{D(T)} \tag{2}$$

where E is the density of eggs (number of eggs per cubic meter), N is the density of prey (number of individuals per cubic meter), and $D(T)$ is the egg developmental duration (in days), which is a function of water temperature (T, in degrees Celsius). The densities of eggs and individuals were averaged across sampling profiles and thermal strata, weighted by the thickness of each thermal layer, to derive estimates of E and N, respectively. $D(T)$ has been derived for *D. mendotae* (Edmonson and Litt 1982) and *Bosmina longirostris* (Hanasato and Yasuno 1985) and can be estimated using the equations

$$D(T) = 1/0.00041 \times T^2 + 0.0108 \times T - 0.0163 \tag{3}$$

and

$$D(T) = 3.102 - 0.261 \times \ln(T^2) \tag{4}$$

respectively. We integrated across the differing temperatures experienced by zooplankton to derive a single estimate of $D(T)$ for each survey (Hoffman et al. 2001) using the equation

$$D(T) = \sum_p D(T)_p w_p \tag{5}$$

where $D(T)_p$ is the mean developmental rate for each profile (p), and w_p is a weighting factor equal to the fraction of a 24-h day each profile represented. For Lake Michigan, the daytime profiles (09:00 and 14:00) and the nighttime profile (01:00) were assigned values of $w_p = 0.30$ and $w_p = 0.20$, respectively. The 21:00 sampling profile captured the day–night transition during which *D. mendotae* migrated. Based on field observations of *D. mendotae* vertical migration (K. L. Pangle and S. D. Peacor, *unpublished data*) and *Daphnia* swimming speed (Dawidowicz and Loose 1992), this sampling profile was assigned a value of $w_p = 0.33$. For Lake Erie, daytime and nighttime profiles were assigned values of $w_p = 0.60$ and $w_p = 0.40$, respectively, for the first survey, and $w_p = 0.53$ and $w_p = 0.47$, respectively, for the second survey, based on sunrise and sunset. $D(T)_p$ was in turn calculated by averaging over the temperature experienced at different depths for each profile:

$$D(T)_p = \sum_z D(T)_{z,p} f_{z,p} \tag{6}$$

where $f_{z,p}$ is the proportion of eggs relative to the total number of eggs in the water column for depth z and profile p, and $D(T)_{z,p}$ is the estimated egg developmental duration using Eq. 3 or 4 given the temperature at depth z for profile p.

The nonlethal effect of the predator (Δb in Eq. 1) was calculated as the difference between the estimated per capita population birth rate using the vertical distributions of prey when *Bythotrephes* was present and when *Bythotrephes* was absent. The latter distributions varied considerably for both species, thus providing us a range of birth rates in the absence of *Bythotrephes*. We used the deepest, the average, and the shallowest observed prey distributions in *Bythotrephes*' absence from our extensive surveys to determine a range of nonlethal effects.

Lethal effects associated with *Bythotrephes* predation, d, were estimated using known light-dependent consumption rates combined with the observed predator–prey spatial overlap from the intensive field survey. We used predation rates derived from a series of laboratory experiments in which *Bythotrephes* preyed on *Daphnia* at natural prey densities in 4-L containers (slowly rotating in a 1500-L incubator) over a large range of light intensities (K. L. Pangle, S. D. Peacor, and H. A. Vanderploeg, *unpublished data*). Note that these predation rates are consistent with those in a previous study that used a bioenergetics approach (Yurista and Schulz 1995). Vanderploeg et al. (1993) found that *Bythotrephes* consumed species of *Daphnia* and *Bosmina* at a similar rate, so we used the same predation rates to estimate *B. longirostis* consumed by *Bythotrephes*. However, *Bythotrephes* are likely better able to detect *D. mendotae* than *Bosmina longirostris* due to *Daphnia*'s larger size (Confer et al. 1978), making our predation estimates for *Bosmina longirostris* conservatively high. The per capita rate of predation by a single *Bythotrephes* (a, prey consumed per cubic meter per *Bythotrephes* per day) was estimated as

