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THE ROLE OF NON-CONSUMPTIVE EFFECTS IN THE NET EFFECT OF AN INVASIVE PREDATOR IN THE LAURENTIAN GREAT LAKES

By

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ABSTRACT

THE ROLE OF NON-CONSUMPTIVE EFFECTS IN THE NET EFFECT OF AN INVASIVE PREDATOR ON LAURENTIAN GREAT LAKES FOOD WEBS

By

Kevin L. Pangle

In ecological food webs, predators can have consumptive effects (CEs) and non-consumptive effects (NCEs) on prey populations, the latter caused by inducing costly changes in prey phenotypes. Studies of NCEs, primarily carried out in laboratory and mesocosm settings, have shown that NCEs can profoundly influence the structure and dynamics of food webs. Whether or not NCEs contribute significantly to ecological patterns and processes observed in the field is still an open question, but one essential to address in the aim of better understanding the mechanisms that regulate food web dynamics in nature and to better inform the management of ecosystems. My goal in this dissertation was to elucidate the importance of NCEs in the complex, natural setting of the Laurentian Great Lakes. I focused my research on the NCEs of the invasive predator, *Bythotrephes longimanus*, and in doing so, I hoped that my dissertation work would also aid in better understanding the detrimental impact of this invader.

The approach I took was necessarily very different than those taken by previous studies of NCEs. Unlike laboratory and mesocosm settings, the Laurentian Great Lakes are not conducive to experimental manipulations. Instead, to evaluate NCEs, I relied on a sequence of steps that integrated experimental findings, field observations, and modeling. First, I tested the phenotypic response of the native prey (zooplankton) to *Bythotrephes* and related their response to zooplankton phenotypes observed in the field. Second, I

evaluated the possible consequences of the phenotypic response of zooplankton on their population growth rate (i.e., NCEs of *Bythotrephes*) in the field. Third, I incorporate NCEs into food web models to quantify the contribution of NCEs to the net effect of *Bythotrephes* on zooplankton populations and to the net indirect effect of *Bythotrephes* on an ecologically and economically important Great Lakes species, alewife (*Alosa pseudoharengus*).

I found that multiple Great Lakes zooplankton species respond to *Bythotrephes* by modifying a behavioral trait. Specifically, the presence of *Bythotrephes* induced zooplankton to migrate downward, which I observed in the field and tested in laboratory settings. Vertical migration is assumed to be adaptive as it reduces the spatial overlap between zooplankton and *Bythotrephes*. To avoid *Bythotrephes*, I found that zooplankton incur a substantial cost to their population growth rate by shifting habitat use to cooler environments. Estimates of the magnitude of these NCEs in Lakes Michigan and Erie indicated that NCEs play a large role in the effect *Bythotrephes* has on zooplankton populations, with NCEs on the same order of magnitude as or greater (up to 10 fold) than CEs. Further, consideration of NCEs greatly influenced the predicted indirect effects of *Bythotrephes* on alewife growth and survival in Lake Michigan.

These results demonstrate the relevance of NCEs to ecological patterns and processes observed in nature. Future consideration of NCEs may substantially improve our understanding of food web function and better inform the management of ecosystems that rely on this understanding. These results also demonstrate the complex impact the introduction of species can have on ecosystems through NCEs.

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GENERAL INTRODUCTION

The concept of food webs is of central importance to the field of ecology, as it has been the foundation for understanding how interactions among organisms shape the structure and dynamics of ecological systems (Elton 1927; MacArthur 1955; Paine 1980). Ecologists have relied on models of food webs to elucidate processes that control ecosystem stability, productivity, biodiversity (e.g., Rosenzweig 1971; May 1973; McCann 2000), and to inform the management of ecosystem services (e.g., Garcia and Cochrane 2003). To construct these food web models, the conventional approach relied on linking predators and prey using pairwise interactions. These interactions are generally defined as the per capita rate of consumption of the prey by the predator, referred to as the predator's consumptive effect (CE). Food web models therefore typically ignore interactions among species in a food web that occur through means other than direct consumption.

One ignored interaction is the effect predators can have on prey phenotype. As a consequence of predation, many prey have evolved plastic anti-predation traits, including behavioral, morphological, and life-history traits, that are modified by prey in a way that optimizes prey fitness (reviewed in Lima 1998; Tollrian and Harvell 1999). As is general in all forms of phenotypic plasticity, the expression of these anti-predation traits represents a trade-off, in this case between the benefit of reduced predation risk and the costs associated with the production and maintenance of the plastic trait. Prey are predicted to incur these cost as long as the net benefit is maximal. Subsequently, these costs, termed the non-consumptive effect (NCE) of the predator on the prey (Abrams 2007), can be substantial and lead to significant reductions in prey somatic growth rate and fecundity (Werner et al. 1983; Peckarsky et al. 1993; Diehl and Eklov 1995; reviewed in Peacor and Werner 2004).

Trait modifications and consequent NCEs may influence how food webs function in several ways. First, recent studies using mesocosm experiments in a damsel bug-pea aphid system (Nelson et al. 2004) and in a *Chaoborus-Daphnia* system (Boeing et al. 2005) have found that the costs incurred due to trait modifications can lead to a substantial NCE on prey population growth rate. This effect is qualitatively different than a predator's CE in that prey population size is being reduced without directly increasing predator population size. Consequently, NCEs may stabilize predator-prey dynamics (Ives and Dobson 1987; Fryxell and Lundberg 1997), or destabilize predator-prey dynamics if there is a time lag between prey and predator population changes (Luttbeg and Schmitz 2000). Second, NCEs may introduce nonlinearities into predator-prey functional relationships that are predicted to profoundly affect food web dynamics (Abrams 1995; Bolker et al. 2003). In particular, a small number of predators may have a disproportionately larger effect on prey density if prey respond to their presence (Abrams 1995; Peacor and Werner 2004). Third, trait modifications that cause NCEs may influence the interactions between prey with other species in the food web. This effect of the predator is termed a trait-mediated indirect effect (Abrams 2007), which is a subset of higher-order interactions (*sensu* Vandermeer 1969). Trait-mediated indirect interactions can lead to counter-intuitive outcomes in food webs (reviewed in Werner and Peacor 2003), such as increased prey growth caused by increased predator density (Peacor 2002).

Although these studies have clearly shown the potential ways that NCEs may influence food webs, whether or not NCEs are relevant to the ecological patterns and processes observed in nature is still an open question. To my knowledge, when I started my dissertation research, no study had quantified NCEs in an uncontrolled, field setting. One obstacle facing such an endeavor is that the inherent complexity of ecosystems makes measuring phenotypic response and their ensuing cost very difficult (Creel and Christianson 2008). Another obstacle is that NCEs may have far reaching effects on the possible multitude of other species in an ecosystem (Abrams 1995). Although challenging, quantifying NCEs in the field may not only help identify mechanisms that regulate food web dynamics in nature, but also inform ecosystem conservation and management (Browman et al. 2004; Pikitch et al. 2004), where consideration for NCEs is largely lacking (Creel and Christianson 2008).

My goal in this dissertation was to elucidate the importance of NCEs in the complex, natural setting of the Laurentian Great Lakes. The Laurentian Great Lakes provide a valuable natural resource for millions of people, supporting a large number of commercial and recreationally activities. However, a number of serious problems threaten this unique system. For example, invasive species are changing the structure and functionality of native Great Lakes communities (Vanderploeg et al. 2002), toxic algae are closing beaches and polluting drinking water (Murphy et al. 2003), and important fisheries are exhibiting drastic declines (Mills et al. 2003; Marsden and Robillard 2004). A commonality among many of the diverse issues is their association with complex, disruptive effects on the food web. Knowledge of food web interactions in the Great Lakes may therefore be vital to gaining the most complete understanding of harmful implications to the aquatic ecosystem.

An invasive species of particular concern to Great Lakes biologists is the invertebrate species *Bythotrephes longimanus*. *Bythotrephes* is a predatory cladoceran that feeds primarily on zooplankton (Vanderploeg et al. 1993; Schulz and Yurista 1999). Originally introduced via ballast water to Lake Ontario over 20 years ago, *Bythotrephes* have spread to all five Great Lakes (Vanderploeg et al. 2002) and many surrounding inland lakes (Boudreau and Yan 2003). Once established in a lake, *Bythotrephes* has been credited with the local extirpation and reduction in density of several zooplankton species (Lehman and Cáceres 1993; Boudreau and Yan 2003; Barbiero et al. 2008). For example, in Lake Michigan, populations of *Daphnia mendotae*, *D. retrocurva*, and *D. pulicaria* collapsed during the first year *Bythotrephes* became abundant in the lake (Lehman 1991). *Daphnia mendotae* have since rebounded to abundances that are equivalent to levels prior to *Bythotrephes* invasion, while the other daphnid species have remained rare (Lehman and Cáceres 1993; Barbiero and Tuchman 2004). Such loss of zooplankton may in turn have detrimental effects on many fish species for which zooplankton serve as a critical food resource (Miller et al. 1990; O'Gorman et al. 1997; Fulford et al. 2006). This threat spurred a recommendation to the Great Lake Fisheries Commission to determine the effects of *Bythotrephes* on the pelagic food web (Shuter and Mason 2001).

Evidence suggests that *Bythotrephes* not only directly consume zooplankton, but may also induce changes in zooplankton traits. Field studies indicate that the vertical distribution of some zooplankton species deepened following the invasion of *Bythotrephes* in Lake Michigan (Lehman and Cáceres 1993) and Lake Erie (O. E. Johansson, unpublished data). These patterns are indicative of diel vertical migration, a plastic behavioral trait commonly observed in zooplankton (Gliwicz 1986; Dodson 1988;

reviewed in DeMeester et al. 1998). Diel vertical migration may reduce the risk of zooplankton being eaten by *Bythotrephes*, as this predator is shallow-dwelling and uses visual cues to detect prey (Muirhead and Sprules 2003), but migration may also come at a cost to zooplankton caused by inhabiting cooler environments (Loose and Dawidowicz 1994). If zooplankton are migrating in response to *Bythotrephes*, the resultant NCEs of *Bythotrephes* may contribute to the net effect of this predator on zooplankton populations and its indirect effect of fish, by reducing the availability of zooplankton.

My doctoral research centered on evaluating the importance of NCEs to the net effect of *Bythotrephes* on the pelagic food web of the Laurentian Great Lakes. The approach I took was necessarily very different than those taken by previous studies. To evaluate NCEs, I relied on a sequence of steps that integrated experimental findings, field observations, and modeling. First, I tested the phenotypic response of the native prey (zooplankton) to *Bythotrephes* and related their response to zooplankton phenotypes observed in the field. Second, I evaluated the possible consequences of the phenotypic response of zooplankton on their population growth rate (i.e., NCEs of *Bythotrephes*) in the field. Third, I incorporate NCEs into food web models to quantify the contribution of NCEs to the net effect of *Bythotrephes* on zooplankton populations and to the net indirect effect of *Bythotrephes* on an ecologically and economically important Great Lakes species, alewife (*Alosa pseudoharengus*).

My dissertation is divided into 6 chapters, which I summarize below. The chapters are ordered in a logical progression, from measuring the traits of individual zooplankton to evaluating the consequences of NCEs food web interactions in the Great Lakes. Two of the chapters are published in peer-reviewed journals (Chapters 1 and 5), one chapter is in review for publication (Chapter 4), and three chapters have not yet been submitted for publication (Chapters 2, 3, and 6) (Appendix A).

Chapter 1 was an initial test to determine if zooplankton respond to *Bythotrephes* by modifying their phenotypes. I focused specifically here and in other parts of my dissertation work on the zooplankton species, *Daphnia mendotae*, which dominates the zooplankton community during the summer in Laurentian Great Lakes (Barbiero and Tuchman 2001). I found that *Daphnia* exposed to *Bythotrephes* kairomones (water borne chemicals extruded by the predator [Lass and Spaak 2003]) migrated downward at substantial cost to their somatic growth rate. Results further indicated that concentrations of *Bythotrephes* kairomones in water taken directly from the field (Lake Michigan) were high enough to induce behavioral shifts that led to these large reductions in somatic growth rate.

Results of Chapter 1 indicated that *Daphnia mendotae* was not naïve to risk posed by *Bythotrephes*. This finding is counter to the notion that prey may be unable to perceive and respond adaptively to novel risk posed by invasive predators because they lack evolutionary experience with the predator. Chapter 2 extends the tests of naïveté to include other Lake Michigan zooplankton prey and another invasive predator, *Cercopagis pengoi*. *Cercopagis* has been present in the Laurentian Great Lakes for six years and is in the same phylogenetic family as *Bythotrephes*, but the relatively small-sized *Cercopagis* poses a lesser risk to some zooplankton than the larger *Bythotrephes*. I also evaluated the migratory response of zooplankton to four common native predators to determine whether the migratory response of *D. mendotae* induced by *Bythotrephes* was a generalized response, thereby providing a possible explanation for the lack of naïveté. I found that zooplankton also responded adaptively to *Cercopagis*, and that downward migration is a generalized response induced by native predators that are functionally, but not phylogenetically similar to *Bythotrephes* and *Cercopagis*. Although native prey in aquatic systems are thought to be prone to naïveté (Cox and Lima 2006), the adaptive response of zooplankton indicates that naïveté currently does not play a role in their interactions with invasive predators.

Chapter 3 examined consequences of such vertical migration on *Daphnia* growth rate in the field. Migratory zooplankton experience fluctuations in their environment due to the multiple environmental gradients associated with the water column. I focused on two gradients, water temperature and food resources, that have been shown to influence zooplankton growth and reproduction in other systems (Williamson et al. 1996; Winder et al. 2003; Kessler and Lampert 2004). In Lake Michigan, these gradients may counter each other, as the highest concentrations of algae, a primary food resource for zooplankton, are found at deep chlorophyll maxima (DCM) where water temperature is relatively cold (Barbiero and Tuchman 2001). Results indicated that variation in water temperature experienced by migrating *Daphnia*, but not variation in food resources, greatly influenced growth rate of *Daphnia* and demonstrated that inhabiting cooler environments is the primarily cost of migration.

In order to determine the net effect of *Bythotrephes* on zooplankton, it was necessary to also accurately predict the CE of *Bythotrephes*. Chapter 4 evaluated predation by *Bythotrephes* over a natural gradient of light intensity. Light intensity may be particularly important to *Bythotrephes* interaction with prey, because *Bythotrephes* encounter most prey during the nighttime and *Bythotrephes'* ability to detect prey decreases with decreased light intensity (Muirhead and Sprules 2003). Results here showed that *Bythotrephes* predation varied among the different light intensities, with predation not detectable under low light intensity (<1 μmol m^{-2} s^{-1}), but increasing with greater light intensity, and eventually asymptoted under high light intensity (>100 μmol m^{-2} s^{-1}). These changes in consumption indicate that *Bythotrephes* predation is more sensitive to light than previously thought, a discrepancy that can be explained after considering the ability of *D. mendotae* to detect *Bythotrephes*' hydromechanic disturbance. In addition to aiding predictions of the CE of *Bythotrephes* in the field, these finding also provide a novel explanation for the tendency of *Bythotrephes* to invade lakes of high water clarity.

Chapter 5 combines the findings of the first four chapters with observations from an intensive field survey to evaluate NCEs of *Bythotrephes* on zooplankton prey populations in Lakes Michigan and Erie. Thus, to my knowledge, this chapter represents the first study that estimated NCEs on prey population growth rate in a natural setting. The results revealed that NCEs of *Bythotrephes* contribute substantially to net effect of *Bythotrephes* on several prey population growth rates, with NCEs on the same order of magnitude as or greater (up to 10 fold) than CEs.

Chapter 6 explored how NCEs of *Bythotrephes* on zooplankton indirectly affected age-0 alewife by incorporating NCEs observed in Chapter 5 into a food web model. Model predictions of seasonal population dynamics of *Daphnia* and consequent growth of alewife indicated that the impact of *Bythotrephes* on alewife depended strongly on whether or not the NCEs of *Bythotrephes* were included. For example, when only CEs of *Bythotrephes* were considered, predicted mean length of alewife entering their first winter was 110 mm and predicted over-winter survival was 87.1 %. When NCEs were added, both by including a cost of migration on *Daphnia* population growth rate and considering the reduction in overlap between alewife and *Daphnia* resulting from migration, predicted mean length of alewife entering winter was 72 mm and predicted over-winter survival was 19 %. These findings provided an example in a natural system of how interactions between competitors can be strongly influenced by behavioral responses of shared prey.

The results of my dissertation research have implications both specific to how biologists assess the impact of *Bythotrephes* on zooplankton prey populations and the Great Lakes pelagic community, and general to predator-prey interactions in nature. Specifically, my research aids Great Lakes managers in an immediate and important problem by providing more comprehensive assessment of *Bythotrephes* impacts. Although I have focused on indirect interactions between *Bythotrephes* and alewife interactions, the approach I took may also be used to identify effects of *Bythotrephes* on other species and the indirect impacts of other invasive species. In general, my research bridged recent knowledge developed in community ecology to large-scale ecological patterns and process, and addressed critical questions, primarily how important are NCEs in ecosystems as complex as Lake Michigan's. The product of this inquiry will hopefully alert researchers of diverse systems to the potential importance of NCEs and provide a mechanistic approach that can be applied to both aquatic and terrestrial environments.

CHAPTER ONE

NON-CONSUMPTIVE EFFECT OF THE INVASIVE PREDATOR *BYTHOTREPHES LONGIMANUS* ON *DAPHNIA MENDOTAE*

ABSTRACT

We evaluated the antipredator behavior of *Daphnia mendotae* to the invasive invertebrate predator, *Bythotrephes longimanus*, and the consequent effect of the predator on prey growth rate (referred to as a non-consumptive effect of the predator). In a laboratory experiment, *Daphnia* in the absence of *Bythotrephes* kairomones remained in the top, warmer regions of experimental columns, whereas in the presence of *Bythotrephes* kairomones, *Daphnia* migrated vertically, occupying a middle region by night and a low, cold region during the day. Over a 4-day experiment, the vertical migration induced by *Bythotrephes* caused a 36 % reduction in the somatic growth rate of *Daphnia*, a level that is sufficient to have an effect on prey population growth rate. A second laboratory experiment indicated that concentrations of *Bythotrephes* kairomones in water taken directly from the field (Lake Michigan) was high enough to induce behavioral shifts that led to these large reductions in somatic growth rate. Our results identify a means by which *Bythotrephes* has substantial effects on native prey populations other than through direct consumption.

INTRODUCTION

Understanding the impact of invasive species is one of the most important challenges facing biologists today (Mack et al. 2000; Byers et al. 2002; Hochberg and Gotelli 2005). One clear effect of invasive species is predation on native prey; however, potential non-consumptive effects are is less well understood. Non-consumptive effects occur when prey respond to predators by a modification of their phenotype (e.g., behavior, morphology, and life-history) that may reduce predation risk (Lima 1998). In theory, this phenotypic response increases fitness, but due to tradeoffs, there are costs, often in the form of reduced growth and fecundity (reviewed in Harvell 1990). Empirical (Lima 1998; Werner and Peacor 2003; Schmitz et al. 2004) and theoretical studies (Abrams 1982; Ives and Dobson 1987; Abrams 1993; Peacor and Werner 2004; Bolker et al. 2003) indicate that such non-consumptive effects can be strong relative to direct consumption. Invasive predators have been shown to have non-consumptive effects on native prey through induced phenotypic changes in several systems, including streams (McIntosh and Townsend 1994), ponds (Shave et al. 1994; Pearl et al. 2003) and terrestrial communities (Wilder and Rypstra 2004). Thus, whereas it is important to understand the non-consumptive effect of invasive predators to understand their impacts fully, our present understanding is derived from a limited number of systems.