$$a = \frac{8.196 \times 10^{-3}}{1 + (L/24.96)^{-1.034}} \tag{7}$$

where L is light intensity (in micromoles per square meter per second). The per capita (of prey) predation rate at a given sampling profile (d_p, per day) was calculated as a weighted average:

$$d_p = \frac{\sum_z a_z N_z P_z w_z}{\sum_z N_z w_z} \tag{8}$$

where a_z is predation rate at the depth z given its midpoint light intensity, N_z and P_z are the prey and *Bythotrephes* density (number per cubic meter), respectively, at depth z, and w_z (m) is the height of the water column represented by depth z. For the Lake Michigan sampling profile representing the day–night transition (21:00), we used the highest light intensity observed during the transition to calculate d_p, thus making our estimate conservatively high. The daily predation rate,

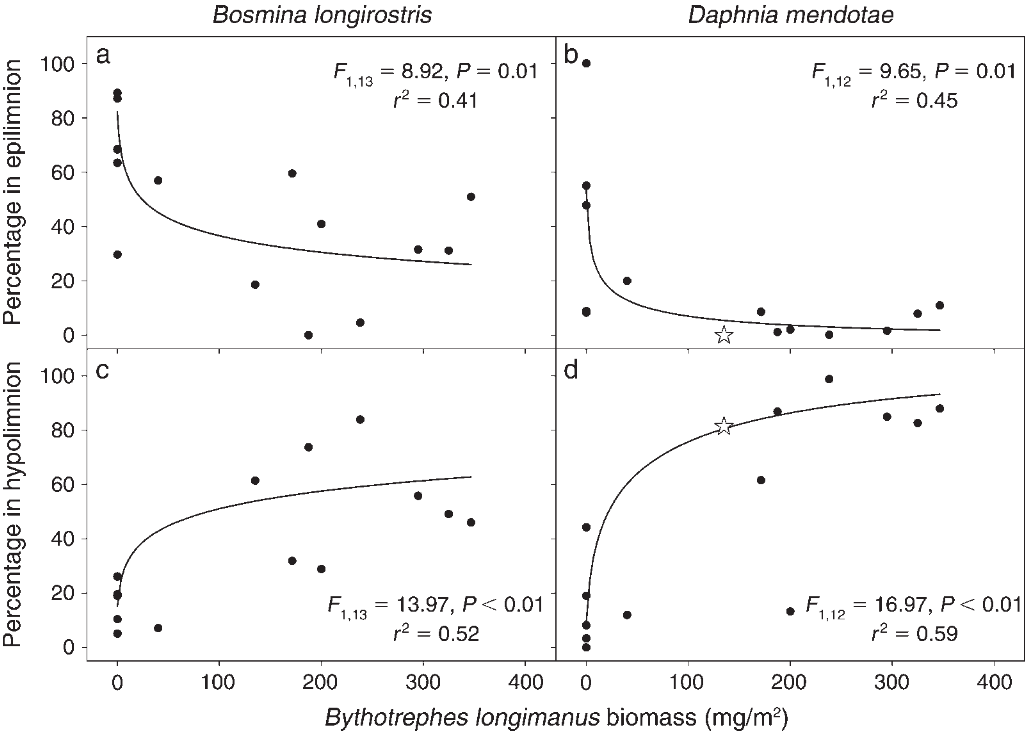

FIG. 1. Percentage of (a, c) *Bosmina longirostris* and (b, d) *Daphnia mendotae* in the epi- and hypolimnion of Lake Michigan over a gradient of *Bythotrephes* biomass. Lines are linear regressions performed on transformed data and plotted on untransformed data, with analysis results reported within each subplot. Stars represent the distribution in the intensive survey (see *Results*).

considered the overall lethal effect of *Bythotrephes*, was calculated as the arithmetic mean of the per capita predation rates using the same weights for sampling profiles as Eq. 5.

RESULTS

Influence of Bythotrephes *on daytime zooplankton vertical distribution*

In Lake Michigan, *Bythotrephes* biomass had a significant negative influence on percentages of both *Daphnia mendotae* and *Bosmina longirostris* in the epilimnion (*Bosmina longirostris*, $F_{1,13} = 8.92$, $P = 0.01$, $r^2 = 0.41$; *D. mendotae*, $F_{1,12} = 9.65$, $P = 0.01$, $r^2 = 0.45$) and had a significant positive influence on percentages in the hypolimnion (*Bosmina longirostris*, $F_{1,13} = 13.97$, $P < 0.01$, $r^2 = 0.52$; *D. mendotae*, $F_{1,12} = 16.97$, $P < 0.01$, $r^2 = 0.59$). When *Bythotrephes* was absent from the pelagic community in Lake Michigan, both prey species primarily inhabited the upper strata of the water column, with a greater percentage of both prey species found in the epilimnion than in the hypolimnion (Fig. 1). With high *Bythotrephes* biomass (i.e., >200 mg/m^2), prey vertical distribution shifted downward and as much as 97% of *D. mendotae* and 74% of *Bosmina longirostris* inhabited the hypolimnion. This was particularly dramatic for *D. mendotae*, which were almost entirely absent from the epilimnion at high *Bythotrephes* biomass.

In Lake Erie (Fig. 2), *Bythotrephes* also had a significant negative influence on percentages of prey, in this case *Bosmina longirostris* and *Daphnia retrocurva,* in the epilimnion (*Bosmina longirostris*, $F_{1,52} = 7.84$, $P = 0.01$, $r^2 = 0.13$; *D. retrocurva*, $F_{1,40} = 4.95$, $P = 0.03$, $r^2 = 0.11$) and had a significant positive influence on percentages in the hypolimnion (*Bosmina longirostris*, $F_{1,52} = 5.47$, $P = 0.02$, $r^2 = 0.10$; *D. retrocurva*, $F_{1,40} = 8.23$, $P < 0.01$, $r^2 = 0.17$). Indeed, both prey species in Lake Erie were almost entirely found in the hypolimnion at high *Bythotrephes* biomass (i.e., >300 mg/m^2), and a decline in the percentage of prey in the epilimnion started at 10 mg *Bythotrephes*/m^2. There was greater variation among sampling events in Lake Erie than in Lake Michigan, particularly when *Bythotrephes* biomass was low (Fig. 2); when *Bythotrephes* was absent from the pelagic community, the percentage of *Bosmina longirostris* and *D. retrocurva* ranged from 0 to 100% in both the epi- and hypolimnion.

Abiotic environmental factors also influenced prey vertical distribution. In particular, a significantly ($P < 0.05$) greater percentage of *Bosmina longirostris* occupied the epilimnion in Lake Erie as both epilimnion depth increased and secchi depth decreased. In the multiple linear regression model, the magnitude of the *Bythotrephes* effect on the percentage of *Bosmina longirostris* occupying the epilimnion increased, a predicted trend; however, this change was not significant ($P =$