Here, we examined non-consumptive effects of an invasive predator, *Bythotrephes longimanus* (Leydig), on zooplankton prey in the pelagic zone of Lake Michigan through a well-known antipredator behavior, vertical migration. *Bythotrephes* is an invasive predatory cladoceran that studies suggest has had an impact on the pelagic ecosystem of the Laurentian Great Lakes (Lehman and Cáceres 1993; Vanderploeg et al. 2002; Barbiero and Tuchman 2004), and smaller surrounding lakes (Yan et al. 2001; Boudreau and Yan 2003). In particular, since its introduction in the early 1980's, *Bythotrephes* has been described as a main factor driving community dynamics in Lake Michigan (Makarewicz et al. 1995). Although research on the effects of *Bythotrephes* on its zooplankton prey has focused primarily on direct consumption, field observations in Lake Michigan indicate that *Bythotrephes* may induce downward migration of zooplankton prey (Lehman and Cáceres 1993; K. L. Pangle, unpublished), which could affect prey growth rate. However, alternative processes could be responsible for the changes in zooplankton vertical distribution including: (1) another factor that is correlated with *Bythotrephes* density; (2) greater *Bythotrephes* predation of the entire prey population near the surface; (3) seasonal shifts in clones within a prey species that exhibit different behavior; or (4) an indirect effect from *Bythotrephes* affecting some other environmental condition, such as attracting fish.

We used an experimental approach to examine if *Bythotrephes* changed the vertical of *Daphnia mendotae* (Birge), and any non-consumptive effect on growth rate caused by such a behavioral modification. *Daphnia mendotae* is an important food for *Bythotrephes* (Lehman et al. 1997; Schulz and Yurista 1999), and *Daphnia* is model organism for the study of predator-induced tactics (Lass and Spaak 2003). *Daphnia mendotae* has also been shown to respond to *Bythotrephes* kairomones (i.e., water-borne chemicals produced by the predator) by growing larger helmets (Bungartz and Branstrator 2003). In the laboratory, we exposed *D. mendotae* to *Bythotrephes* kairomone over a 5-day period. We hypothesised that *D. mendotae* would respond by migrating downward, particularly during the day, because *Bythotrephes* is a visual predator (Muirhead and Sprules 2003) that inhabits the epi- and metalimnetic portions of the water column in Lake Michigan (Lehman and Cáceres 1993; K. L. Pangle, unpublished). Further, we hypothesised that vertical migration into deeper, colder water would incur a cost to growth. A second laboratory experiment was conducted to link our laboratory results with the concentrations of *Bythotrephes* kairomones in water collected from Lake Michigan.

METHODS

We measured the effect of *Bythotrephes* kairomones on the behavior and growth rate of *Daphnia mendotae* in experimental cylinders with a thermal gradient spanning a similar temperature range as that found in Lake Michigan. Experiment 1 was conducted to examine the effects of *Bythotrephes* kairomones on the vertical distribution of *Daphnia* and on individual (i.e. somatic) growth. Experiment 2 compared the response of *Daphnia* to lake water collected from regions with and without *Bythotrephes* and to a range of *Bythotrephes* kairomone concentrations prepared in the laboratory.

The experimental system followed that of Loose and Dawidowicz (1994). During the experiments, the vertical position of *Daphnia* was measured in 80-cm tall, 19-mm diameter, clear acrylic cylinders that were filled with experimental water and submerged vertically in a transparent, 300-L aquarium. The aquarium acted as a thermally-stratified water bath, with water temperatures regulated to 23°C at the surface and 12°C at the bottom, using an external chiller unit. The cylinders were illuminated by diffused light from directly above using four, 50W halogen bulbs. Light conditions followed a 14 h light : 10 h dark regime centred at 12:00, with a photon flux density of 20.0 μmol m^{-2} s^{-1} at the top of the cylinder and 4.0 μmol m^{-2} s^{-1} at the bottom during midday. During the transitions from day to night or *vice versa*, light intensity was gradually increased or decreased over a 2-h period. Water was pumped into each cylinder using two 24-channel peristaltic pumps via individual 0.38 mm-diameter tygon tubes at a rate of 13.3 ml h^{-1}, creating a 12-h residence time for the water in each cylinder. Given this rate of water flow, the supply rate of resources was approximately 20 times greater than the expected maximum clearance rate of the *Daphnia* (0.6 ml h^{-1} $individual^{-1}$; Lurling 2001), and therefore any effects of *Daphnia* grazing of food were negligible.

In both experiments, we measured the vertical position of *Daphnia* by recording the depth interval occupied. Cylinders were demarcated into 10 intervals total, with two 5-cm intervals at the top, two 5-cm intervals at the bottom, and six 10-cm intervals in the middle. We used mean depth (cm) and the percentage of individuals in the upper and lower 5-cm extremes of the cylinder as measures the vertical position of *Daphnia.* "Depth" was defined as the midpoint of the depth interval in which *Daphnia* were observed.

Daphnia mendotae were collected from Lake Michigan on 12 July 2004 using a zooplankton net with a closed bucket towed vertically through the entire water column. Collections occurred approximately 8 km offshore of Muskegon, Michigan, an area inhabited by *Bythotrephes* (K. L. Pangle, personal observation). The *Daphnia* were then maintained in 4-L vessels in aged Lake Michigan water at 20°C with a 14 h light : 10 h dark light regime. They were fed *Nanochloropsis limnetica* (Hibberd) (SAG 18.99, University of Gottingen, Sag, Germany) at approximately 6 mg C L^{-1}. The *Bythotrephes* used in the experiments were collected in a similar fashion at the same location on 6 August and 7 September 2004, and maintained individually in 50-ml glass containers at the same temperature and light conditions as *Daphnia* and were fed 5 *Daphnia* d^{-1}.

Experiment 1 was conducted from 9 to 13 August 2004. During the experiment, *Daphnia* were kept in either a control water treatment or in a *Bythotrephes* water treatment. Control water was lake water passed through a 0.45-μm filter and aged at room temperature over a 14-d period, a sufficient duration for breakdown of pre-existing kairomones (Loose et al. 1993). To create *Bythotrephes* water (density, 5 *Bythotrephes* L^{-1}), individual *Bythotrephes* were incubated in control water in separate 200-ml containers for a 24-h period. Fresh *Bythotrephes* water was created on seven separate occasions over the course of the experiment, so it could be replaced every 12 hours. *Bythotrephes* were not fed during the incubation period. The control water used in the experiment was maintained under similar condition with no *Bythotrephes* added. Two hours prior to the experiment, *Bythotrephes* were removed from each container, and *Bythotrephes* water and control water passed through a 64-μm filter to remove any debris. For food, *Nanochloropsis* was added to all experimental water (6 mg L^{-1}). Some of the experimental water was used to fill respective cylinders, while the remainder was transferred to reservoirs that supplied the peristaltic pump system. Treatments were assigned to cylinders using a randomized block design; each of the two treatments was represented in 10 spatial blocks, with each consecutive two cylinders representing a block (20 cylinders aligned side by side in total).

Daphnia used in the experiment were neonates, born four to five days beforehand. This ensured that the organisms were initially of uniform size and developmental state, and the young age reduced the chance of *Daphnia* producing offspring during the experiment. One *Daphnia* was transferred into each cylinder and allowed to acclimate to experimental conditions for 1 h before observations began. An additional 20 *Daphnia* were picked haphazardly and measured to estimate the initial size.

The experiment started at noon and continued for four days. The vertical position of each *Daphnia* was determined every 12 hours (nine observations in total), coinciding with noon and midnight. At the end of the experiment, the *Daphnia* were removed from each cylinder and preserved in a sugar-formalin solution. Standard body length of each *Daphnia* was later measured under 40x magnification using a drawing tube and digitizer (Roff and Hopcroft 1986). Standard body length was converted to dry weight using a standard equation (Dorazio et al. 1987) to determine the absolute weight gain over the duration of the experiment. In addition, specific growth rate (*SGR*) in mass was calculated as:

$$(1.1)\quad SGR = \frac{\ln(W_f) - \ln(W_i)}{d}$$

where W_f is final dry weight (µg), W_i is initial dry weight (µg), and d is the duration of the experiment (days).

Experiment 2 was conducted on 8 September 2004. *Daphnia* were kept in one of six water treatments including: control water; three concentrations of laboratory prepared *Bythotrephes* water, low, medium, and high; lake water not inhabited by *Bythotrephes*; and lake water inhabited by *Bythotrephes*. This design allowed us both to compare the concentrations of kairomones in Lake Michigan with those created in the laboratory, and also to evaluate the effect of predator density on vertical migration. Lake water was collected from depths of the water column where *Bythotrephes* is known to be most and least abundant (K. L. Pangle, unpublished). Specifically, 1000 L of lake water was pumped from 1-m and 20-m depths where *Bythotrephes* was absent (no *Bythotrephes* were found) and present (approximately 0.010 *Bythotrephes* L^{-1}), respectively, at 16:00

on 7 September 2004 at the same site where experimental *Daphnia* and *Bythotrephes* were collected. At the time of sampling, the Lake Michigan water column was stratified, with a thermocline at approximately 20-m. During the period between water collection and the start of the experiment, lake water was maintained in the dark at 4°C to reduce kairomone breakdown. The control water and water prepared in the laboratory with a high density of *Bythotrephes* (5 L^{-1}) was made in a similar fashion as Experiment 1. Laboratory prepared water with low and medium *Bythotrephes* density (0.05 and 0.5 L^{-1}, respectively) was made through serial dilutions of the "high density" prepared water. For food, *Nanochloropsis* (6 mg L^{-1}) was added to all experimental water. In contrast to Experiment 1, six replicate cylinders were designated to each treatment, and each cylinder received six *D. mendotae*. Treatments were assigned to cylinders using a randomized block design; each of the six treatments was represented in six spatial blocks, with each consecutive six cylinders representing a block (36 cylinders aligned side by side in total). Five observations were taken from 10:00 to 14:00 in 1-h intervals. All other experimental conditions were as described in Experiment 1.

In Experiment 1, a repeated-measures analysis of variance (ANOVA) was used to evaluate the effect of *Bythotrephes* kairomone on *Daphnia* vertical position during the day and night over the duration of the experiment. In addition, the secondary effects of *Bythotrephes* kairomone on standard body length and specific growth rate of *Daphnia* were evaluated using a blocked one-way ANOVA. In Experiment 2, the behavioral responses were averaged over all *Daphnia* within each cylinder over the duration of the experiment. The behavioral response of *Daphnia* to each treatment was analyzed using a blocked one-way ANOVA. When significant differences among treatments were detected, a Tukey pair-wise comparison was used to separate the means. All percentage data were arc-sin transformed prior to analysis (Zar 1999).

RESULTS

Daphnia responded to *Bythotrephes* kairomones by migrating downwards into cooler water. In Experiment 1, *Daphnia* remained high in the experimental columns by both day and night in the absence of *Bythotrephes* kairomones but, when in the *Bythotrephes* water, the *Daphnia* were significantly deeper ($F_{1,157} = 91.06$; $p < 0.01$), particularly during the day (significant interaction between kairomones and photoperiod [$F_{1,157} = 16.93$; $p < 0.01$]). Thus, in the presence of *Bythotrephes*, *Daphnia* displayed a diel vertical migration, but not in the predator's absence (Figure 1.1). The percentage of individuals in the upper 5-cm section of the cylinder was also significantly lower for *Daphnia* in the *Bythotrephes* water than for those in the control water ($F_{1,157} = 37.50$, $p < 0.01$), with no significant difference between day and night ($F_{1,157} = 1.97$, $p = 0.16$). Further, the percentage of individuals in the lowest 5-cm section of the cylinder was significantly greater for the *Daphnia* in the *Bythotrephes* water than for those in the control water during the day, but not at night, leading to a significant interaction ($F_{1,157} = 5.20$, $p = 0.02$).

Bythotrephes kairomones also affected *Daphnia* growth. Over the duration of the experiment, the mean weight gained by *Daphnia* in the *Bythotrephes* water (1.2 ± 0.2 μg) was less than one half that in the control water (2.7 ± 0.2 μg, $F_{1,18}= 22.34$; $p < 0.01$). *Daphnia* mean specific growth rate in *Bythotrephes* water, 29.5 ± 3.3 % d^{-1}, was 36 % lower than in the control water, 45.7 ± 1.8 % d^{-1} ($F_{1,18}= 13.02$; $p < 0.01$). In Experiment

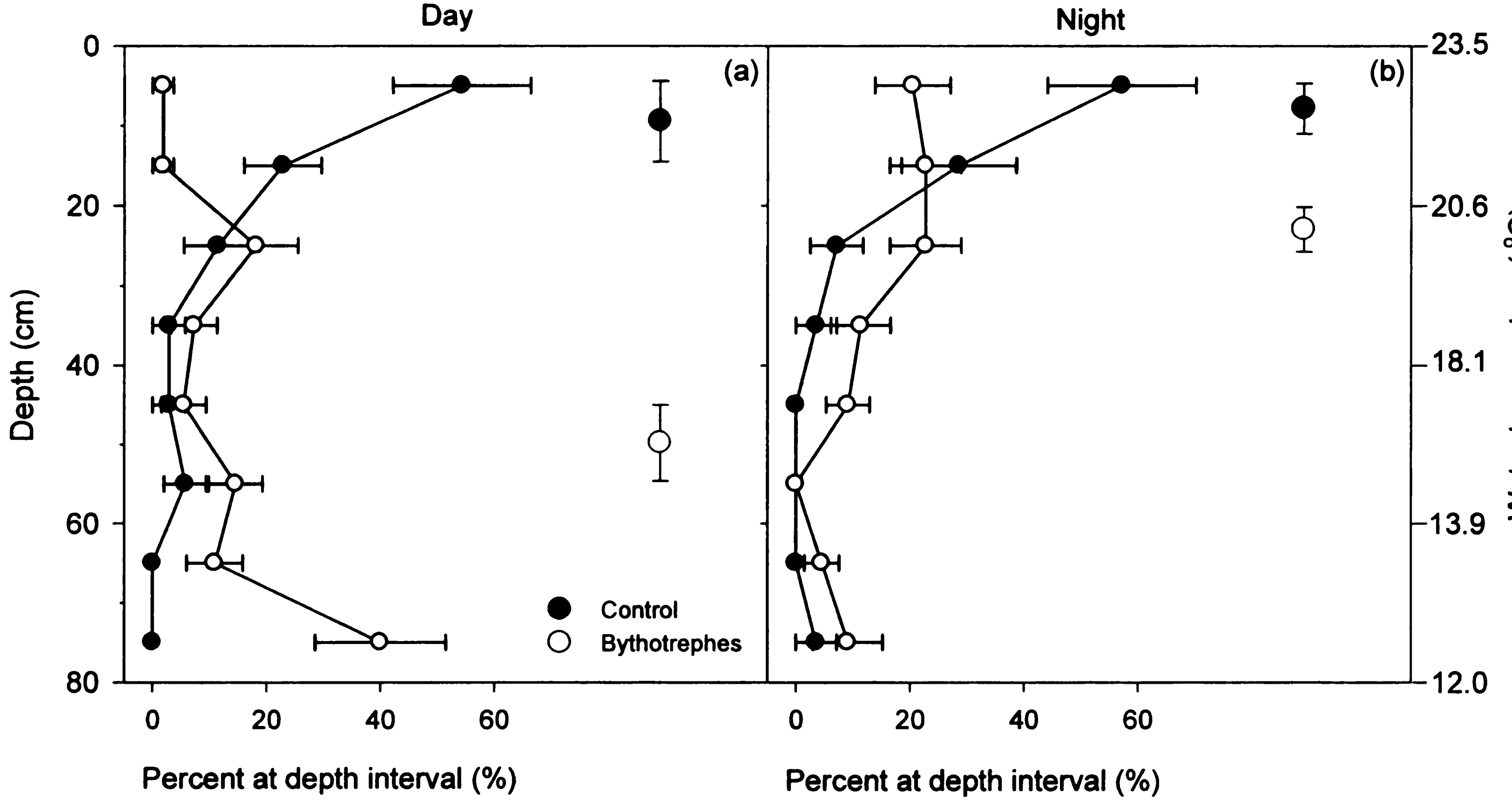

Figure 1.1. Results of Experiment 1. Day (a) and night (b) vertical position, plotted as a function of depth (left hand axis) and temperature (right hand axis), of *D. mendotae* exposed to aged lake water without (solid circles [•]) and with (open circles[○]) *Bythotrephes* kairomone. The left-hand frequency distributions represent the mean percentage (± SE bars) of *Daphnia* at each depth interval (points have been positioned on the y-axis at the midpoint of their respective depth interval). Mean percentages for the top 2 5-cm intervals have been combined, as have those for the bottom 2 5-cm intervals. The right-hand points represent the mean depth (± SE bars).

2, *D. mendotae* responded similarly to a gradient of *Bythotrephes* kairomone concentration in both water collected directly from the lake and prepared in the laboratory. Mean depth of *Daphnia* differed significantly among treatments ($F_{3,27}$ = 45.32; $p < 0.01$), so pair-wise comparisons were made between treatments (denoted significant below if p was less than 0.05). Relative to the control, mean depth was not significantly different for *Daphnia* in lake water not inhabited by *Bythotrephes*, but was significantly deeper for *Daphnia* in lake water inhabited by *Bythotrephes* (Figure 1.2a). Likewise, the vertical position of *Daphnia* was significantly deeper as *Bythotrephes* kairomone concentration increased in laboratory-prepared treatments. The behavior of *Daphnia* in lake water not inhabited by *Bythotrephes* closely resembled those in control water, whereas the behavior of *Daphnia* in lake water inhabited by *Bythotrephes* was similar to that in water with *Bythotrephes* kairomones that had been prepared in the laboratory (Figure 1.2a). Significant differences were also found among treatment in the percentage of individuals in the extreme sections of the cylinder (Figures 1.2b & c). Pair-wise comparisons between treatments indicated that *Daphnia* in lake water not inhabited by *Bythotrephes* and in control water were found more frequently in the upper 5-cm section than *Daphnia* in water from *Bythotrephes* kairomone treatments ($F_{3,27}$ = 12.50; p < 0.01). Further, a significantly greater percentage of *Daphnia* were observed in the lower 5-cm extreme of the cylinder in water from *Bythotrephes* kairomone treatments than those in lake water not inhabited by *Bythotrephes* and control water ($F_{3,27}$ = 11.32; p < 0.01).

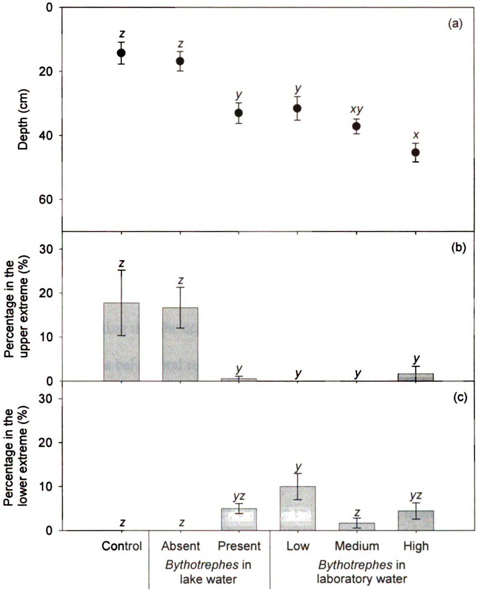

Figure 1.2. Mean depth (a) and the percentage of *D. mendotae* in the upper and lower 5-cm extremes (b and c, respectively) in Experiment 2. Treatments included: control water; lake water not inhabited by *Bythotrephes*; lake water inhabited by *Bythotrephes* (approximately 0.010 *Bythotrephes* L^{-1}); low *Bythotrephes*-density laboratory-prepared water (0.05 *Bythotrephes* L^{-1}); medium *Bythotrephes*-density laboratory-prepared water (0.5 *Bythotrephes* L^{-1}); and high *Bythotrephes*-density laboratory-prepared water (five *Bythotrephes* L^{-1}). Values reported are treatment means (± SE). Means with different lowercase letters were significantly different as determined by ANOVA and Tukey's HSD tests ($p < 0.05$).