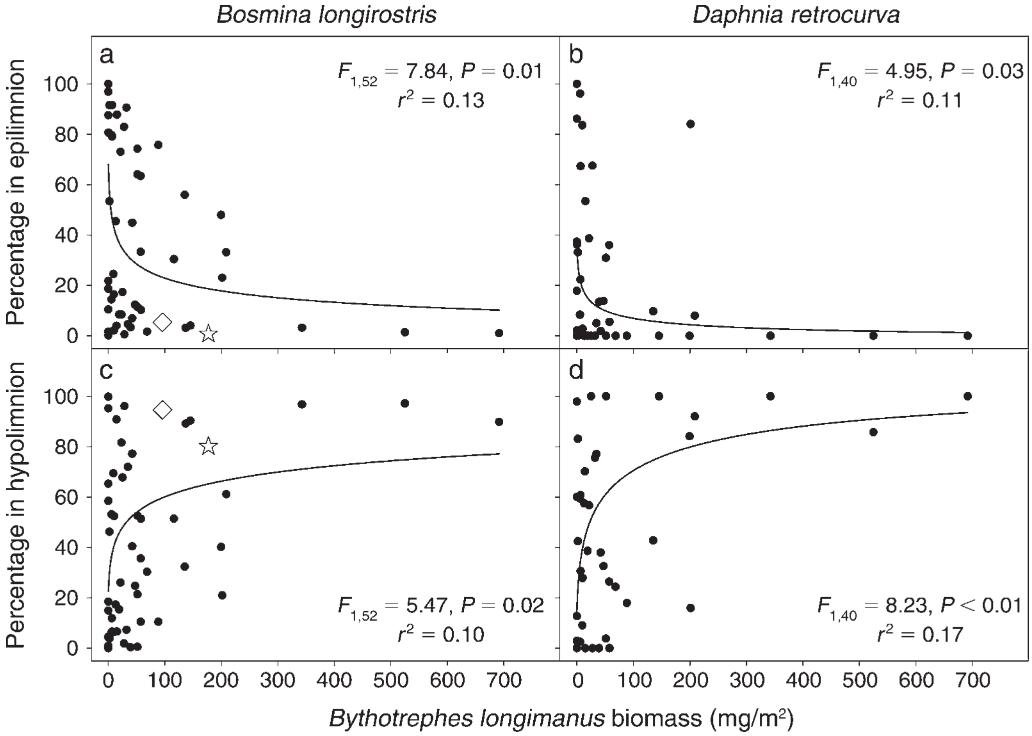

FIG. 2. Percentage of (a, c) *Bosmina longirostris* and (b, d) *Daphnia retrocurva* in the epi- and hypolimnion of Lake Erie over a gradient of *Bythotrephes* biomass. Lines are linear regressions performed on transformed data and plotted on untransformed data, with analysis results reported within each subplot. Stars and diamonds represent distributions in the first and second intensive surveys, respectively (see *Results: Influence of* Bythotrephes *on zooplankton daytime vertical distribution*).

0.18). There was no effect of epilimnion depth and secchi depth on the percentage of *D. retrocurva* occupying the epilimnion ($P > 0.05$).

The vertical distribution of *Bythotrephes* remained constant throughout the Lake Michigan intensive field survey, while a strong migratory behavior was observed for *D. mendotae* (Fig. 3). During the middle of the day, *D. mendotae* were distributed deep in the water column, at dusk they had begun to move into upper vertical strata and warmer temperatures, until at night, *D.*

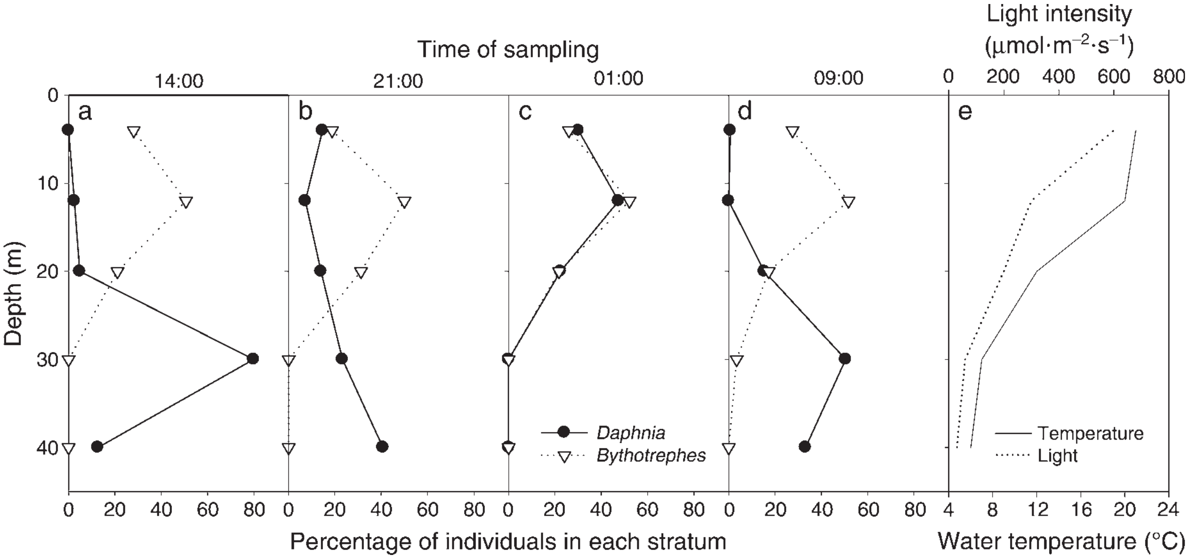

FIG. 3. (a–d) Vertical distribution of *Daphnia mendotae* and *Bythotrephes* and (e) midday temperature and light conditions of the water column during the Lake Michigan intensive field survey. Each of four sampling profiles is reported in chronological order.

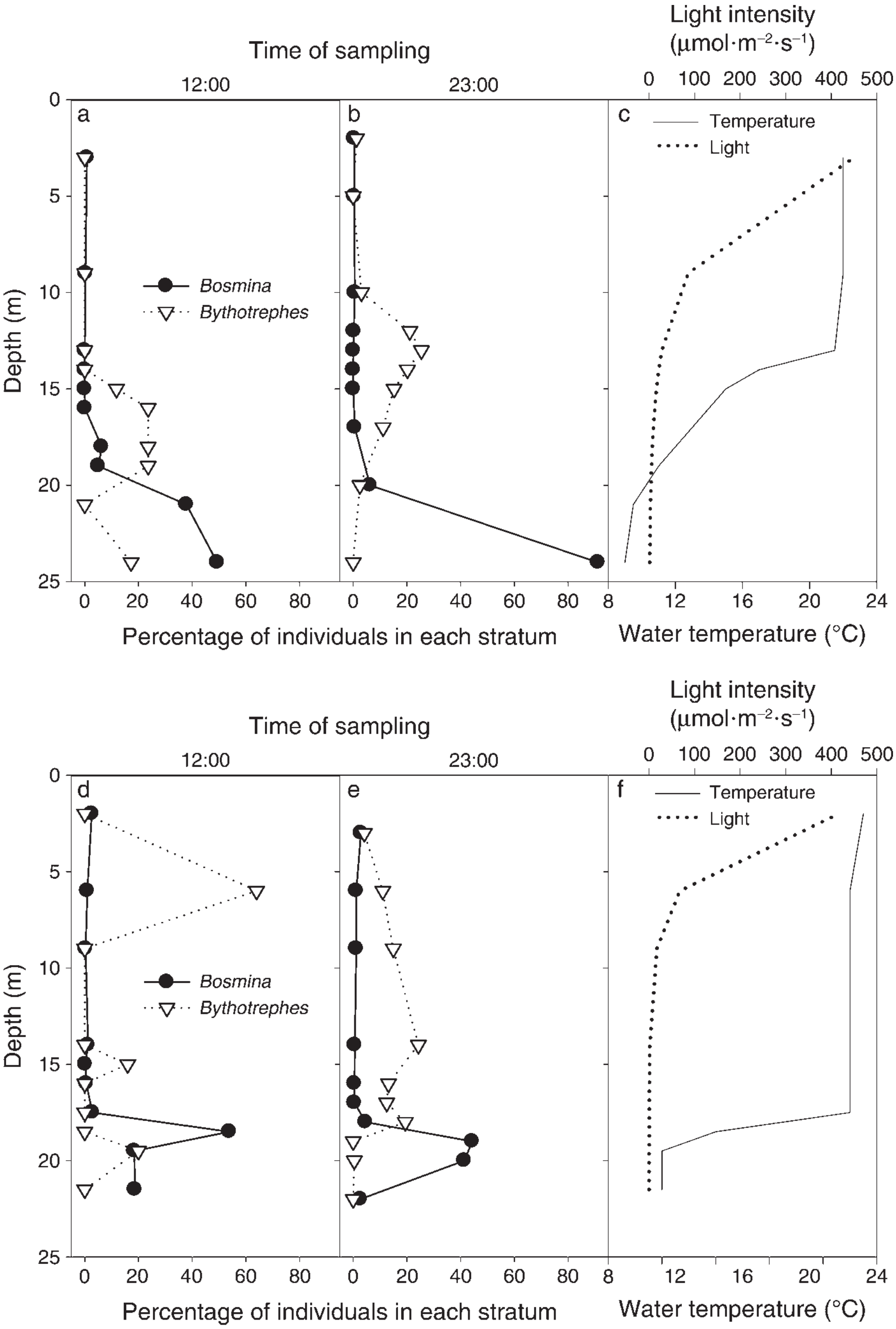

FIG. 4. (a, b, d, e) Vertical distribution of *Bosmina longirostris* and *Bythotrephes* and (c, f) midday temperature and light conditions of the water column during the first and second Lake Erie intensive field surveys (a–c and d–e, respectively). Sampling profiles were conducted near midday (a, d) and midnight (b, e) during both surveys.