DISCUSSION

Our results support the hypothesis that the presence of *Bythotrephes* induces a behavioral response by *Daphnia*. In both laboratory experiments, *Daphnia* exposed to *Bythotrephes* kairomones during the day were found in lower, cooler regions of the experimental columns, while *Daphnia* exposed to water with no kairomones inhabited upper, warmer regions. The difference between treatments lessened in magnitude when light intensity decreased, as seen in Experiment 1, in which *Daphnia* exposed to *Bythotrephes* kairomones migrated upward during the night, while the vertical distribution of *Daphnia* in the control treatment remained unchanged. Experiment 2 also showed that *Daphnia* responded in similar ways to lake water inhabited by *Bythotrephes*, but not without, suggesting that the concentration of kairomones in the field is sufficient concentrations to illicit a behavioral response by *Daphnia*.

The alternating day-night movement of *Daphnia* observed in our study (i.e., diel vertical migration), normally associated with a response to vertebrate planktivores (Stich and Lampert 1981; Gliwicz 1986; Loose and Dawidowicz 1994; De Meester et al. 1998), could optimize the fitness of *Daphnia* when exposed to predation risk from *Bythotrephes*. *Bythotrephes*, unlike many aquatic invertebrate planktivores (Riessen et al. 1988; Roche 1990), uses visual cues to detect prey and may be five times more effective as a predator in the photic zone of the water column than in the aphotic zone (Muirhead and Sprules 2003). Subsequently, inhabiting deeper, darker regions of the water column during the day would greatly reduce predation risk for *Daphnia*. At night, *Daphnia* can increase growth and developmental rates by migrating upwards into warmer near-surface regions when the risk from *Bythotrephes* is lower.

Our results are consistent with changes in *Daphnia* vertical distribution observed in pelagic systems invaded by *Bythotrephes*. For example, in Lake Michigan, a downward shift of *D. mendotae* in the water column corresponded with the invasion of *Bythotrephes* (Lehman and Cáceres 1993), and there is a strong positive relationship between the percentage of *D. mendotae* in the hypolimnion and *Bythotrephes* abundance that occurs seasonally in Lake Michigan (K. L. Pangle, unpublished). In Harp Lake, Ontario, *D. mendotae* maintained a deeper vertical distribution than that of *Bythotrephes* during the day, but overlapped with the predator at night (Dumitru et al. 2001; Muirhead and Sprules 2003). In each case, the vertical migration induced by *Bythotrephes* could be responsible for the vertical distribution observed in the field. Note, however, that there are a number of possible alternative mechanisms for the observed field patterns (listed in the Introduction), and therefore this laboratory study makes clear the potential contribution of the behavioral response.

We predicted that predator-induced diel vertical migration would be associated with a cost, as is general to anti-predator tactics (reviewed in Harvell 1990; Lima 1998). In Experiment 1, the vertical migration of *Daphnia* to *Bythotrephes* kairomone led to a 36 % reduction in somatic growth. This reduction could have been caused by several mechanisms including inhabiting cooler water (Loose and Dawidowicz 1994) and allocating more energy to early reproduction and morphological defenses relative to somatic growth (Tollrian 1995).We evaluated how these possibilities contributed to the non-consumptive effects on *Daphnia* in Experiment 1.We calculated a predicted somatic growth rate (*SGR*) for each individual (given their thermal experience during the experiment) using the equation:

(1.2) $SGR = -0.0009\,T^2 + 0.0476\,T - 0.1882$

where T is water temperature (°C). This equation was derived by fitting a nonlinear model to published data (Hall 1964) that reported *D. mendotae* growth rate under saturated food resource conditions over a wide range of temperatures (11 to 25°C). The predicted reduction in *Daphnia* growth in the *Bythotrephes* treatment was close to the actual reduction (Figure 1.3). This suggests that migratory behavior into cooler water, and not modifications to morphology and life history, were principally responsible for the non-consumptive effect on growth rate.

For *Daphnia* species, somatic growth can be used as an approximation of fitness, as it is known to correlate strongly with population growth rate (Lampert and Trubetskova 1996); thus, our results show a means by which *Bythotrephes* affects prey populations other than by direct consumption (i.e., non-consumptive effect). These so-called non-consumptive effects are predicted theoretically to play a critical role in predator-prey interactions (Abrams 1982; Ives and Dobson 1987; Abrams 1993). Indeed, using simple models, Peacor and Werner (2004) showed that predator-induced reductions in growth rates on the order observed here (36 %) are large enough to contribute substantially to the net effect of the predator on prey fitness. Empirical studies performed in mesocosms have also shown that the magnitude of non-consumptive effects on prey population growth rates can be as large as or larger than that of lethal effects (Nelson et al. 2004; Boeing et al. 2005). Note that, in addition, such non-consumptive effects may extend indirectly to affect prey food resources and competitors (reviewed in Abrams 1995; Bolker et al. 2003; Werner and Peacor 2003; Schmitz et al. 2004) via trait-mediated indirect interactions, further contributing to the net predator-prey interaction.

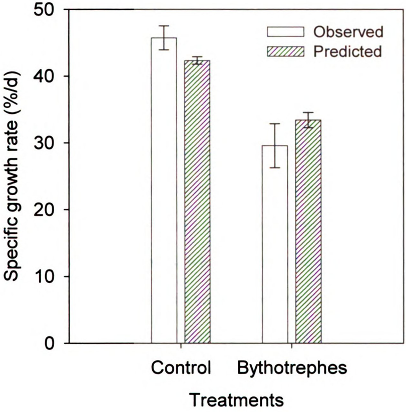

Figure 1.3. Observed (open bars) and predicted (using a growth model, hatched bars) specific growth rate of *D. mendotae* in Experiment 1 exposed to aged lake water without and with *Bythotrephes* kairomone. Values reported are treatment means (± SE).

These results, combined with our study, suggest that the induction of diel vertical migration may be as important to *Daphnia* population dynamics as changes caused by the direct consumption of *Daphnia* by *Bythotrephes*.

In conclusion, this study demonstrated the behavioral response of *D. mendotae* to *Bythotrephes* and a consequent non-consumptive effect on growth. Our findings may be applicable to other systems, as *Bythotrephes* density used in the experiments were not only typical of Lake Michigan (Pothoven et al. 2003), but also of those observed in Lakes Erie and Huron (Barbiero and Tuchman 2004), smaller Canadian inland lakes (Boudreau and Yan 2003), and lakes in the native range of *Bythotrephes* (Manca et al. 2000; Palmer et al. 2001). Moreover, our study emphasizes the complex nature of the impact of invasive species as well as provides an avenue for research into better understanding Lake Michigan food web dynamics. What is the relative magnitude of non-consumptive effects compared to lethal effects and how are they transmitted through the food web via trait-mediated indirect interactions? Further, how do non-consumptive effects occur under such short-term evolutionary periods? Addressing these questions could shed light into both the ecology and evolution of invasive species.

CHAPTER 2

LACK OF NAÏVETÉ IN LAKE MICHIGAN ZOOPLANKTON PREY TO RISK POSED BY INVASIVE PREDATORS

ABSTRACT

Prey have evolved traits that enable them to perceive and respond adaptively to predation risk. However, prey may be naïve towards novel risk posed by invasive predators, and prey naïveté could profoundly influence the nature of invasive-predator-prey interactions. Here, using a series of laboratory experiments, we tested the naïveté of three Lake Michigan zooplankton species by evaluating their behavioral response (i.e., vertical migration) to the presence of two invasive invertebrate predators, *Bythotrephes longimanus* and *Cercopagis pengoi. Bythotrephes* can consume all three zooplankton species used in the study, but the smaller *Cercopagis* is hindered by the large-sized prey, and subsequently posed a real risk to only the smallest one of the zooplankton species. We also evaluated the behavioral response of zooplankton in the presence of four native predator species, *Perca flavescens*, *Leptodora kindtii*, *Polyphemus pediculus*, and *Mysis relicta*, which vary in their phylogenetic and functional similarity to the invasive predators. The results indicated that prey were able to distinguish between the presence and absence of *Bythotrephes* and *Cercopagis* and responded behaviorally by migrating downward only when it was adaptive. Thus, zooplankton appeared not be naïve towards the risk posed by these invasive predators. Downward migration was also induced by a functionally similar native predator, suggesting that this behavioral trait is an exadaption that is sufficiently general to be co-opted to avoid invasive predators. Although aquatic

systems are thought to be prone to naïveté, the results suggest that naïveté does not contribute to current impact of *Bythotrephes* and *Cercopagis* in Lake Michigan.

INTRODUCTION

Prey can evolve traits that reduce their risk of being consumed by predators. However, prey may lack appropriate traits to reduce novel risk posed by invasive predators due to lack of co-evolution, a condition referred to as prey naïveté. Naïveté may leave prey extraordinarily vulnerable to the invader, and has been linked to enhanced growth of invasive predator populations, extirpation of prey populations, and an overall destabilization of invaded systems (Fritts and Rodda 1998; Blackburn et al. 2004; Cox and Lima 2006; Salo et al. 2007). However, lack of co-evolution does not guarantee an easy meal for invasive predators. Prey may have evolved antipredator traits through experience with native predator (exadaptations) that are sufficiently general to be co-opted to thwart invasive predators (Wilder and Rypstra 2004). Due to the potentially strong selection pressures posed by invasive predators, native prey may also adapt traits or learn strategies that minimize novel risk at a rate that outpaces extinction (Griffin 2004; Strauss et al. 2006).

Whether or not prey naïveté occurs may be dependent on the characteristics of the invaded ecosystem, and variation in naïveté may provide insights into why some ecosystem types tend to be more impacted by invasive predators than others. A primary factor driving differences among ecosystem types is insularity. In insular ecosystems, prey tend to adapt defenses to combat local predator archetypes but lack evolutionary experience and thus possibly appropriate traits to respond to predator archetypes outside of their system. Classic and extreme examples of such insular ecosystems are oceanic island ecosystems that support prey populations with few or no native predators. The lack of evolutionary experience with predators can render island prey highly susceptible to invaders (Case and Bolger 1991; Fritts and Rodda 1998), and may be an underlying reason for the greater impact invasive predators have on native prey of islands relative to mainlands (Simberloff 1995; Blackburn et al. 2004; Salo et al. 2007). Like islands, lake ecosystems may isolate prey populations due to surrounding land barriers that hinder dispersal among systems, and, like islands, the insularity of lakes may foster naïveté in lake prey species to invasive predators (Cox and Lima 2006). Although prey naïveté in aquatic systems is not yet well understood, the notion that lake prey are generally naïve could provide powerful insights into the nature of the impact invasive predators have in lakes, as well as explain broader patterns among invaded ecosystems. For example, Cox and Lima (2006) recently proposed that differential naïveté is an underlying cause for the greater impact of invasive species observed in aquatic systems relative to terrestrial systems (Vermeij 1991; Ricciardi and Rasmussen 1999; Bruno et al. 2005).

In our study, we evaluated the naïveté of Lake Michigan zooplankton species towards invasive planktivores. Previous laboratory and field studies indicate that the invasive predatory cladoceran, *Bythotrephes longimanus*, induce downward migration in one Lake Michigan zooplankton species, *Daphnia mendotae* (Lehman and Cáceres 1993; Chapter 1; Chapter 5). In this case, vertical migration is a plastic behavioral trait that can be used by *Daphnia mendotae* to reduce spatial overlap with the shallow-dwelling *Bythotrephes* during the daylight hours during which *Bythotrephes* pose the greatest risk. *Bythotrephes* has only been present in Lake Michigan for about twenty years and belongs to a phylogenetic family (Cercopagidae) previously unrepresented in North America (Dodson and Frey 2001), a characteristic generally used to designate novel predator archetypes (Cox and Lima 2006). Induction of vertical migration suggests that *D. mendotae* is not naïve to *Bythotrephes*, a result contrary to the prediction of naïveté in lake prey.

The goals of our study were two-fold. First, we wanted to determine whether the migratory response of *D. mendotae* induced by *Bythotrephes* was a general response induced by native Lake Michigan planktivores, thereby providing a possible explanation for the lack of naïveté in *D. mendotae*. Second, we wanted to expand tests of naïveté to other Lake Michigan zooplankton species and to another shallow-dwelling invasive planktivore, *Cercopagis pengoi*. *Cercopagis* has been present in Lake Michigan for six years and is in the same phylogenetic family as *Bythotrephes*, but the relatively small-sized *Cercopagis* poses a lower risk to some zooplankton than the larger *Bythotrephes*. Understanding the response (or lack of response) *Bythotrephes* evoke in native zooplankton relative to *Cercopagis* and native predators can provide insights into the nature of the impact of *Bythotrephes* and *Cercopagis* in Lake Michigan, as well as potentially alter expectations regarding the generality of naïveté in aquatic systems.

METHODS

We measured the migratory response of Lake Michigan zooplankton species using a series of laboratory experiments. To address the first goal, we compared the response of *Daphnia mendotae* induced by *Bythotrephes* to the responses induced by four native predators to determine if any of these predators also induced downward migration.

We chose a set of native predators that encompassed the primary predator archetypes found in Lake Michigan. They included two predatory cladocerans, *Leptodora kindtii* and *Polyphemus pediculus*, a freshwater shrimp *Mysis relicta* and a juvenile fish *Perca flavescens* (Table 2.1).

The native predators varied in the phylogenetic and functional similarity with *Bythotrephes*, thus providing a means to evaluate if downward migration was general to either phylogeny or functional characteristics of the predator. *Leptodora* and *Polyphemus* are the most similar to *Bythotrephes* phylogenetically, all belonging to the suborder Cladocera (Dodson and Frey 2001). If the lack of naïveté of *Daphnia* towards *Bythotrephes* is linked to phylogenetic relatedness of *Bythotrephes* to native predators, we would expect that *Leptodora* and *Polyphemus* would induce a downward migration in *Daphnia*. However, *Leptodora* and *Polyphemus* are hindered by the relatively large size of *Daphnia* (Herzig and Auer 1990; Packard 2001), a characteristic that makes them functionally different than *Bythotrephes* (Schulz and Yurista 1998). Subsequently, vertical migration may be unnecessary for *D. mendotae* when facing *Leptodora* and *Polyphemus,* or *D. mendotae* may modify other traits that may be more adaptive for this risk than vertical migration. For example, the presence of *Leptodora* is known to induce enlarged helmets in *D. mendotae* (Tanner and Branstrator 2006). In contrast to *Leptodora* and *Polyphemus*, juvenile *Perca* is phylogenetically disparate, but functionally similar, to *Bythotrephes*. Juvenile *Perca* are not hindered by the relatively large size of *Daphnia* (Fulford et al. 2006) and uses visual cues to detect prey (Jansen and Mackay 1992), as does *Bythotrephes* (Muirhead and Sprules 2003). Further, although migratory response of

Table 2.1. Names and characteristics of the native and invasive plantivores used in the experiments.

Scientific names	Origin	Phylum, Class, Order	Size (mg DW)	Habitat use*
Bythotrephes longimanus	invasive	Arthropoda, Branchiopoda, Cladocera	0.3	shallow
Cercopagis pengoi	invasive	Arthropoda, Branchiopoda, Cladocera	0.01	shallow
Perca flavescens	native	Chordata, Actinopterygii, Perciformes	10	shallow
Leptodora kindtii	native	Arthropoda, Branchiopoda, Cladocera	0.02	shallow
Polyphemus pediculus	native	Arthropoda, Branchiopoda, Cladocera	0.01	shallow
Mysis relicta	native	Arthropoda, Malacostraca, Mysidacea	0.5	deep

*Habitat use based on 2-year average of observations at the site in Lake Michigan where zooplankton prey used in the experiments were collected (K. L. Pangle, unpublished data).

D. mendotae, to our knowledge, has never been tested using the presence of juvenile *Perca*, other fish species have induced downward migration in other *Daphnia* species (e.g., Loose and Dawidowicz 1994). If the lack of naïveté of *Daphnia* towards *Bythotrephes* is linked to functional relatedness of *Bythotrephes* to native predators, we would expect that *Perca* would induce a downward migration in *Daphnia*. *Mysis relicta* is both phylogenetically and functionally disparate to *Bythotrephes*, and served as a control in our study. *Mysis* are only related to *Bythotrephes* at the subphylum level, and, unlike all of the other predators in this study, *Mysis* are deep-dwelling, thus downward migration by *Daphnia* in response to *Mysis* presence would actually increase spatial overlap with *Mysis*. If the lack of naïveté of *Daphnia* towards *Bythotrephes* is linked to either functional or phylogenetic relatedness of *Bythotrephes* to native predators, we would expect that *Mysis* would not induce a downward migration in *Daphnia*.

To address our second goal, we tested the naïveté of *Daphnia mendotae* and two other native zooplankton, *Daphnia pulicaria* and *Bosmina longirostris,* to the other invasive predator, *Cercopagis*. Because of its small size, *Cercopagis* only poses a substantial risk to *Bosmina* and not to either *Daphnia* species. Thus, in this case, a response by the *Daphnia* species to *Cercopagis* would be unnecessary and an indication of naïveté. Below we first provide our general experimental methodology and then describe the details of each experiment.

Methodology general to all experiments:

We measured migratory response of zooplankton by maintaining them in vertical columns and observing their behavior in the presence and absence of predators. The columns were clear acrylic, 80-cm tall and 19-mm diameter, and submerged in a transparent, 300-L aquarium. The aquarium acted as a thermally stratified water bath, with water temperatures regulated to 23°C at the surface and 12°C at the bottom, using an external chiller unit. The cylinders were illuminated by diffused light from directly above using four, 50 W halogen bulbs. The lighting created a light gradient in the columns, in which photon flux density was 20.0 μmol m^{-2} s^{-1} at the top and 4.0 μmol m^{-2} s^{-1} at the bottom. We mimicked the presence of a predator in the columns by using predator kairomones. Kairomones are waterborne chemicals that are released by predators (Lass and Spaak 2003). Zooplankton can detect kairomones and use them to perceive and differentiate different types of risk (Dodson 1988; Laforsch and Tollrian 2004). In our study, zooplankton were exposed to kairomones by filling the columns with water that had been incubated with the predators over the 24 hrs prior to the start of the experiments.

Experiments lasted 4 to 4.5 hours and zooplankton behavior during this period was quantified by recording their location in the columns. Columns were demarcated into 10 intervals, with two 5-cm intervals at the top, two 5-cm intervals at the bottom, and six 10-cm intervals in the middle. We used the average depth (cm) of individuals within each column averaged over all observations as measures of the vertical position of zooplankton. 'Depth' was defined as the midpoint of the depth interval in which individuals were observed. Because vertical movement of zooplankton was constrained by the water's surface and the bottom of the columns, zooplankton evading predation risk may collect at the extremes of the columns. Thus we also used the percentage of individuals in the upper and lower 5-cm extremes of each column as a second measure of the vertical position of zooplankton, which was calculated based on all individuals within each column and averaged over all observation periods.

All zooplankton prey species were collected from Lake Michigan using a 64-µm-mesh zooplankton net with a closed bucket towed vertically through the entire water column. Collections occurred approximately eight km offshore of Muskegon, Michigan. Prior to the experiments, zooplankton were maintained in 4-L vessels in aged Lake Michigan water at 20°C with a 14 h light : 10 h dark light regime. They were fed *Nanochloropsis limnetica* (SAG 18.99, University of Gottingen, Sag, Germany) at approximately 6 mg C L^{-1}. Five of the six predators (all but juvenile *Perca*) were collected in a similar fashion at multiple sites offshore of Muskegon, Michigan, and immediately used for production of kairomone water. Specific collection sites for the predators varied between experiments, so we provide details of collection for each experiment separately. The sixth type of predator, juvenile *Perca,* was collected by hook-and-line from nearshore areas of Lake Michigan and maintained in a 50-l glass aquaria, and fed a mixture of zooplankton collected from Lake Michigan prior to their use for production of kairomone water.