mendotae were found only in the upper stratum. At dawn (09:00), *D. mendotae* migrated back downward as light levels increased. This migration resulted in a change in temperature to which prey were exposed (colder during the day, Fig. 3) and the degree of vertical overlap with *Bythotrephes,* which was high during the nighttime but low during the day (Fig. 3).

The vertical distribution of *Bosmina longirostris* in the Lake Erie intensive field surveys was below that of *Bythotrephes* during the day and nighttime sampling profiles (Fig. 4). In the first survey, *Bosmina longirostris* were found almost entirely in the hypolimnion at midday and midnight, while *Bythotrephes* were found in the metalimnion at the same times. In the second survey, *Bosmina longirostris* were found in the hypolimnion and *Bythotrephes* were found in the epilimnion at midday and midnight. In both Lake Erie surveys, vertical overlap between predator and prey was low and changed little between sampling profiles. Overall, *Bythotrephes* biomass during intensive surveys was in the midrange of *Bythotrephes* densities seen during extensive surveys (Figs. 1 and 2).

Estimates of lethal and nonlethal effects of Bythotrephes

In Lake Michigan, the estimated lethal effect (d) of *Bythotrephes* on *D. mendotae* population growth rate was 0.013 d^{-1}. Estimates of the nonlethal effect (Δb) of *Bythotrephes* on *D. mendotae* were 0, 0.038, and 0.174 d^{-1}, respectively, for scenarios that used the deepest, mean, and shallowest observed prey distributions in the absence of *Bythotrephes* (Fig. 5). In Lake Erie, d was estimated as 0.006 and 0.007 d^{-1} in the first and second surveys, respectively (Fig. 5). Estimates of nonlethal effects in the first survey were 0, 0.015, and 0.061 d^{-1}, respectively, based on three depth scenarios, and in the second survey were 0, 0.024, and 0.079 d^{-1}, respectively. These estimates were similar to those produced independently using a somatic growth rate model (Appendix A).

DISCUSSION

This study demonstrates that nonlethal effects can contribute strongly to, and even predominate, the net effects of predators on prey population growth rate in a natural setting. Variability in estimated effects among our different scenarios shows how the importance of nonlethal effects may fluctuate over time. For example, at times at which prey occupy deep waters independent of the presence of *Bythotrephes*, *Bythotrephes* will not affect prey position and nonlethal effects are necessarily absent. At other times, prey vertical migration appeared to be driven entirely by *Bythotrephes*' presence, and, in this scenario, nonlethal effects were estimated to be up to 10 times greater than lethal effects. Whereas the nonlethal effect of *Bythotrephes* may range from low to very large values in time and space, the relatively frequent distribution of prey high in the water column in *Bythotrephes* absence indicates that larger values are common.

If planktivorous fish biomass positively correlates with *Bythotrephes* biomass then fish may underlie or contribute to the observed prey vertical distribution. We therefore examined the correlation between planktivorous fish biomass and *Bythotrephes* biomass and found that they do not positively correlate. In particular, in Lake Michigan during July and August 2004, acoustic estimates of fish biomass were relatively constant in offshore areas where both *Bythotrephes* biomass and prey vertical distribution fluctuated greatly (D. M. Kreuger, *unpublished data*). Low variation in Lake Michigan offshore fish biomass was also observed between May and September 1987 (Brandt et al. 1991) and is considered a general phenomenon (S. A. Pothoven and C. P. Madenjian, *personal communications*). Other lines of evidence further support that *Bythotrephes*, rather than fish, caused the vertical migration of