Water used to fill the experimental columns was lake water passed through a 0.45-lm filter and aged at room temperature over a 14-day period, a sufficient duration for breakdown of pre-existing kairomones (Loose et al. 1993). Predators were not fed while they were incubated in the experimental water, so that kairomones extruded into water and used for the experiments were associated with prey they had consumed in the lake prior to collection, or in the case of *Perca*, prey they had consumed from the mixture of zooplankton collected from Lake Michigan. Some water received no planktivores and acted as a control. All experimental water received *Nanochloropsis* algae (6 mg C L^{-1}) to provide zooplankton with a saturated level of food resource during the experiment.

Methodology specific to each experiment:

In the first experiment, *Daphnia mendotae* was exposed to a control treatment (no kairomones) and five different kairomone treatments created using *Bythotrephes*, *Cercopagis*, *Leptodora*, *Polyphemus*, and *Perca flavescens*. Invertebrate predators were collected in two different locations in Lake Michigan. *Bythotrephes* and *Polyphemus* were collected from the same site as *D. mendotae*. During the collection event, we did observe *Cercopagis* and *Leptodora* in the samples, but in very low numbers. Subsequently, *Cercopagis* and *Leptodora* used in the experiment were collected from a nearshore site where *D. mendotae* was still present. Because predator size varied by orders-of-magnitude (Table 2.1),we used different densities (number L^{-1}) of each planktivore for the production of kairomone water so that their biomass (mg L^{-1}) was approximately equal. Experimental planktivore densities were 0.01 individuals L^{-1} for *Perca*, 1 individual L^{-1} for *Bythotrephes*, and 10 individuals L^{-1} for *Cercopagis*, *Leptodora* and *Polyphemus*. Although the relationship between body mass and kairomone production is unknown, here we assumed direct proportionality as a first approximation. To create kairomone water for invertebrate planktivores, ten individuals of each planktivore species were transferred into separate 25-ml vials filled with aged lake water and allowed to incubate at 20°C. To create *Perca* kairomone water, four fish were transferred into a 4-L beaker filled with aged lake water and the water was incubated under similar conditions. Afterwards, kairomone waters were passed through a 64-micron filter and then diluted with aged lake water to achieve experimental kairomone concentrations. For the experiment, six replicate cylinders were assigned to each treatment (36 cylinders total), and three *D. mendotae* (mean standard length, 1 mm) were transferred into each cylinder. Vertical position of the zooplankton was observed hourly over 4-h period (five observations total).

In Experiment 2, the same prey species, *Daphnia mendotae,* was exposed to a control treatment and two different kairomone treatments created using *Bythotrephes* and *Mysis.* Both predators were collected from the same site as *D. mendotae*. Experimental planktivore densities were both five individuals L^{-1}. To produce *Mysis* kairomone water, 10 *Mysis* were transferred into a 2-L beaker filled with aged lake water and incubated at 6°C. Production of *Bythotrephes* kairomone water was the same as in Experiment 1. For the experiment, 12 replicate cylinders were assigned to each treatment (36 cylinders total), and three *D. mendotae* (mean standard length, 1 mm) were transferred into each cylinder. Vertical position of the zooplankton was observed in 30-min intervals over 4.5-h period (10 observations total).

In the Experiment 3, *Bosmina longirostris* and *Daphnia pulicaria* were exposed to a control treatment and two different kairomone treatments created using *Cercopagis* and *Perca.* Production of kairomone waters and the planktivore densities was the same as in Experiment 1. Six replicate cylinders were designated to each treatment (36 tubes total) and three individuals were transferred into each cylinder. Vertical position was recorded every 1 hr over a 4-h period (five observations total).

Statistical Analyses

Prior to analyses of treatment effects, we tested assumptions of analysis-of-variance (ANOVA) for our response variables and evaluated potential confounding factors that occurred during the experiments. Assumptions of normality and homogeneity of variance were tested using the Wilks-Shapiro Test and the Levene Test, respectively. One variable, mean depth, met assumptions in all experiments, while the other two variables, the percentage of individuals in the upper and lower column extremes, violated assumptions in all experiments, even after arc-sine transformation.

Prior to analyses of treatment effects, we also evaluated potential confounding factors that occurred during the experiments. One factor was the change in the number of zooplankton in some columns due to birth of offspring or death. In addition, some zooplankton adhered to the surface or to air bubbles on the side of the cylinders and were not included in observations. We tested whether the final number of individuals in a column affected our behavioral variables in each experiment using ordinary linear regression, and found that it was never a significant factor (all ps > 0.2). Another potentially confounding factor occurred in Experiment 3, in which the zooplankter, *Bosmina longirostris*, was difficult to see in the columns due to its small size. For two columns, one replicate in the *Cercopagis* treatment and one replicate in the *Perca* treatment, all individuals could not be accounted for so these replicates were removed from the analysis. In addition, for some columns, not all individuals could be accounted for during a particular observation, so these observation periods were not included in the average of the behavioral variables. We tested whether the number of observations for a given column during the experiment affected our behavioral variables using ordinary linear regression, and found that it was never a significant factor ($p > 0.1$).

Treatment effects were analyzed using ANOVA for mean depth and nonparametric methods for the percentage of individuals at extremes. For Experiments 1 and 2,we tested for significant differences among treatments using one-way ANOVAs and Kruskal-Wallis tests (Zar 1999). When significant differences among treatments were detected, we used parametric and nonparametric Dunnett's tests to identify the predator-kairomone treatments that significantly differed from the control treatment (Zar 1999). For Experiment 3,we used a full factorial ANOVA and Kruskal-Wallis tests to evaluate the effects of kairomones, prey species, and their interaction. We also evaluated the simple main effects of species within each kairomone treatment (Kuehl 2000).

RESULTS

In Experiment 1, the migratory response of *Daphnia mendotae* varied among the different predator kairomone treatments. Mean depth of *D. mendotae* in *Bythotrephes* and *Perca* kairomone treatment columns was significantly deeper than those in the control treatment and in kairomone treatments of *Cercopagis*, *Leptodora*, and *Polyphemus* ($F_{5,30} = 7.66, p < 0.01$; Figure 2.1a). The latter kairomone treatments did not significantly differ in mean depth from the control treatment. The percentage of *D. mendotae* at the upper extreme of the column in *Bythotrephes* and *Perca* kairomone treatments was also

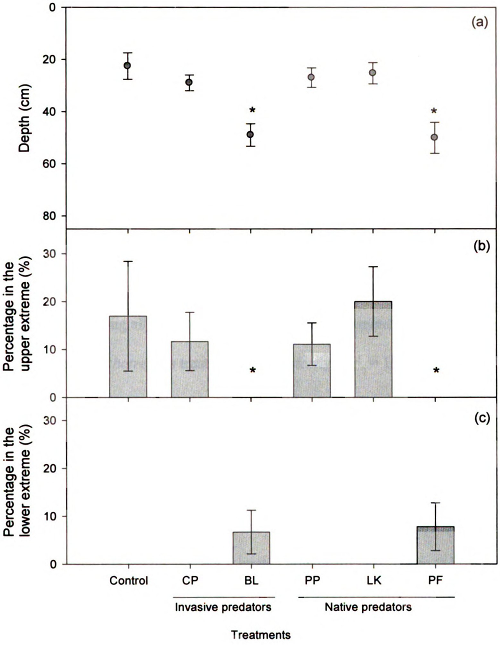

Figure 2.1. Mean depth (panel a) and the percentage of *D. mendotae* in the upper and lower 5-cm extremes (panels b and c, respectively) in Experiment 1. Values reported are treatment means (± SE). Treatments included: control water or water with kairomones from the invasive predators *Cercopagis* (CP) or *Bythotrephes* (BL) or from the native predators, *Polyphemus* (PP), *Leptodora* (LK), or *Perca* (PF). Asterisks indicate predator treatments that were significantly different ($p < 0.05$) from the control.

significantly lower than that for the control, while other treatments did not differ from the control ($\chi^2_5 = 13.3, p = 0.02$; Figure 2.1b). The percentage of individuals at the lower extreme of the column did not significantly vary among treatments ($\chi^2_5 = 9.06, p = 0.11$; Figure 2.1c)

In Experiment 2, *D. mendotae* responded to both kairomone treatments, but in opposite directions. Mean depth varied significantly between all treatments, with the shallowest value for the *Mysis* treatment, the middle value for the control treatment, and the deepest value for the *Bythotrephes* treatments ($F_{2,33} = 23.26, p < 0.01$; Figure 2.2a). The percentage of individuals at the upper extreme of the column also varied significantly among all treatments, with 12 % and no *Daphnia* found near the surface in the *Mysis* and *Bythotrephes* treatments, respectively ($\chi^2_2 = 18.54, p < 0.01$; Figure 2.2b). The percentage of individuals at the lower extreme of the column was significantly greater in the *Bythotrephes* treatment than in *Mysis* treatment, but neither differed significantly from the control ($\chi^2_2 = 6.14, p = 0.05$; Figure 2.2c).

In Experiment 3, *Daphnia pulicaria* showed no response to kairomones of the invasive predator, *Cercopagis*, but migrated downward in response to kairomones of the native predator, *Perca*. Mean depth of *D. pulicaria* was significantly deeper for the *Perca* treatment than the control and did not differ between *Cercopagis* and control treatments ($F_{2,27} = 6.52, p = 0.01$; Figure 2.3b). The percentage of *D. pulicaria* at the upper and lower extremes of the column did not vary significantly among treatments (all *ps* > 0.05). In contrast to *D. pulicaria*, the smaller prey species, *Bosmina longirostris*, migrated downward in response to kairomones of both the invasive and native predator. Mean

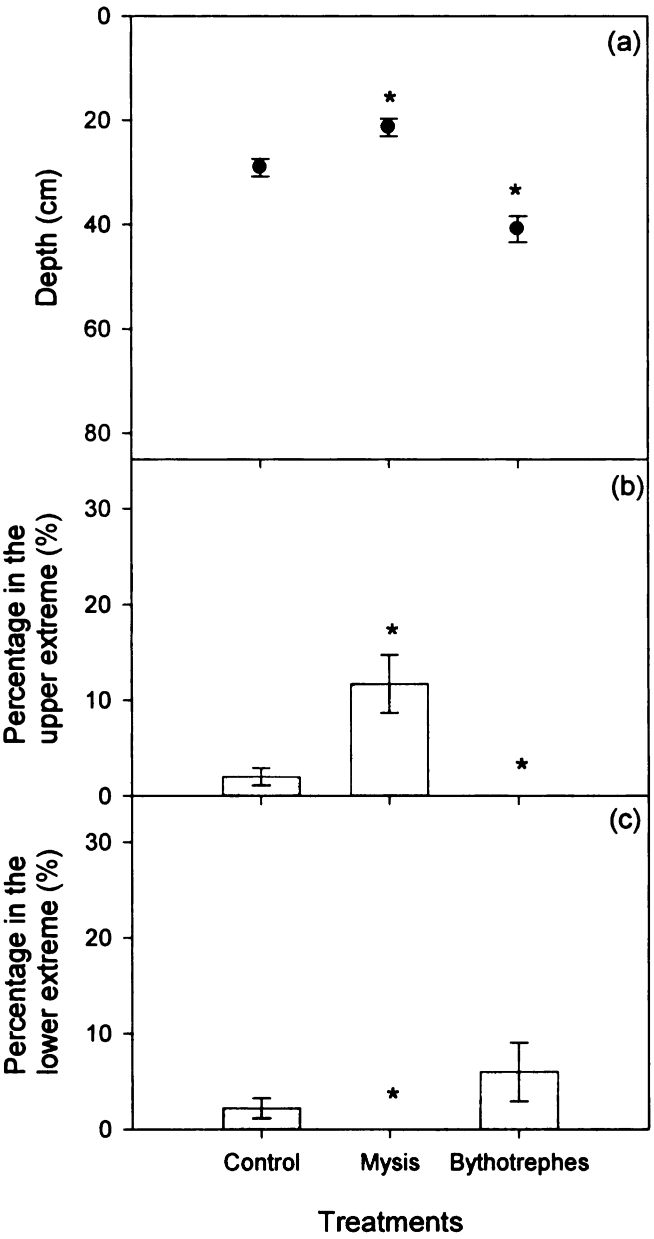

Figure 2.2. Mean depth (panel a) and the percentage of *D. mendotae* in the upper and lower 5-cm extremes (panels b and c, respectively) in Experiment 2. Values reported are treatment means (± SE). Treatments included: control water or water with kairomones from the native, deep-dwelling predator, *Mysis*, or the invasive, shallow-dwelling predator, *Bythotrephes*. Asterisks indicate treatments that were significantly different ($p < 0.05$) from the control.

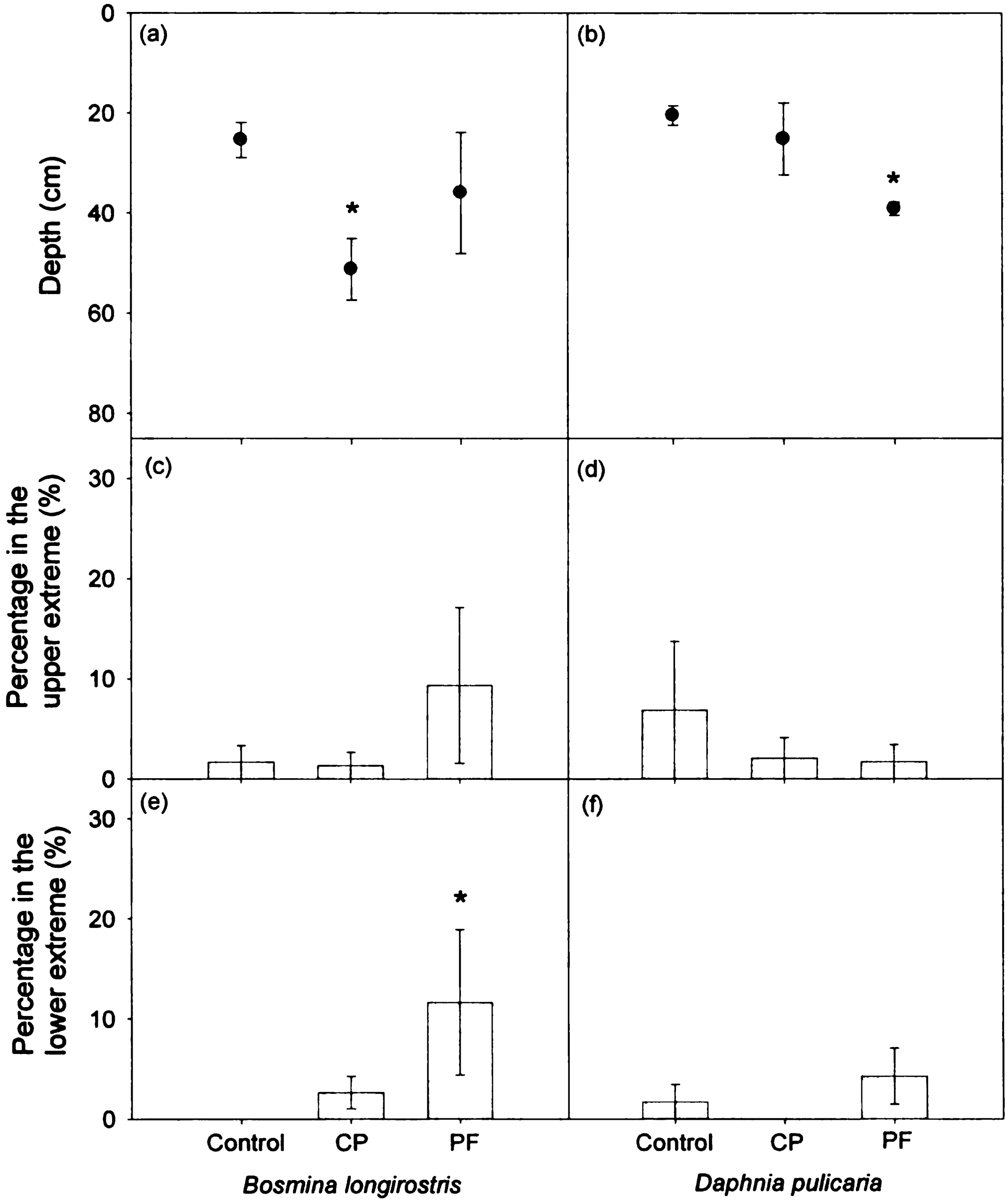

Figure 2.3. Mean depth (panel a, b) and the percentage of individuals in the upper and lower 5-cm extremes (panels c,d and e,f respectively) in Experiment 3. Left panels give results for *Bosmina longirostris* and right panels give results for *Daphnia pulicaria*. Values reported are treatment means (± SE). Treatments included: control water or water with kairomones from the small invasive predator, *Cercopagis* (CP), or the large, native predator, *Perca* (PF). Asterisks indicate treatments that were significantly different ($p <$ 0.05) from the control.

depth of *B. longirostris* was significantly deeper for the *Cercopagis* treatment than the control treatment and did not differ between *Perca* and control treatments ($F_{2,27} = 4.71$, $p = 0.02$; Figure 2.3a). The percentage of *B. longirostris* at lower extremes of the column was significantly greater for the *Perca* treatment than the control and did not differ between *Cercopagis* and control treatments (Figure 2.3a), while the percentage of *B. longirostris* at the upper extremes did not significantly vary among treatments (all *p*s > 0.5).

DISCUSSION

Our results indicate that Lake Michigan zooplankton generally lack naïveté towards invasive predators. As shown for *Bythotrephes* in this study and in a previous study (Pangle and Peacor 2007), three species of zooplankton all responded adaptively to the invasive predator *Cercopagis*, despite having only six years experience with the predator. In the first and third experiments, *Cercopagis* induced downward migration in the relatively vulnerable prey species, *Bosmina*, but not in less vulnerable prey species, *D. mendotae* and *D. pulicaria.* Although this study is the first of our knowledge to experimentally evaluate the response of zooplankton to *Cercopagis*, the differential response to *Cercopagis* corresponds with field observations in Lake Ontario, in which small zooplankton species exhibit deeper distributions and less overlap with *Cercopagis* relative to large zooplankton species (Benoit et al. 2002).

Our results also suggest that migration induced by the invasive predators is a more general trait that is also induced by native predators. In the first experiment, both *Bythotrephes* and the functionally similar, but phylogenetically disparate native predator

Perca induced downward migration in *D. mendotae*. In contrast, *D. mendotae* exhibited no migratory response to the native predators *Leptodora* and *Polyphemus*, which are much more phylogenetically but less functionally similar to *Bythotrephes* relative to *Perca*. Further, *D. mendotae* migrated upwards in response to kairomones of *Mysis*, a predator that is functionally and phylogenetically disparate to *Bythotrephes* relative to the other native predators. Although not predicted *a priori*, upward migration seems an appropriate response to the deep dwelling *Mysis* and is consistent with field observations of zooplankton avoidance of *Mysis* in Lake Michigan (Schulze and Brooks 1987).

The behavioral responses we observed in zooplankton therefore challenge the notion that native prey in aquatic systems are generally naïve to invasive predators. The basis for this notion is that aquatic prey tend to lack evolutionary experience and thus possibly appropriate traits to respond to predators outside of their system. However, characteristics of zooplankton may allow them to perceive and respond adaptively to novel risk. First, zooplankton can assess the level of risk via kairomones, as multiple studies have shown that zooplankton respond more strongly to kairomones of predators that had recently consumed conspecifics, than to predators that were unfed or fed other zooplankton species (Stabell et al. 2003; Laforsch et al. 2006). Thus, consumption of conspecifics by invasive predator may be sufficient to alert zooplankton of their presence. Second, zooplankton tend to use qualitatively-generalized antipredator traits that are adaptive for multiple predators. For example, growing larger helmets and tail spines is adaptive for *Daphnia* facing three functionally similar invertebrate predators (Laforsch and Tollrian 2004). In our study, downward migration is a trait that likely evolved due fish predation, but may have been co-opted for *Cercopagis* and *Bythotrephes*. Although we have focused here on zooplankton, these characteristics, and thus mechanisms that reduce naïveté, are also present in other aquatic prey that use kairomones to perceive risk and have qualitatively-generalized responses to multiple predators (e.g., protozoa [Kuhlmann et al. 1999], rotifers [Stemberger and Gilbert 1987], and amphibians [Relyea 2001]).

However, it remains unclear how zooplankton came to associate *Bythotrephes* and *Cercopagis* with the appropriate predator functional type. For example, why did zooplankton not migrate upwards in response to *Bythotrephes*, as they did in the presence of *Mysis*? One explanation is that downward migration rapidly evolved in response to selection pressures of the invasive predators. The rapid evolution hypothesis is supported by changes observed in prey populations in Lake Michigan following the introduction of invasive predators. The density of *D. mendotae* was extraordinarily low during the year following the introduction of *Bythotrephes*, but then rebounded to pre-invasion densities during subsequent years (Lehman and Cáceres 1993). These population changes may represent a bottleneck in which strong selection occurred for *Daphnia* genotypes that migrated downwards in *Bythotrephes* presence. There is growing evidence that evolutionary processes generally contribute to the ecology of invasions over relatively short time scales (reviewed in Mooney and Cleland 2001; Strauss et al. 2006). Zooplankton have characteristics that are particularly conducive to rapid evolution, such as short generations and cyclo-parthenogenic reproduction, and have been shown to evolve rapidly in response to changes in their environment over periods as short as ten years (Hairston et al. 1999; Cousyn et al. 2001; Kerfoot and Weider 2004). Although we are unable to test this explanation given the methods of our study, future research may be able to do so by hatching resting eggs of zooplankton collected from Lake Michigan that were deposited before and after the introduction of *Bythotrephes* and *Cercopagis* and test whether the response of zooplankton changed over this time period. Such research could not only provide insights on the role rapid evolution plays in the prey naïveté, but also identify a mechanism that leads to the change of interactions between native and invasive species often observed over time (Strayer et al. 2006).

Identifying mechanisms underlying the detrimental impact of invasive species is one of the most important challenges facing biologists today (Mack et al. 2000; Byers et al. 2002; Hochberg and Gotelli 2005). Naïveté is thought to exacerbate this impact, particularly in lakes (Cox and Lima 2006); however, results of this study indicate that some lake species are not naïve, thus changing the interactions predicted between invader and prey. Although migration is expected to reduce direct consumption of zooplankton by *Bythotrephes* and *Cercopagis*, migration may lower birth rate of zooplankton due to inhabiting regions of lower temperature (Chapters 3, 5), referred to as a non-consumptive effect (Abrams 2007). These non-consumptive effects may lead to large reductions in prey population growth rate (Chapter 5), and change how zooplankton interact with competitors and other predators due to the shift in zooplankton habitat use (Chapter 6), a trait-mediated indirect effect (Abrams 2007). Thus, although prey are not naïve, understanding how they are responding to invasive predators may still paramount to understanding the ecology of invaded systems.

CHAPTER 3

TEMPERATURE GRADIENTS, BUT NOT FOOD RESOURCE GRADIENTS, AFFECT GROWTH RATE OF *DAPHNIA MENDOTAE* IN LAKE MICHIGAN

ABSTRACT

We evaluated the effects of water temperature and food resource gradients on the growth rate of zooplankton undergoing vertical migration in Lake Michigan. In two laboratory experiments, juvenile *Daphnia mendotae*, a native herbivorous cladoceran, were incubated for five days at water temperatures associated with the epilimnion and deep chlorophyll maxima (DCM) of Lake Michigan and fed food resources collected directly from these regions. Juvenile growth rate was strongly dependent on water temperature, as *Daphnia* incubated at the epilimnetic temperature (21°C) exhibited a 42 % higher growth rate than those at the DCM temperature (8°C). Juvenile growth rate of *Daphnia* that alternated between the two temperatures every 12 hours (10.8 % day^{-1}) was similar to the arithmetic average growth rate of the two extreme water temperature treatments (11.0 % day^{-1}), suggesting fluctuating temperatures itself does not substantially influence *Daphnia* growth. Contrary to water temperature, the depth at which food resources were obtained had no effect on juvenile growth rate of *Daphnia*, nor was there a significant interaction between food resource and water temperature effects. The results of our study show a dominant influence of variation in water temperature relative to variation in food resources on the growth rate of migrating Lake Michigan *Daphnia* and demonstrate the need to account for the different water temperatures *Daphnia* encounter over the course of a day when estimating their production. These findings may extend to other migrating

zooplankton species and to other Laurentian Great Lakes, though gradients other than water temperature may also need to be considered (e.g., oxygen gradient in Lake Erie).

INTRODUCTION

The production of zooplankton is important to Great Lakes ecosystems, as zooplankton serve as a critical food resource to many fish species (Miller et al. 1990; O'Gorman et al. 1997; Fulford et al. 2006) and may also influence density and composition of phytoplankton (Makarewicz et al. 1998), which may in turn affect water clarity of the lakes (Scavia et al. 1986). Making accurate predictions of zooplankton production relies on knowledge of the environment they inhabit (Shuter and Ing 1997; Kuns and Sprules 2000); however, predictions may be complicated by the migratory behavior of zooplankton. Many species of zooplankton in the Laurentian Great Lakes undergo diel vertical migration (Wells 1960; Schulze and Brooks 1987; Barbiero et al. 2000; Chapter 5), a behavior that is general to freshwater and marine systems (DeMeester et al. 1998). Although the ultimate causes of migration by zooplankton may vary among lakes (Leech et al. 2005), migration may occur in the Great Lakes as means for zooplankton to avoid predation risk (Schulze and Brooks 1987; Chapter 5). A consequence of migration is that the environment zooplankton experience can greatly change over the course of a day, particularly when migration occurs during periods of the year when the lakes are vertically stratified. Changing environments could influence the production of zooplankton, but exactly how is unclear; there are multiple environmental gradients associated with the water column, and to our knowledge, the effects of these gradients on zooplankton migrating in the Great Lakes have yet to be evaluated.

Water temperature and food resources are two vertical gradients that have been shown to influence zooplankton growth and reproduction in other systems (Williamson et al. 1996; Winder et al. 2003; Kessler and Lampert. 2004). During stratified periods, zooplankton migrating in lakes will generally encounter a water temperature gradient, and the amount of time zooplankton spend at each temperature stratum may strongly influence their metabolic and reproductive rates (Bottrell 1975; Orcutt and Porter 1983; Stich and Lampert 1984). Migrating zooplankton may also encounter variation in food resources, particularly in lakes that exhibit deep chlorophyll maxima (DCM). The DCM is a peak in phytoplankton biomass that is observed in lakes, including the Great Lakes (Barbiero and Tuchman 2001), at the base of the thermocline, and zooplankton fed food resources from the DCM have been shown to sometimes exhibit greater growth and reproduction than zooplankton fed food resources from shallow regions of the water column (Williamson et al. 1996; Winder et al. 2003; Park et al. 2004; Kessler and Lampert 2004). The relative importance of temperature and food resource gradients to zooplankton growth has been shown to vary considerably among different lakes, with temperature being relatively more important in some lakes (Williamson et al. 1996; Park et al. 2004) and food resources being relatively more important in others (Cole et al. 2002; Winder et al. 2003). This variation among lakes may be influenced by differences in the severity of the water temperature gradient (Winder et al. 2003) and zooplankton's utilization of food resources other than phytoplankton, such as ciliates, bacteria, and detritus (Rothhaupt 1991; Williamson et al. 1997).

In this study, we evaluated the effects and relative importance of temperature and food resource gradients found in Lake Michigan on the growth of the zooplankton species, *Daphnia mendotae*. *Daphnia mendotae* is a dominant zooplankton species during the summer in Lake Michigan (Barbiero and Tuchman 2001b) and is known to undergo diel vertical migration in the lake, aggregating near the DCM during the day and in the epilimnion during the night (Chapter 5). Using laboratory experiments, we mimicked the variation in environments experienced by *D. mendotae*, by incubating them at water temperatures of and feeding them food resources collected from either the DCM or the epilimnion of Lake Michigan. Our results demonstrate the relative effects of water temperature, food resources, and their possible interactions on *D. mendotae* in Lake Michigan and have implications to estimating zooplankton production in the Great Lakes.

METHODS

We conducted two experiments during the summer 2005 in which we evaluated juvenile *Daphnia* growth rate under different water temperature and food resource treatments. Our treatments were designed to 1) tease apart the effects of water temperature and food resource gradients associated with vertical migration by varying one of the factors while holding the other constant; 2) identify possible interactions between the effects of water temperature and food resources; and 3) determine if fluctuating environments themselves affect growth rate. We chose to use juvenile growth rate as a response variable, because it is strongly correlated to the intrinsic rate of population growth (Lampert and Trubetskova 1996). To ensure that *Daphnia* did not mature over the course of the experiment, we limited the duration of each experiment to 5 days. For both experiments, we obtained food resources and *Daphnia* from Lake

Michigan in an identical fashion, which we describe first before presenting the specific details of each experiment.

Food resources fed to *Daphnia* during the experiments was seston, including phytoplankton, ciliates, bacteria, and detritus, collected at ambient densities from the DCM and epilimnion of Lake Michigan. We were unable to make daily seston collections from Lake Michigan due to logistical limitations. Instead, seston was collected once two days prior to the start of each experiment and maintained over the duration of the experiment in light and temperature conditions that were similar to the depths seston was collected from following techniques used by Fahnenstiel et al. (2000) and Lohrenz et al. (2004). Collections for the first and second experiments occurred on 22 August and 17 September 2005, respectively, at a site approximately 10 km west of Muskegon, Michigan. Prior to collection, a vertical profiler (Sea-Bird Electronics, Inc., Bellevue, WA) equipped with an *in situ* chlorophyll fluorometer (Seapoint Sensors, Inc., Exeter, NH) was deployed to identify thermal structure of the water column and the location of the DCM. Vertical profiles of water temperature and chlorophyll concentration on the collection dates are presented in Figure 3.1. Seston was collected by pumping lake water from the center of the epilimnion and the DCM (Figure 3.1). Pumped lake water was passed through a 300-μm sieve and into separate 25-L transparent, polycarbonate carboys. The sieve retained planktivores (e.g., *Bythotrephes longimanus*, *Leptodora kindtii*), while allowing the seston and herbivorous zooplankton to remain in the collected lake water at ambient densities. The carboys were immediately placed in dark coolers and transported to the National Oceanic and Atmospheric Administration Lake Michigan Field Station in Muskegon, MI. At the field station, carboys were maintained for seven

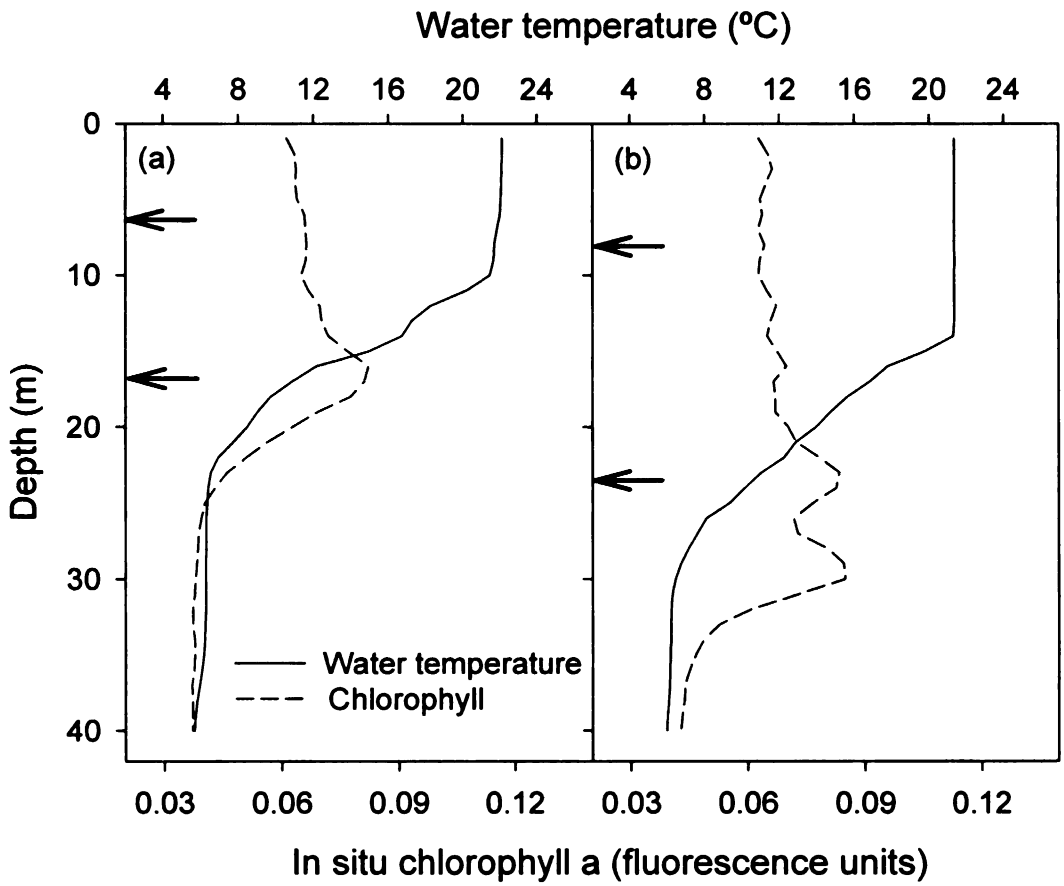

Figure 3.1. Water temperature (solid line) and *in situ* chlorophyll fluorescence (dashed line) in Lake Michigan during water collection for the first and second experiments (panels a and b, respectively). Arrows indicate the depths at which food resources were collected from for each experiment.

days (two days prior and five days after the start of the experiment) in translucent, water-filled environmental chambers that mimicked light and temperature conditions observed in the epilimnetic and DCM regions of the water column, respectively. The environmental chambers were exposed to full sunlight and were lined with theatrical gels to manipulate the spectra of sunlight entering the chambers. Water temperature inside the chambers was regulated using an external chiller. To avoid the settling of seston, the carboys were gently rotated three times end-over-end every 12 hours. Our maintenance of lake water, including the use of these specific chambers, has been shown to maintain ambient densities of seston for at least 10 days (G. L. Fahnenstiel, personal communication, 2004).

Daphnia used in the experiments were neonates born from adults collected from Lake Michigan. Adult *Daphnia* were collected at the same time as lake water using a 0.5 diameter 64-μm zooplankton net with a closed bucket towed vertically through the entire water column. From the netted zooplankton, 200 egg-bearing *Daphnia* were transferred into a 2-L container 13 hours prior to each experiment, and neonates born from these *Daphnia* were collected one hour prior to each experiment. An additional 25 neonates were collected for an estimate of initial size.

At the start of each experiment, four *Daphnia* neonates were transferred into 300-ml replicate bottles filled with either epilimnetic or DCM lake water. Bottles were housed in incubators for the duration of the 5-day experiments and rotated at 0.25 rpm using plankton wheels. Incubators maintained the bottles at different experimental temperatures and regulated photoperiod to 14 h light : 10 hr dark.

In our first experiment, we used a factorial design, with six treatments in total: we used two food resources (epilimnetic and DCM seston) under three thermal regimes (Table 3.1). The first two thermal regime treatments consisted of exposing *Daphnia* to either 21 or 8°C, which are typical water temperatures found in the epilimnetic (21°C) or DCM (8°C) region of the water column. The third treatment consisted of exposing *Daphnia* to alternating temperatures of 21°C and 8°C, switching at 12-hour intervals. Based on the approximate linear relationship between water temperature and growth of *Daphnia* under non-saturating food resource conditions (Hall 1964),we expected that growth rate in the alternating temperature treatment would be approximately the arithmetic average of growth rates of the high and low temperature treatments; a growth rate lower than this average would indicate a growth reduction due to fluctuating temperatures (Reichwaldt et al. 2005). The factorial design also allowed us to evaluate the interacting effects that may occur between food resource conditions and temperature on *Daphnia* growth. For example, Gielbelhausen and Lampert (2001) showed that temperature had a greater effect on *Daphnia magna* growth in high relative to low concentrations of food resources. Each treatment in the first experiment had four replicate bottles (total, 24 bottles), and *Daphnia* in all treatments were transferred into a new bottle filled with fresh treatment water every 24 hours. Transfers were done to ensure 1) that *Daphnia* did not consume more than 25% of the available food resources, based on known clearance rates, and 2) that bottles did not foul.

In our second experiment, we tested the effect of simultaneous changes in water temperature and food resources that *Daphnia* would experience when migrating in Lake Michigan. Specifically, we included one treatment in which we alternated epilimnion and

Table 3.1. Temperature and food resource treatments used in the first and second experiments.

	Treatment	Temperature (°C)	Food resource
Experiment 1	1	21	Epilimnetic
	2	21	DMC
	3	8	Epilimnetic
	4	8	DMC
	5	alternate 8 and 21	Epilimnetic
	6	alternate 8 and 21	DMC
Experiment 2	1	alternate 8 and 21	Epilimnetic at 21°C and DCM at 8°C
	2	alternate 8 and 21	Epilimnetic
	3	alternate 8 and 21	DCM
	4	21	Epilimnetic

DCM = deep chlorophyll maxima

DCM water temperature and food resources every 12 hours and two treatments in which we alternated water temperature but not food resources (Table 3.1). Comparing the first treatment with the latter two provided a means to determine whether *Daphnia* benefited from the combination of food resources and water temperature experienced during migration. We also included a fourth treatment in which *Daphnia* were maintained at a constant 21°C and fed epilimnetic food resources. The difference between this treatment and the first treatment provided an estimate of the growth cost incurred by migrating *Daphnia* relative to remaining the epilimnion. In addition, the last three treatments were similar to treatments in the first experiment, thus providing a means to reaffirm results of the first experiment with food resources taken on a different date. Each treatment in the second experiment had four replicate bottles (total, 16 bottles), and *Daphnia* in all treatments were transferred into a new bottle filled with fresh treatment water every 12 hours.

For both experiments, juvenile growth rate (g, day^{-1}) was calculated as:

$$g = \frac{\ln(l_f) - \ln(l_i)}{d} \tag{3.1}$$

where l_f and l_i were the final and initial standard length and d was number of experimental days. The initial length of *Daphnia* (mean ± standard deviation) in the first and second experiments was 552 ± 22 and 566 ± 64 μm, respectively. Mean survival rate of *Daphnia* over the course of the experiments varied among treatments, ranging from 89 to 94 % in both the first and second experiments. To ensure that juvenile growth rate was not confounded by survival, we conducted two tests. First, we compared survival rate among treatments using ANOVA. Second, we evaluated the effect of survival on growth rate among replicates of all treatments using linear regression. The tests showed that survival did not differ among treatments and did not significantly affect juvenile growth rate.

We analyzed the effects of water temperature and food resource treatments on juvenile growth rates using general linear models. For the first experiment, we evaluated the effect of water temperature and food resources and their interaction using a two-way ANOVA. For the second experiment, we determined if treatments varied significantly using a one-way ANOVA. If a significant difference was found, we used a Tukey's HSD test to separate treatment differences.