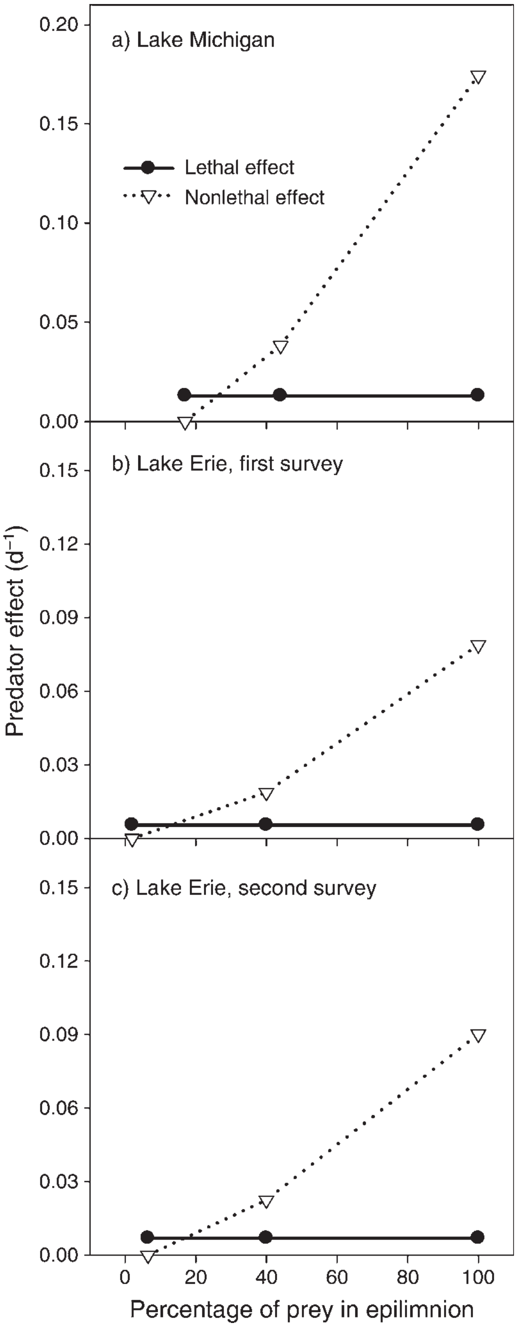

FIG. 5. Estimated lethal and nonlethal effects of *Bythotrephes* on (a) *Daphnia mendotae* in Lake Michigan and (b, c) *Bosmina longirostris* in Lake Erie. Nonlethal effects were estimated based on three different scenarios (see *Methods*) that assumed different prey distribution in *Bythotrephes*' absence to reflect the natural variation. This range is represented on the x-axis as the percentage of the prey species in the epilimnion in *Bythotrephes*' absence for the different scenarios.

zooplankton prey. Following the introduction of *Bythotrephes* in Lake Michigan, zooplankton vertical distribution deepened (Lehman and Caceres 1993), but the biomass of alewife, the primary species of planktivorous fish, remained relatively constant (Madenjian et al. 2002). Further, the underlying mechanism is supported by laboratory experiments in which zooplankton prey have been shown to respond strongly to *Bythotrephes* kairomones by migrating downward in experimental columns (Pangle and Peacor 2006).

Because *Bythotrephes* consume prey at higher rates near the surface, we consider whether predation could underlie the change in prey distribution observed in *Bythotrephes'* presence, rather than a behavioral mechanism. We believe this alternative is not plausible because: (1) *Bythotrephes* has been demonstrated experimentally to induce strong vertical migration in zooplankton (including *D. mendotae* and *Bosmina longirostris*) in a manner identical to that reported here (Pangle and Peacor 2006; K. L. Pangle and S. D. Peacor, *unpublished data*); (2) prey vertical migration was observed in our intensive field surveys, particularly in Lake Michigan, where prey inhabited very different regions of the water column during the day, night, and transitional periods (Fig. 3); (3) analysis of the extensive survey data (Appendix B) indicated that absolute prey abundance in the hypolimnion increased with *Bythotrephes* biomass, which is more indicative of a shift in prey habitat use than predation.