RESULTS

In the first experiment, the juvenile growth rate of *Daphnia* significantly varied over the range of temperatures associated with the water column in Lake Michigan ($F_{2,20} = 37.37, p < 0.01$). *Daphnia* incubated at the epilimnetic water temperature (21°C) grew at a 42 % greater rate than those at the DCM water temperature (8°C) and a 29 % greater rate than those that alternated between these water temperatures (Figure 3.2). The average juvenile growth rate of *Daphnia* switched between the two temperatures (0.108 day^{-1}) fell close to the arithmetic average growth rate of the two extreme water temperature treatments (0.110 day^{-1}). Contrary to water temperature, the juvenile growth rate of *Daphnia* was not significantly affected by the location that their food resources were collected from ($F_{1,20} = 0.66, p = 0.43$). *Daphnia* grew at a similar rate in epilimnetic and DCM water under each temperature treatment, as further indicated by the non-significant

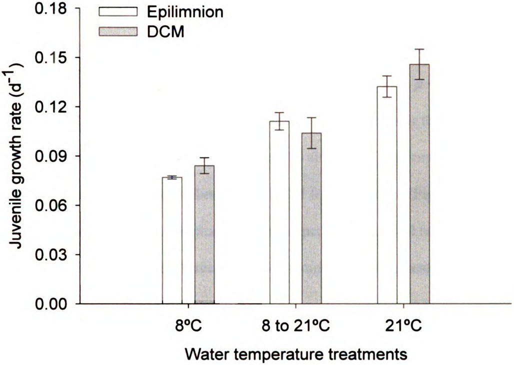

Figure 3.2. Growth rates of *Daphnia* in Experiment 1. Juvenile *Daphnia* experienced three temperature treatments (8°C, alternating 8 and 21°C, and 21°C) and two food resource treatments (water from the epilimnion and the deep chlorophyll maxima [DCM]). Values reported are treatment means (± SE).

interaction between food resource and water temperature effects ($F_{2,18} = 1.26, p = 0.31$). The interaction term was subsequently removed from the ANOVA.

In the second experiment, the juvenile growth rate of *Daphnia* indicated that simultaneous changes in water temperature and food resources did not have a substantial effect on *Daphnia* relative to only changes in water temperature. Although juvenile growth rate varied significantly among treatments ($F_{3,12} = 16.51, p < 0.01$), growth of *Daphnia* that experienced alternating epilimnetic and DCM water temperatures and food resources were similar to those that experienced alternating epilimnetic and DCM water temperatures, but fed either epilimnetic or DCM food resources (Figure 3.3). *Daphnia* that experienced constant epilimnetic water temperature and food resources grew at 34 % greater rate than those in the three alternative temperature treatments on average (Figure 3.3).

DISCUSSION

Daphnia migrating in Lake Michigan experience gradients in both water temperature and food resources; however, our results indicate that changes in water temperature has a much greater effect on *Daphnia* than changes in food resources. In both experiments, increased water temperature had positive effects on *Daphnia* growth rate, most likely caused by a heightening of metabolic rates (Orcutt and Porter 1983;Stich and Lampert 1984). Contrary to water temperature, food resources taken from the deep chlorophyll maxima did not improve *Daphnia* growth rate relative to epilimnetic food resources. There was also no interactive effect between water temperature and food

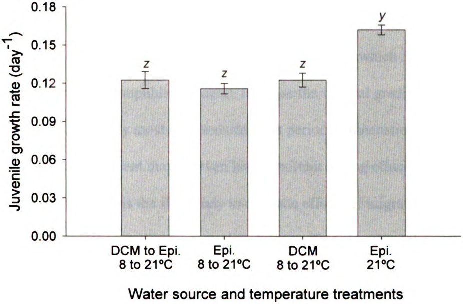

Figure 3.3. Growth rates of juvenile *Daphnia* in Experiment 2. *Daphnia* experienced one of four treatments including: deep chlorophyll maxima (DCM) water at 8°C for 12 h and epilimnetic water at 21°C for 12 h; epilimnetic water at 21°C; epilimnetic water at 21°C for 12 h and at 8°C for 12 h; and DCM water at 21°C for 12 h and at 8°C for 12 h. Values reported are treatment means (± SE). Means with different lowercase letters were significantly different as determined by ANOVA and Tukey's HSD tests ($p < 0.05$).

resources. A previous study that had found such interactions concluded that they occur only when food resources go from a limiting to non-limiting state (Gielbelhausen and Lampert 2001). Thus, the lack of interaction may have occurred because food resources were limiting for *D. mendotae* in both the DCM and the epilimnion. In addition, although food resources for the experiments were collected on different dates (August and September), the consistent lack of a food resource effect suggests that our findings are general to the late summer and early fall months during which *Daphnia* are most abundant (Pangle, unpublished data). Because the vertical gradient in phytoplankton biomass is generally most severe during this period (Fahnenstiel and Scavia 1987), the food resource gradient may be even less important during other months of the year.

While ours is the first study to evaluate effects of migration on zooplankton in the Great Lakes, other studies have explored these effects in other lake systems. In a lake that had a similar temperature gradient and a more severe food resources gradient than Lake Michigan, Park et al. (2004) showed *Daphnia rosea* fed DCM seston grew faster than those fed epilimnetic seston; however, consistent with our results, this food resource effect was relatively minor compared to corresponding water temperature effects. Similar results have been shown for both *Daphnia pulicaria* and a copepod, *Diaptomus oregonensis* (Williamson et al. 1997), indicating that the findings of our study may also be applicable to other non-*Daphnia* zooplankton in Lake Michigan. Contrary to our results, Winder et al. (2003) found that the food resources gradient in a Switzerland lake had a greater influence on the growth of *Daphnia galeata* than water temperature gradient. However, their water temperature gradient was much less severe than in Lake Michigan, with only a change of 6°C. Further, food resource gradients may vary among systems in ways that are difficult to quantify, particularly because *Daphnia* consume food other than phytoplankton, including ciliates, bacteria, and detritus, with maxima that may not correspond with the DCM (Rothhaupt 1991; Williamson et al. 1997).

The results of our study have multiple implications on estimating zooplankton production in Lake Michigan. First, our study experimentally validates the assumption taken by many studies that production of zooplankton is a function of water temperature (e.g. Shuter and Ing 1997). Second, our study indicates that production estimates should consider the possible variation in water temperature experienced daily by zooplankton. Doing this may require depth-stratified sampling of zooplankton, as described in a previous study (Kuns and Sprules 2000), carried out several times over 24-hours periods. Although our study focused on Lake Michigan, these implications may have direct applications to the other Laurentian Great Lakes, as these lakes can exhibit similar temperature and food resource gradients to Lake Michigan (Barbiero and Tuchman 2001a). However, other gradients may also be in important in the other lakes. In particular, oxygen gradients that can develop in Lake Erie during the summer associated with the "Dead Zone" (Rosa and Burns 1987) has the potential to strongly influence zooplankton production (Weider and Lampert 1985; Wright and Shapiro 1990).

Our study also shows how planktivores can affect zooplankton in Lake Michigan through means other than direct predation. Vertical migration by *Daphnia mendotae* functions as means to avoid predation risk and varies according to densities of shallow-dwelling planktivores such as *Bythotrephes* (Chapter 5). Thus, the cost of migration, as demonstrated in our experiments, can be considered a non-consumptive effect of planktivores on *Daphnia* populations. Non-consumptive effects have been shown to contribute substantially to the net effect of predators and influence predator-prey dynamics in qualitatively different ways than direct consumption of prey (Ives and Dobson). Incorporating these non-consumptive effects is therefore necessary to understanding dynamics *Daphnia* and other migrating zooplankton in the context of the Lake Michigan food web.

CHAPTER 4

LIGHT-DEPENDENT PREDATION BY THE INVERTEBRATE PLANKTIVORE, *BYTHOTREPHES LONGIMANUS*

ABSTRACT

We evaluated predation by the invasive invertebrate planktivore, *Bythotrephes longimanus*, on a Lake Michigan prey assemblage as a function of light intensity. *Daphnia mendotae* was the only prey type significantly reduced and light intensity strongly affected this reduction. Specifically, *Bythotrephes* consumption of *D. mendotae* was not detected under low light intensity (< 1 μmol m^{-2} s^{-1}), but increased with greater light intensity, and leveled off under high light intensity (> 100 μmol m^{-2} s^{-1}), at which point *Bythotrephes* ingestion rate was 2.1 *Daphnia*/h. These results indicate that *Bythotrephes* predation is more sensitive to light than previously thought, a discrepancy that can be explained after considering the ability of *D. mendotae* to detect *Bythotrephes*' hydromechanic disturbance. The observed effect of light intensity on *Bythotrephes* predation is more like that of planktivorous fish than that of other previously-studied invertebrate planktivores. Our findings elucidate the role *Bythotrephes* plays in the food web and provide a novel explanation for its tendency to invade lakes of high water clarity. The importance of light-dependent predation found here may extend to other visually oriented predatory cladocerans.

INTRODUCTION

Light can strongly influence the composition and dynamics of communities in aquatic systems (Interlandi and Kilham 2001; Wissel et al. 2003; Sørnes and Aksnes

2006). One mechanism underlying this effect relates to the role light plays in predator-prey interactions (Aksnes 2007). For example, some planktivores have consumption rates that are order-of-magnitudes greater in lit environments than in the dark because they rely on visual cues to detect prey (Ali 1959). Such predation pressure can drive visually-conspicuous prey to extirpation (Brooks and Dodson 1965) and shift habitat use of remaining prey (Clark and Levy 1988; DeMeester et al. 1998), both having potentially strong indirect effects on aquatic communities (Carpenter and Kitchell 1993).

Since planktivores can play a dominant role in aquatic communities, the potential consequences of the invasive predatory cladoceran, *Bythotrephes longimanus*, in the Laurentian Great lakes and surrounding inland lakes has received much attention (Lehman and Cáceres 1993; Vanderploeg et al. 1993; Boudreau and Yan 2003; Barbiero and Tuchman 2004; Strecker et al. 2006). Since its arrival in the Great Lakes two decades ago, *Bythotrephes* has been implicated with the extirpation and reduction in density of several zooplankton species (Lehman and Cáceres 1993; Yan et al. 2002). This disruption to pelagic food web can have indirect consequences on other organisms, including fish (Hoffman et al. 2001) and rotifers (Hovius et al. 2007). Understanding the long-term effects of *Bythotrephes* will require continued monitoring (Neilson et al. 2003) and a better understanding of the mechanisms governing its effect (Schulz and Yurista 1999, Boudreau and Yan 2003).

Muirhead and Sprules (2003) showed that *Bythotrephes'* ability to detect prey increased with increased light intensity using experiments that measured the response of tethered *Bythotrephes* to prey. This type of prey detection is different from that associated with more commonly studied invertebrate planktivores, such as *Chaoborus* spp. and predatory copepods, which depend primarily on hydromechanical cues for tactile detection of prey. In confirmation of the importance of light, *Bythotrephes* generally inhabit the most lit portions (i.e., epi- and metalimnion) of the water column (Evans 1988; Lehman and Cáceres 1993). Further, field surveys (Lehman and Cáceres 1993, Chapter 5) and laboratory experiments (Chapter 1) indicate that *Bythotrephes* induce a strong downward migration in prey during the day, but not at night. Such behavioral responses are presumably an adaptive response to reduce predation risk associated with light intensity (reviewed in DeMeester et al. 1998).

Despite its importance to accurately quantifying and modeling *Bythotrephes* predation rate as a function of time and among systems, the functional relationship between *Bythotrephes* predation and light intensity is still not well understood. To our knowledge, there has not been a study that has experimentally measured predation rate of *Bythotrephes* at different light intensities. This gap in knowledge is also true for predatory cladocera in general, despite their dominance in many lakes (Manca et al. 2000; Pichlová and Brandl 2003; Halversen et al. 2004; McNaught et al. 2004; Ojaveer et al. 2004; Wojtal et al. 2004). Further, when quantifying *Bythotrephes* predation rate using encounter models (Muirhead and Sprules 2003), *Bythotrephes* is predicted to consume prey even in the absence of light; however, we found that *Bythotrephes* predation rates were below detection limits in an experiment using low light intensity (< 0.1 μmol m^{-2} s^{-1}; K. L. Pangle, unpublished data). The goal of this study was to evaluate the effect of light intensity on *Bythotrephes* predation using experiments designed to encompass the variation of light intensity and prey observed in nature. Our findings will improve predictions of *Bythotrephes* influence on pelagic communities across its current and expanding geographical range.

METHODS

We conducted two separate predation experiments in which *Bythotrephes* were incubated with prey at different light intensities, one occurring on 1 September 2005 and the other on 13 October 2005. Each experiment had three light intensity treatments, which we labeled high, mid and low (Table 4.1). The second experiment explored a light intensity gradient lower than the first gradient; the lowest light intensity was 30 times lower than the lowest light intensity in the first experiment, with the middle and highest intensities approximating those from lowest and middle light intensities from the first experiment (Table 4.1).

The prey consisted of a natural assemblage of zooplankton to make our results most applicable to predation occurring in natural systems (Colton 1987). For both experiments, 4-L glass bottles containing *Bythotrephes* and prey were submerged in an incubation chamber, and predation rate was estimated by comparing the final density of zooplankton in bottles that contained *Bythotrephes* to that in control bottles lacking *Bythotrephes*. To manipulate light intensity among treatments, bottles were wrapped with varying layers of neutral density vinyl screening to reduce the fraction of light entering the bottle during the experiment. We designed the experiments so that the loss of zooplankton due to *Bythotrephes* predation would be kept low enough to avoid severe prey depletion, and high enough to still be detectable statistically (Vanderploeg et al.

Table 4.1. Summary of the different *Bythotrephes* densities and light intensities used for each treatment in Experiments 1 and 2.

	Light treatments	*Bythotrephes* per bottle	Light intensity (μmol m^{-2} s^{-1}) minimum	mean	maximum
Experiment 1	High	1	55	170	397
	Mid	1	8	25	60
	Low	3	1	3	8
	Control	0	55	170	397
Experiment 2	High	1	8	22	71
	Mid	3	1	3	11
	Low	3	0.02	0.06	0.21
	Control	0	8	22	71

1982; Båmstedt et al. 2000). Zooplankton densities were also chosen to be within a range observed in the field (K. L. Pangle, unpublished data).

Our incubator chamber allowed for 36 bottles per experiment. Consequently, we decided to only have one control treatment, using the high light intensity for each experiment, thus allowing for more replicates of each treatment. The high light intensity treatment was chosen because it is in this treatment that potential of prey loss is highest in *Bythotrephes* absence, because predation rate is likely greatest from other predators in the community sampled (e.g., *Epischura lacustris*, *Polyphemus pediculus*, and *Leptodora kindtii*), which may also display light-dependent predation (Young and Taylor 1987). While we expected minor prey loss in the absence of *Bythotrephes*, we believe our use of a high light intensity control would, if anything, lead to underestimates of the effects of light intensity on *Bythotrephes* predation rates, and thus is conservative in the context of this experiment.

On the day of each experiment, live *Bythotrephes* and zooplankton prey were obtained from Lake Michigan at a site 5 km west of Muskegon, Michigan (43° 11'29"N, 86° 25'92"W, bottom depth = 45 m). Prior to the initiation of each experiment, approximately equal amounts of zooplankton were added to each *Bythotrephes* treatment bottle (27 bottles), each control bottle (9 bottles). An additional 18 samples were also taken and used to assess initial zooplankton densities. At the start of each experiment, *Bythotrephes* were added into *Bythotrephes* treatment bottles (27 bottles total), while control treatment bottles received no *Bythotrephes*. We anticipated lower predation rates as light intensity decreased, and therefore added more *Bythotrephes* to treatments with lower light (Table 4.1).

Bythotrephes were collected by towing a 1-m diameter, 500-µm-mesh plankton net equipped with a 4-L collection bottle from 25 meters depth to the surface. Captured *Bythotrephes* were immediately transferred into 15-ml vials (1 individual per vial) that were filled with lake water that had been passed through a 64-micron filter to remove all zooplankton prey. To reduce variability among *Bythotrephes*, we separated individuals by instar and used individuals of the 2nd instar in the experiments (mean individual weight in both experiments was 0.3 mg DW). The experiment started when *Bythotrephes* were poured from the vials into the experimental bottles.

Zooplankton prey were collected using a 0.5 m diameter, 64-µm-mesh plankton net equipped with a 1-L collection bottle at the cod end towed over the same area. Captured zooplankton prey were gently poured into a 30-L aquarium, which was filled with filtered lake water. Cetyl alcohol was added to the aquarium to prevent zooplankton from adhering to the surface of the water (Desmarais 1997). Zooplankton prey were added to the experimental bottles by taking 10-ml subsamples of water from the center of the aquarium and releasing subsamples into the bottles. We took subsamples by lowering an 8-mm diameter cylinder into the water until it touched the bottom of the aquarium at which point we capped the top of the cylinder to retain the water and organisms inside. This subsampling approach allowed us to capture organisms regardless of their vertical position in the aquarium and also did not require producing a suction field that could potentially be sensed and avoided by some zooplankton. Subsamples were transferred to bottles according to a randomized-block design, a technique that minimized the variation in zooplankton density between bottles, and one subsample was added to each bottle (both the 36, 4-L experimental bottles and the 18, 0.5-L sample bottles was used to estimate initial zooplankton densities) sequentially, until each bottle received 16 subsamples total. Initial zooplankton densities samples were preserved with buffered sugar-formalin solution.

The incubation chamber in which experiments were carried out was 2,000-L in size and maintained an environment similar to that observed in Lake Michigan. The incubation chamber was illuminated with natural sun. Light entering the chamber passed through theatrical gels (Peacock Blue Roscolux, Rosco Laboratories Inc., Stamford, Connecticut, USA) that mimicked the pelagic light spectra and neutral density vinyl screening that reduced light intensity (Lohrenz et al. 2004). Ambient light intensity was measured using a 4-pi sensor over the course of the experiments, and the number of neutral vinyl layers was changed as sunlight intensity changed. In comparison with light intensity observed in Lake Michigan's water column, 25 and 170 μmol m^{-2} s^{-1} would be typical at the thermocline and at the center of epilimnion, respectively, on a summer day, whereas 0.06 μmol m^{-2} s^{-1} would be typical at the surface on a moonlit night (K. L. Pangle, unpublished data). Water temperature inside the incubation chamber was kept at a level typical of the Lake Michigan metalimnion (16°C) using an external water chiller.

Bottles were attached to a motorized cage located inside the incubation chamber, which rotated the bottles end-over-end during the experiment at a constant rate (approximately 0.5 rpm) to reduce aggregation of zooplankton inside the bottles. Both experiments ran for 7 hours, from 1300 to 2000 EDT. At the end of each experiment, bottles were removed from the incubation chamber, and organisms were immediately narcotized by adding Alka-Seltzer® tablets to each bottle. Organisms were siphoned from the bottles onto a 64-µm filter and then transferred into 0.2 L bottles with buffered sugar-formalin solution. Later, all zooplankton prey and *Bythotrephes* were identified and counted using a microscope and their body lengths were measured using a drawing tube and digitizer (Roff and Hopcroft 1986). Prey were grouped into one of 7 prey types including: *Daphnia mendotae*, *Bosmina longirostris*, copepod nauplii, juvenile *Diaptomus* spp., adult *Diaptomus* spp., juvenile *Diacyclops thomasi*, and adult *D. thomasi*.

Statistical analyses and predation rate calculations

Prior to analyses of light effect, we first tested assumptions of normality and homogeneity of variance using the Wilks-Shapiro Test and the Levene's Test, respectively. In addition, we evaluated whether prey density was substantially different in the control bottles at the end of the experiment than it was at the start of the experiment due to predation by other predators in the community sampled. This was done by comparing the average initial prey density based on the preserved initial samples with the average prey density in the control bottles at the end of the experiment. While the predatory copepod, *Epischura lacustris*, was found in two and seventeen bottles in Experiment 1 and 2, respectively, its presence did not vary among treatments (one-way ANOVA: both *ps* > 0.05) and the prey density in initial samples and control treatments did not differ significantly (Student's t-test: all *ps* > 0.05) in both experiments. Hence we combined data from the initial prey densities to those from the control treatments, and used the average as an estimate of initial prey density in each experiment to increase statistical power. We also removed one 25 μmol m^{-2} s^{-1} replicate and one 3 μmol m^{-2} s^{-1} replicate in Experiment 1 and one 22 μmol m^{-2} s^{-1} replicate in Experiment 2 from analyses, because an individual *Bythotrephes* was not found in these bottles at the end of the experiments.

We tested the hypothesis that light intensity led to different final densities of zooplankton using a one-way ANOVA and separated differences between specific treatments using Tukey HSD tests (Zar 1999).We followed this by calculating estimated clearance rates (F, L hour^{-1} predator^{-1}) and ingestion rates (I, prey hour^{-1} predator^{-1}) and (a) testing for variation in clearance and ingestion rates for each experiment by one-way ANOVA and then (b) combining data from the two experiments to estimate a relationship between ingestion rate and light intensity. Clearance rate was calculated as:

$$(4.1) \quad F = \frac{-\ln\left({N_f}/{\hat{N}_i} \right) V}{tP}$$

where N_f is final prey density (individuals L^{-1}) in a *Bythotrephes* bottle, $\hat{N}_i$ is average initial prey density (individuals L^{-1}), V is the volume of the bottle (L), t is the duration of the experiment (hours), and P is the number of *Bythotrephes* in the bottle (Båmstedt et al. 2000). Ingestion rate was calculated as:

$$(4.2) \quad I = F\hat{N}_i$$

We used standard error propagation techniques (Meyer 1975) to calculate standard errors associated with mean clearance and ingestion rates of each *Bythotrephes* treatment. Propagated standard errors are reported with treatment means and used in a subsequent analysis, but not included in ANOVAs of clearance and ingestion rates because the error associated with the initial prey density was common among *Bythotrephes* treatments.

We pooled estimates of ingestion rates from both experiments to better describe *Bythotrephes* consumption over a broad range of light intensity (0.06 - 170 μmol m^{-2} s^{-1}). Using weighted non-linear least squares regression, the relationship between light intensity and *Bythotrephes* ingestion rate was fit to the logistic model:

$$(4.3) \quad I = \frac{a}{1+\left(\frac{L}{b}\right)^{c}}$$

where a, b, and c are fitted parameter representing the maximum ingestion rate, the light intensity at which ingestion rate is half of its maximum, and the exponential rate of increase, respectively, and L is light intensity (μmol m^{-2} s^{-1}). Data used for the regression were treatment means weighted with their respective propagated standard error (Gurevitch and Hedges 1999).We chose this logistic model because, for visual predators, ingestion rate is often constant over low light intensities and then increases to an asymptote as light intensity increases (Fraser and Metcalfe 1997).We chose to use ingestion rate rather than clearance rate in this analysis, because the prey densities used in both experiments were greater than that at which *Bythotrephes* predation is saturated at high light intensities (K. L. Pangle, unpublished data.).

RESULTS

In both experiments, *Daphnia mendotae* was the only of the seven prey types in the prey assemblage whose density was significantly reduced (Experiment 1, $F_{3,48} = 19.53, p < 0.01$; Experiment 2, $F_{3,49} = 5.51, p < 0.01$; Figure 4.1). In Experiment 1,

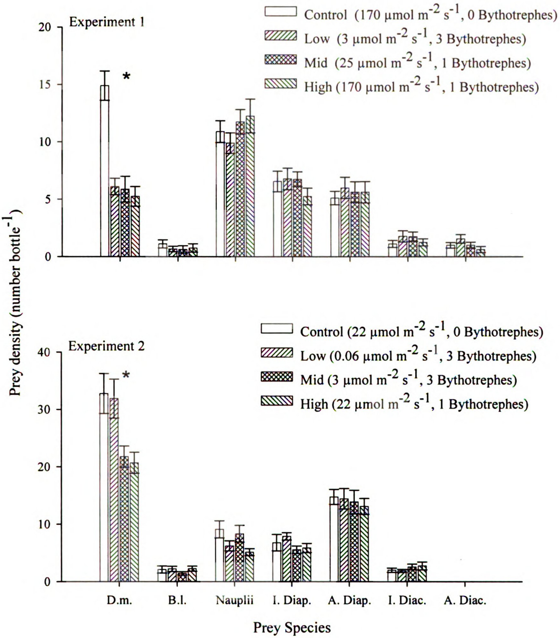

Figure 4.1. Densities of different prey types in *Bythotrephes* and control treatments in Experiments 1 and 2. In each experiment, bottles were exposed to different light intensities and received 0, 1, or 3 *Bythotrephes* depending on the treatment (see figure legends). Bars are means with standard errors and reflect total, not per capita predator effect. Data from initial prey density are included in mean densities of the control treatment. Prey types included *Daphnia mendotae* (D.m.), *Bosmina longirostris* (B.l.), copepod nauplii, immature *Diaptomus* (I. Diap.), adult *Diaptomus* (A. Diap.), immature *Diacyclops thomasi* (I. Diac.), and adult *D. thomasi* (A. Diac.). Asterisks denote significant differences.

Bythotrephes clearance and ingestion rates of *D. mendotae* did not differ significantly between the 22 and 175 μmol m^{-2} s^{-1} treatments; however, rates in these treatments were significantly greater than those in the 3 μmol m^{-2} s^{-1} treatment (Table 4.2), with values approximately 4 times greater in the highest than the lowest light intensity treatment. In Experiment 2, *Bythotrephes* clearance and ingestion rates of *D. mendotae* were significantly greater in the 22 μmol m^{-2} s^{-1} treatment than those in the 0.06 and 3 μmol m^{-2} s^{-1} treatments (Table 4.2). An additional analysis using data from only the lowest light intensity treatment showed that clearance and ingestion rates at this light intensity did not differ significantly from zero (Student's t-test: $t = 0.50, p = 0.63$, df = 8; $t_8 = 0.13, p = 0.90$, df = 8, respectively) and had upper bounds of 0.05 L h^{-1} and 0.31 *Daphnia* h^{-1} in 95% confidence intervals.

We pooled ingestion rate data found in Experiments 1 and 2 to examine the functional relationship between *Bythotrephes* consumption of *D. mendotae* and light intensity. The combined data fit a logistic model well ($r^2 = 0.98$; Figure 4.2) with a half-saturation point at 6.8 μmol m^{-2} s^{-1} and maximum ingestion rate at 2.1 *Daphnia* h^{-1}.

DISCUSSION

Light strongly influenced the predation rate of the invasive planktivore, *Bythotrephes* on the cladoceran *Daphnia mendotae*, a prey type shown to be highly selected for by *Bythotrephes* (Vanderploeg et al. 1993; Lehman and Branstrator 1995; Dumitru et al. 2001). Consumption of *Daphnia* was not detectable under low light intensity (< 1 μmol m^{-2} s^{-1}), but increased with greater light intensity, and eventually leveled off at high light intensity (> 100 μmol m^{-2} s^{-1}; Figure 4.2). The steepness of the

Table 4.2. *Bythotrephes* clearance rates (L hr^{-1}) and ingestion rates (number hr^{-1}) of *Daphnia mendotae* observed in Experiments 1 and 2 at different intensities (description of light intensities in Table 1).

		Light intensity treatment		
	Variable	Low	Mid	High
Experiment 1	Clearance rate	0.16 ± 0.03 *z*	0.58 ± 0.11 *y*	0.59 ± 0.10 *y*
	Ingestion rate	0.56 ± 0.07 *z*	2.06 ± 0.40 *y*	2.08 ± 0.34 *y*
Experiment 2	Clearance rate	0.00 ± 0.02 *z*	0.07 ± 0.02 *z*	0.22 ± 0.09 *y*
	Ingestion rate	-0.02 ± 0.17 *z*	0.49 ± 0.15 *z*	1.66 ± 0.46 *y*

Note: Values are means ± propagated standard errors and were calculated using equations 1 and 2. Mean row values with different lowercase letters were significantly different as determined by ANOVA and Tukey's HSD tests ($p < 0.05$).

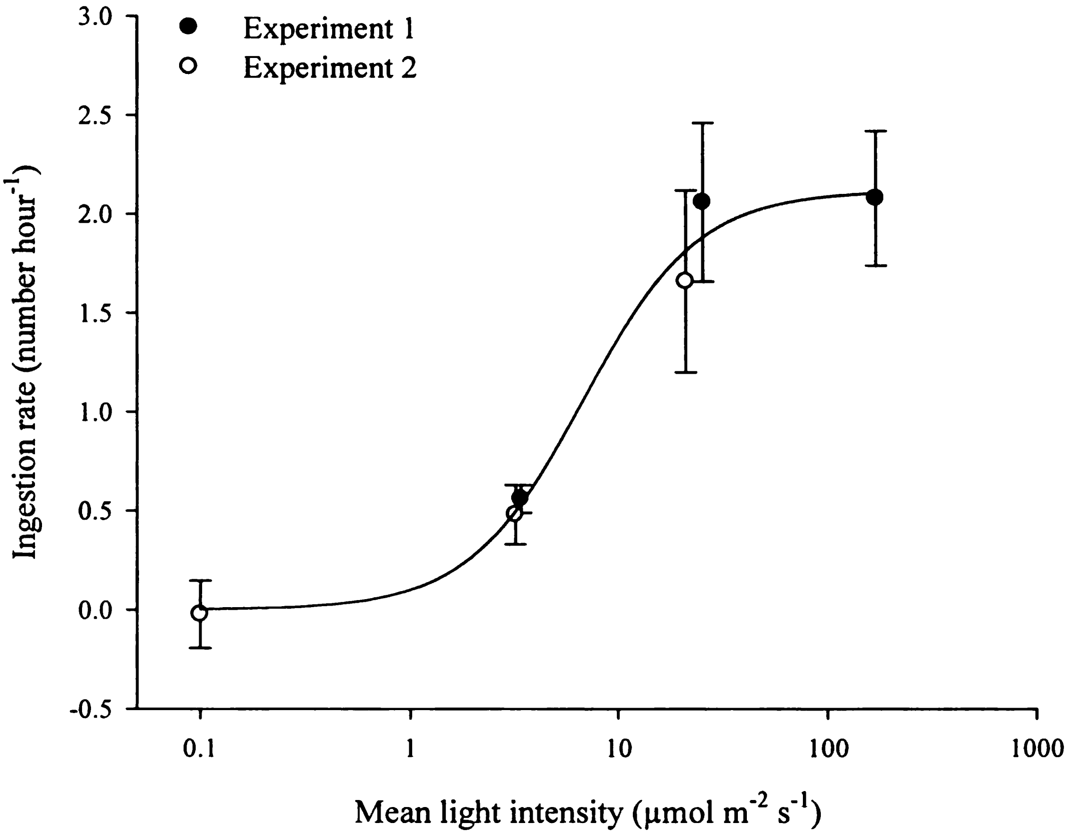

Figure 4.2. Effect of light intensity on *Bythotrephes* ingestion rate. Data of ingestion rates of *Daphnia mendotae* in Experiments 1 and 2 were combined to evaluate *Bythotrephes* predation over a broad range of light intensities. Points are means with propagated standard error bars that were calculated using equations 1 and 2. In this analysis, the relationship between light intensity and ingestion rate was described using a logistic regression model ($y = 2.12 / [1 + (x / 6.79)^{-1.57}]$), shown by the fitted line.

increase in predation rate at intermediate light intensities is difficult to ascertain given our experimental design; however, the increase depicted in Figure 4.2 is similar to the increase Muirhead and Sprules (2003) found for the reaction distance of *Bythotrephes* to prey over a similar range of light intensities. Whereas we did not observe consumption of other prey at any light intensity, our ability to detect predation for some of these prey may have been limited due to their low density, particularly *Bosmina longirostris*, which is another preferred prey of *Bythotrephes* (Vanderploeg et al. 1993).

Previous studies indicate that invertebrate planktivores primarily use tactile, rather than visual cues, as the primary means to detect prey (Pastorok 1981; Kiørboe and Visser 1999). Exceptions include studies on predation by mysids (Ramcharan and Sprules 1986) and notonectids (Dieguez and Gilbert 2003); however, in both of these cases, these invertebrate planktivores still relied strongly on tactile means to detect prey and, in contrast to *Bythotrephes*, their feeding was not substantially reduced in total darkness. Thus, the strong dependence of *Bythotrephes* on light intensity found here is unique among known aquatic invertebrates and is comparable to planktivorous fish predation that is often strongly affected by light intensity. Indeed, zooplankton prey have evolved behavior known as diel vertical migration to avoid overlap with fish in areas and at times of high light intensity (DeMeester et al. 1998). Laboratory experiments (Chapter 1) and field observations (Chapter 5) have shown that zooplankton prey also migrate vertically in the presence of *Bythotrephes*, suggesting that *Bythotrephes* may be driving selection for zooplankton to perceive its risk and respond behaviorally.

A previous laboratory study by Muirhead and Sprules (2003) that evaluated prey detection by *Bythotrephes* as a function of light also predicted that *Bythotrephes* predation rate decreased with decreasing light intensity, but the predicted light effect was less than what we found in our experiments. Their predictions were derived from a model of the rate of prey encountered by a single *Bythotrephes* given the density and swimming velocity of *Bythotrephes* and prey, and *Bythotrephes* reaction distance, which is a function of light intensity (details of the model and its application provided in Appendix A). The model was parameterized with data from laboratory observations of tethered *Bythotrephes'* detection of prey. Given the densities in Experiment 2, the number of *D. mendotae* encountered by *Bythotrephes* is predicted by the model to decline 29.1 % as light intensity changes from 3 to 0.06 μmol m^{-2} s^{-1} (Appendix B); in contrast, the observed mean decline in ingestion rate was actually 100 %.

The discrepancy between our results and the model predictions may result from the ability of *D. mendotae* to detect *Bythotrephes*, which is not included in the model. Zooplankton prey are known to avoid predators through hydromechanical signals prior to an attack (Heath 1993; Viitasalo et al. 1998), such that the ability of prey to detect predators is not dependent on light. To test the role of predator detection by *Daphnia* on *Bythotrephes* predation rate at low light, we can apply models developed by Tiselius and Jonsson (1990) parameterized with data from our study and other studies of *Daphnia* and *Bythotrephes* (Brewer et al. 1999; Muirhead and Sprules 2003). These models predict the hydro-mechanical signals produced by *Bythotrephes* and the distance from *Bythotrephes* that *D. mendotae* would be able to detect these signals (details of the model and its application provided in Appendix C). Results of the hydro-mechanical models show that the predicted distance *Bythotrephes* is able to perceive prey is less than the predicted distance that *D. mendotae* can detect *Bythotrephes* at low light intensity, but greater at the mid light intensity. The model predictions suggest that *D. mendotae* may be able to perceive *Bythotrephes* before being attacked at light intensities less than 2.7 μmol m^{-2} s^{-1}, which could account for the dramatic decrease in predation observed, and the discrepancy with the predation rate prediction by the Muirhead and Sprules (2003) model. These idealized models provide a qualitative explanation for the patterns observed in our study, however more research is needed on prey detection ability and how it influences predation by *Bythotrephe*s on *D. mendotae*. Building on previous studies that have emphasized the importance of prey escape capabilities (Brenner et al. 1978; Heath 1993; Viitasalo et al. 1998), our results suggest that light-mediated changes to the relative ability of prey and predator to detect each other can substantially affect predation rate.

Light-dependent predation has implications for predicting *Bythotrephes*' impact on zooplankton communities. Our results suggest that *Bythotrephes* effect could be strongly influenced by the depth and time at which *Bythotrephes* and zooplankton overlap. For example, there are periods in Lake Michigan in which the only overlap in the vertical distribution of *D. mendotae* and *Bythotrephes* occurs at night (Chapter 5); thus, *Bythotrephes* ability to consume *D. mendotae* would be greatly reduced. *Bythotrephes* is also known to migrate downward itself when facing fish predation (Straile and Halbich 2000). In lakes with high fish predation, predation by *Bythotrephes* that are forced to inhabit deeper, darker regions of the water column would also be greatly reduced (Lehman and Cáceres 1993; Palmer et al. 2001).

The spread of *Bythotrephes* is of concern to management of lake ecosystems given their potential impacts. Understanding factors controlling the establishment of *Bythotrephes* in a lake can aid in identifying lakes to focus management efforts

(Muirhead and MacIsaac 2005). Our results suggest that the success of *Bythotrephes*, in terms of its predation, would increase in lakes with increased water transparency; indeed, this relationship has been observed in nature. MacIsaac et al. (2000) found that high secchi depth values, a surrogate for high water transparency, was a strong predictor of *Bythotrephes* presence in lakes within *Bythotrephes* native range. In addition, Branstrator et al. (2006) reported a similar finding in Minnesota lakes that were recently invaded by *Bythotrephes*. These studies propose different explanations for why *Bythotrephes* were found more often in clear lakes. MacIsaac et al. (2000) suggest that high transparency was indicative of systems with low productivity that could not support high densities of planktivorous fish thereby providing *Bythotrephes* a release from both a predator and a competitor. Branstrator et al. (2006) suggest that high transparency was not the primary reason for the establishment of *Bythotrephes*, but rather an indicator that the systems also have a warm, low-light, mid-depth water layer. This layer may be beneficial to *Bythotrephes* populations by acting as a visual refuge from warmwater fish and a thermal refuge from coldwater fish (Yan et al. 2001). Based on our results, we propose that light-dependent predation by *Bythotrephes* should be added to the list of potential factors contributing to its establishment in clear lakes.

There is evidence that the type of predation observed in this study may be general to other predatory cladocera. An experiment using *Polyphemus pediculus* found its predation varied with light intensity and was not detectable in the absence of light (A. T. Packard, unpublished data). A large, complex eye like the one *Bythotrephes* and *Polyphemus* use to detect prey is a trait common to *Cercopagis pengoi*, *Leptodora kindtii*, and ponids (Rivier 1998). The maintenance of a large eye is costly because it makes predatory cladocera more visible to fish (Branstrator and Holl 2000). This large cost must be associated with a large benefit, suggesting that the eye plays an important role in detecting prey. In addition, the distribution of predatory cladocera in natural systems indicates light influences their prey consumption, as they primarily inhabit well-lit areas, such as the littoral zone and the epi- and metalimnion of the pelagic (Palmer et al. 2001; Benoit et al. 2002). Future studies of light-dependent predation in other predatory cladocera may aid in better understanding the role these organisms play in aquatic communities and their relative success in different systems.

CHAPTER 5

LARGE NON-CONSUMPTIVE EFFECTS OF AN INVASIVE PREDATOR ON ZOOPLANKTON POPULATION GROWTH RATE

ABSTRACT

We evaluated the non-consumptive 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 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 non-consumptive (i.e., resulting from reduced birth rate) and lethal (i.e., consumptive) effects of *Bythotrephes* on *D. mendotae* and *B. 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 non-consumptive effects played a substantial role in the net effect of *Bythotrephes* on several prey population growth rates in the field, with non-consumptive 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 non-consumptive, behaviorally-based effects, despite short evolutionary coexistence with prey species.

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 Mittelbach 1990; Werner and Peacor 2003; Schmitz et al. 2004, also termed interaction modifications, Wootton 1994). Therefore, "non-consumptive" 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 non-consumptive 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 non-consumptive 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 non-consumptive effects contribute to the net effect of a predator on prey populations. Nevertheless, little is known of either population-level non-consumptive effects or the relative importance of lethal and non-consumptive effects in natural (uncontrolled) field environments.

We quantified both the lethal and non-consumptive effects of an invasive invertebrate predator, *Bythotrephes longimanus* Leydig, 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 Cáceres 1993; Barbiero and Tuchman 2004) and smaller surrounding lakes (Hoffman et al. 2001; 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 Cáceres 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 (Chapter 1), whereas a field study indicates that *Daphnia mendotae* Birge vertical distribution deepened in Lake Michigan after the invasion of *Bythotrephes* (Lehman and Cáceres 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 non-consumptive 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 if *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 non-consumptive 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 *B. 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 et al., 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 5.1). 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 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-weight relationship (Yan and Pawson 1998).

Percentage of prey in the epi- and hypolimnion (%), and *Bythotrephes* biomass (mg/m^2) 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 *B. 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 Non-consumptive Effects of Bythotrephes

We estimated the non-consumptive 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:

$$(5.1)\quad \frac{1}{N}\frac{dN}{dt} = b - \Delta b - d - m$$

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 non-consumptive (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.