We have argued that the nonlethal effect of *Bythotrephes* on prey birth rate was a result of inhabiting lower temperatures. It is possible that different resource levels experienced due to migration could also affect growth rate. However, results from bioassay experiments showed that the growth of *D. mendotae* did not vary significantly when cultured in Lake Michigan water taken from each of the thermal layers and held at the same temperature (K. L. Pangle and S. D. Peacor, *unpublished data*). Further, other studies have found that vertical migration affects zooplankton birth rate primarily through differences in temperatures and not from food resource differences (Winder et al. 2003, Park et al. 2004). It is also possible that natural variation in resource levels could affect prey growth rate over time and space and therefore confound comparisons of growth rate in the presence and absence of *Bythotrephes*. This factor does not affect our results, because we compared the predicted prey population growth rate in the presence and absence of *Bythotrephes* at the same location and time.

Our results extend previous studies that indicate a strong contribution of nonlethal effects to the net interaction between predator and prey. Previous work has primarily evaluated predator-induced reductions in prey somatic growth as a surrogate for population growth (e.g., Diehl and Eklov 1995, reviewed in Peacor and Werner 2004). However, although effects on somatic growth rate may translate into change in population dynamics, it is also necessary to directly evaluate nonlethal predator effects at the population level (Nelson et al. 2004, Boeing et al. 2005) if we are to make robust comparisons with lethal predator effects. Further, thus far, studies at the population level have been performed in controlled mesocosm settings. It is essential to translate experimental findings to patterns in natural settings to improve our understanding of the hierarchy of processes that regulate ecosystems (Carpenter and Kitchell 1988, Levin 1992, Schmitz 2005). By working in a setting as large and complex as the Great Lakes, our approach is novel and necessarily very different than that used in laboratory and mesocosm studies (e.g., rather than measure densities in a factorially designed experiment, we made inferences from established relationships of growth and predation). Overall, our results provide a demonstration that nonlethal effects can strongly influence population-level responses, even exerting greater effect on prey populations than do lethal effects in large-scale, natural settings.

The results of our study have implications for the manner in which biologists assess the impact of *Bythotrephes* on zooplankton prey populations and the Great Lakes pelagic community and the impact of predator–prey interactions in general. Nonlethal effects can introduce nonlinearities into predator–prey functional relationships, which could result in a small number of predators having a disproportionately larger effect on prey density (Abrams 1995, Peacor and Werner 2004) and could affect the stability of predator–prey interactions (Luttbeg and Schmitz 2000). Furthermore, nonlethal effects may initiate trait-mediated indirect interactions (TMIIs) within food webs because changes in the fitness and population size of responding prey may in turn affect interactions of the responding prey with other species (reviewed in Werner and Peacor 2003, Schmitz et al. 2004). For example, other herbivorous zooplankton species less preferred by *Bythotrephes* (Vanderploeg et al. 1993, Schulz and Yurista 1999) may respond differently to *Bythotrephes* predation risk, thus altering competitive interactions (Dawidowicz and Wielanier 2004). In addition, changes in the assemblage and densities of zooplankton may affect other predators, like young-of-year fish, which can clearly have cascading effects on the food web.

Finally, the evolutionary history of species interactions may strongly influence the phenotypic responses of a prey species to a predator (Abrams 2000, Trussell 2000, Cousyn et al. 2001) and therefore nonlethal effects. Whereas there are few studies of phenotypic responses of prey to invasive predators, the magnitude of the response has been shown to vary greatly from no change at all (Pearl et al. 2003) to strong changes (McIntosh and Townsend 1995). Further, the magnitude of the response has been shown to change through time (Cousyn et al. 2001). Given the variation in the phenotypic response, the magnitude of the nonlethal effect will vary accordingly. In the case studied here, native zooplankton prey in the Great Lakes respond strongly to the presence of *Bythotrephes* after a relatively short evolutionary history (~20 years). Is this predator-induced response a result of rapid evolution, or did prey have this ability prior to the invasion of *Bythotrephes* due to adaptation to native predators? Exploration of this evolutionary question could shed light on changes in nonlethal effects on Great Lakes zooplankton over the last two decades and further our understanding of the nonlethal effects of invasive species in general.

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APPENDIX A

Estimates of nonlethal effect produced using a prey somatic growth rate model (*Ecological Archives* E088-025-A1).

APPENDIX B

The relationship between *Bythotrephes* biomass and absolute prey abundance in the hypolimnion (*Ecological Archives* E088-025-A2).