Non-consumptive 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 approximately 10 km west of Muskegon, Michigan (Table 5.1). Four sampling profiles were carried out over a 24-hr period, and profiles were initiated consecutively at 1400, 2100, 0100, and 0900 h. 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. Non-consumptive effects in Lake Erie were estimated from samplings collected on 30 July and 8 September 1997 in Long Point Bay (Table 4.1). 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, and then water was filtered through a 64-micron mesh net. Samples were processed and counted in the same fashion as described for the extensive survey.

Field-derived estimates of *D. mendotae* and *B. 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:

Table 5.1. Sampling locations and dates for Lake Michigan and Lake Erie field surveys.

System (basin)	Latitude	Longitude	Depth (m)	Sampling months, year	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 June - October, 1994 June - October, 1998	6 16 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 5 different locations, all of which were located close to the reported coordinates.

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

E is the density of eggs (eggs/m^3), N is the density of prey (individuals/m^3), and $D(T)$ is the egg developmental duration (d), which is a function of water temperature (T, °C). 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 *B. longirostris* (Hanasato and Yasuno 1985) and can be estimated using the equations:

(5.3) $D(T) = 1 / (0.00041 \cdot T^2 + 0.0108 \cdot T - 0.0163)$

and

(5.4) $D(T) = 3.102 - 0.261 \cdot \ln(T^2)$,

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:

(5.5) $$D(T) = \sum_p D(T)_p w_p$$

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 hour day each profile represented. For Lake Michigan, the daytime profiles (0900 and 1400 h) and the nighttime profile (0100 h) were assigned values of $w_p = 0.30$ and $w_p = 0.20$, respectively. The 2100 h sampling profile captured the day-night transition during which *D. mendotae* migrated. Based on field observations of *D. mendotae* vertical migration (K. L. Pangle et al., 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

$$(5.6) \quad D(T)_p = \sum_z D(T)_{z,p} f_{z,p}$$

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 Equation 3 or 4 given the temperature at depth z for profile p.

The non-consumptive effect of the predator (Δb in Equation 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 non-consumptive 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 et al., 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. longirostris* consumed by *Bythotrephes*. However, *Bythotrephes* are likely better able to detect *D. mendotae* than *B. longirostris* due to *Daphnia*'s larger size (Confer et al. 1978), making our predation estimates for *B. longirostris* conservatively high. The per capita rate of predation by a single *Bythotrephes* (a, prey consumed · m^3 · *Bythotrephes*$^{-1}$ · d^{-1}) was estimated as:

$$(5.7)\quad a = \frac{8.196\text{E}-03}{1+(L/24.96)^{-1.034}}$$

where L is light intensity (μmol · m^{-2} · s^{-1}). The per capita (of prey) predation rate at a given sampling profile (d_p, /d) was calculated as a weighted average:

$$(5.8)\quad d_p = \frac{\sum_z a_z N_z P_z w_z}{\sum_z N_z w_z}$$

where a_z was predation rate at the depth z given its midpoint light intensity, N_z and P_z were the prey and *Bythotrephes* density (number/m^3), respectively, at depth z, and w_z (m) was the height of the water column represented by depth z. For the Lake Michigan sampling profile representing the day-night transition (2100 H),we used the highest light intensity observed during the transition to calculate d_p, thus making our estimate conservatively high. The daily predation rate, considered the overall lethal effect of *Bythotrephes*, was calculated as the arithmetic mean of the d_ps using the same weights for sampling profiles as Equation 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 (*B. 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 (*B. 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 (Figure 5.1). 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 *B. 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 (Figure 5.2), *Bythotrephes* also had a significant negative influence on percentages of prey, in this case *B. longirostris* and *Daphnia retrocurva,* in the epilimnion (*B. 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 (*B. longirostris*: $F_{1,52} = 5.47, p = 0.02, r^2 = 0.10$; *D. retrocurva*: $F_{1,12} = 8.23, p < 0.01, r^2 = 0.17$). 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

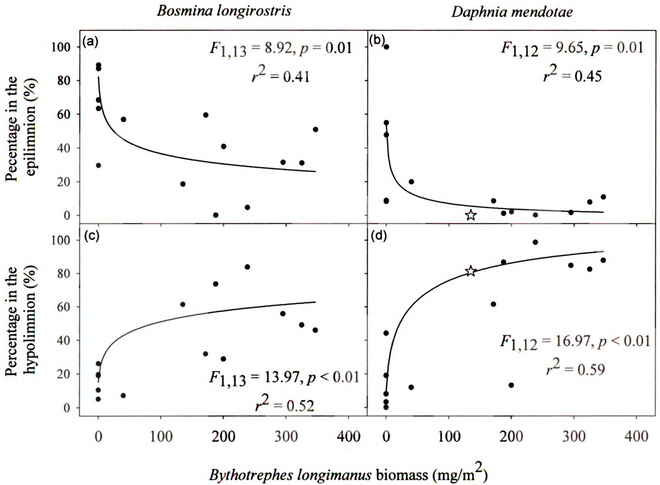

Figure 5.1. Percentage of *B. longirostris* (a, c) and *D. mendotae* (b, d) in the epi- and hypolimnion of Lake Michigan over a gradient of *Bythotrephes* biomass (mg/m^2). Lines are linear regressions performed on transformed data and plotted on untransformed data, with analysis results reported within each subplot. Stars (☆) represent the distribution in the intensive survey (see text).

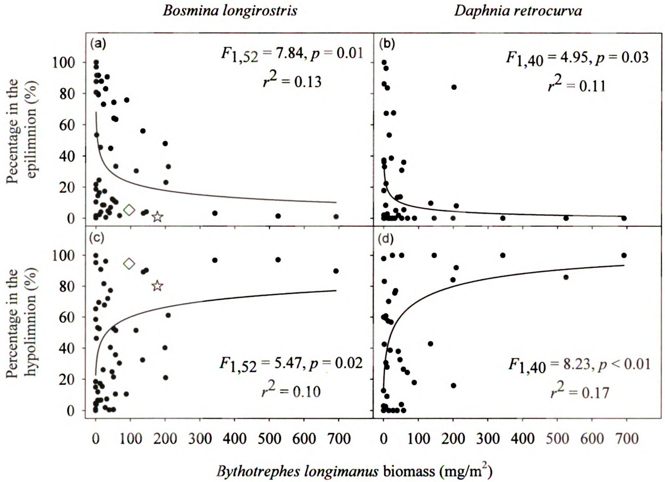

Figure 5.2. Percentage of *B. longirostris* (a, c) and *D. retrocurva* (b, d) in the epi- and hypolimnion of Lake Erie over a gradient of *Bythotrephes* biomass (mg/m^2). Lines are linear regressions performed on transformed data and plotted on untransformed data, with analysis results reported within each subplot. Stars (☆) and diamonds (◊) represent distributions in the first and second intensive surveys, respectively (see text).

Bythotrephes biomass was low (Figure 5.2); when *Bythotrephes* was absent from the pelagic community, the percentage of *B. 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 *B. longirostris* occupied the epilimnion in Lake Erie as both epilimnion depth increased and secchi depth deceased. In the multiple linear regression model, the magnitude of the *Bythotrephes* effect on the percentage of *B. longirostris* occupying the epilimnion increased, a predicted trend; however, this change was not significant ($p = 0.18$). 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* (Figure 5.3). 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. mendotae* were found only in the upper stratum. At dawn (0900 h), *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, Figure 5.3) and the degree of vertical overlap with *Bythotrephes,* which was high during the nighttime but low during the day (Figure 5.3).

The vertical distribution of *B. longirostris* in the Lake Erie intensive field surveys was below that of *Bythotrephes* during the day and nighttime sampling profiles (Figure 5.4). In the first survey, *B. longirostris* were found almost entirely in the hypolimnion at

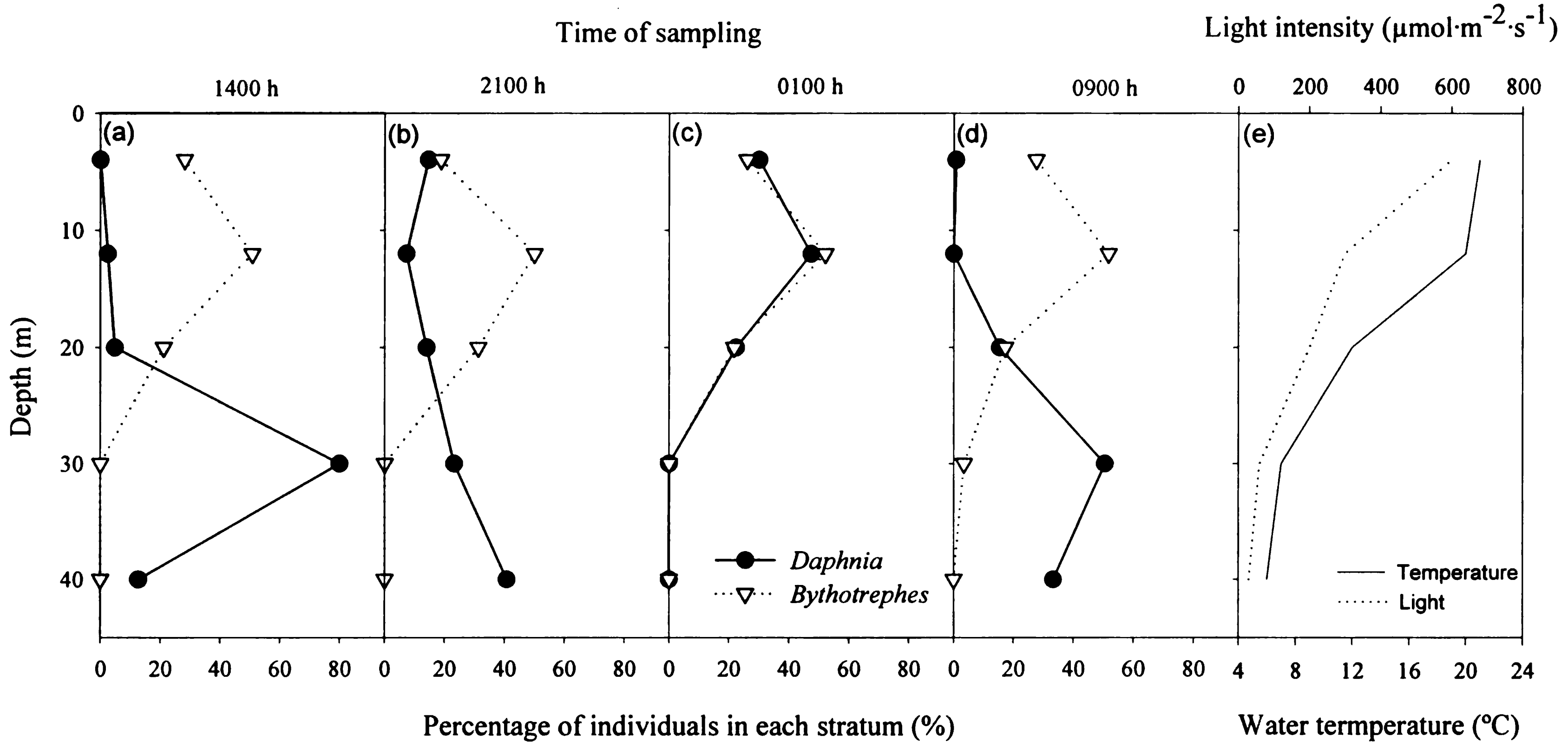

Figure 5.3. Vertical distribution of *D. mendotae* (solid line) and *Bythotrephes* (dashed line), and mid-day temperature and light conditions of the water column (e) during the Lake Michigan intensive field survey. Each of four sampling profiles are reported in chronological order.

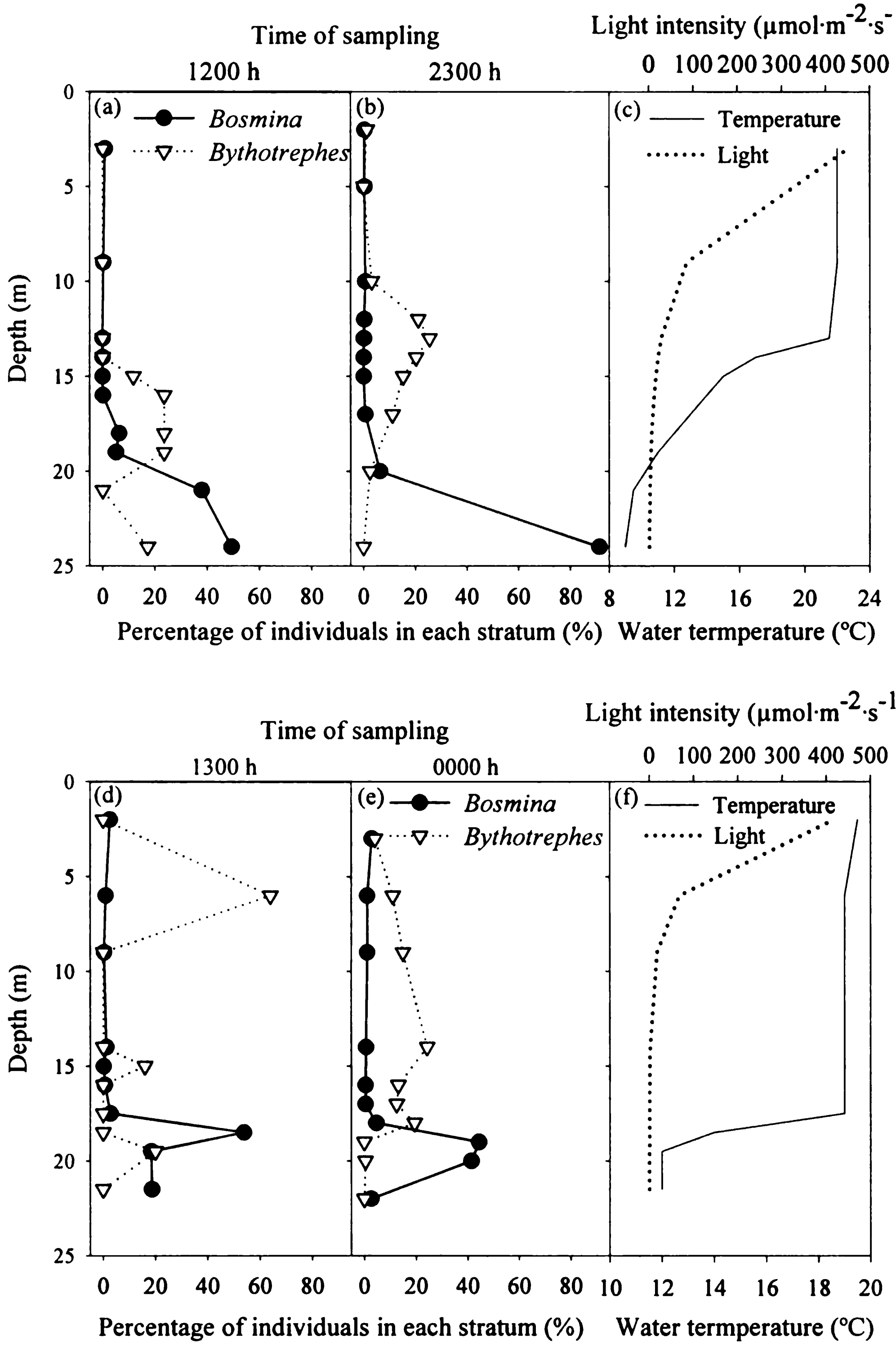

Figure 5.4. Vertical distribution of *B. longirostris* (solid line) and *Bythotrephes* (dashed line), and mid-day temperature and light conditions of the water column during the first and second Lake Erie intensive field surveys (a-c and d-e, respectively). Sampling profiles were conducted near midday (a,d) and midnight (b,e) during both surveys.

midday and midnight, while *Bythotrephes* were found in the metalimnion at the same times. In the second survey, *B. 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 (Figures 5.1 and 5.2).

Estimates of Lethal and Non-consumptive Effects of Bythotrephes

In Lake Michigan, the estimated lethal effect (*d*) of *Bythotrephes* on *D. mendotae* population growth rate was 0.013 /d. Estimates of the non-consumptive effect (Δb) of *Bythotrephes* on *D. mendotae* was 0, 0.038, and 0.174 /d, respectively, for scenarios that used the deepest, average, and shallowest observed prey distributions in the absence of *Bythotrephes* (Figure 5.5). In Lake Erie, *d* was estimated as 0.006 and 0.007 /d in the first and second surveys, respectively (Figure 5.5). Estimates of non-consumptive effects in the first survey were 0, 0.015, and 0.061 /d, respectively, based on three depth scenarios, and in the second survey were 0, 0.024, and 0.079 /d, respectively. These estimates were similar to those produced independently using a somatic growth rate model (Appendix D).

DISCUSSION

This study demonstrates that non-consumptive 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

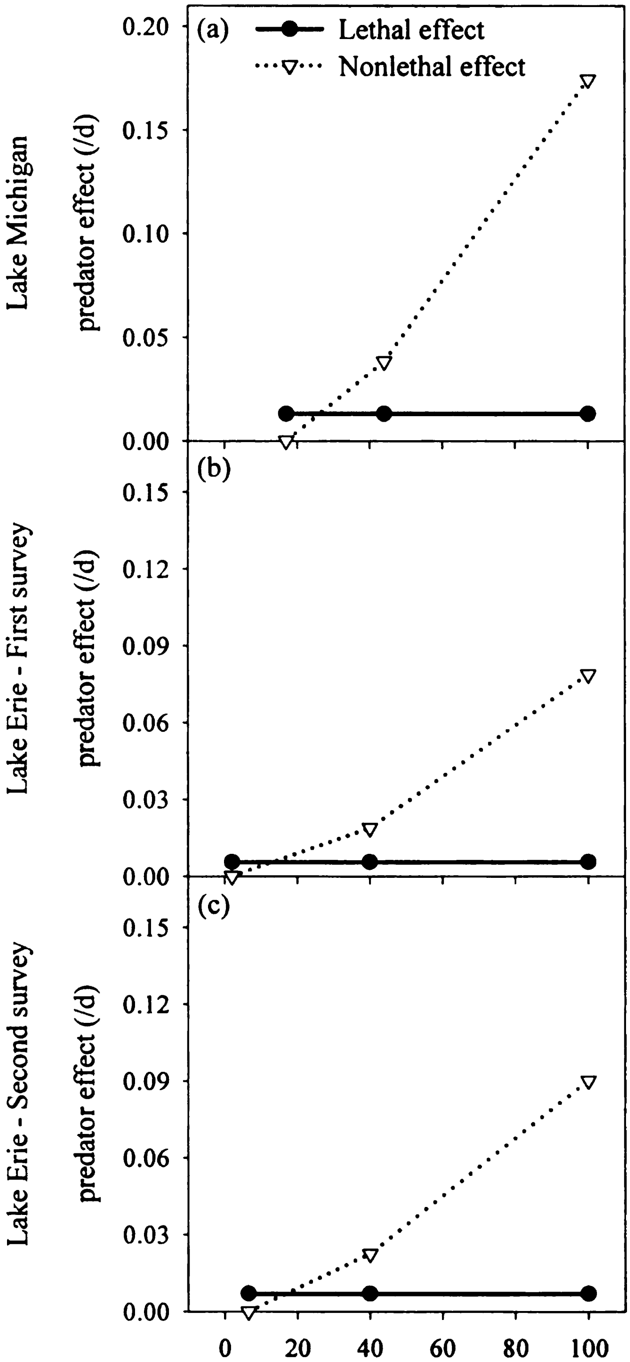

Figure 5.5. Estimated lethal and non-consumptive effects of *Bythotrephes* on *D. mendotae* in Lake Michigan (a) and *B. longirostris* in Lake Erie (b, c). Non-consumptive effects (dotted line with open triangles) were estimated based on three different scenarios (see Methods section) that assumed different 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.

the importance of non-consumptive 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 non-consumptive effects are necessarily absent. At other times, prey vertical migration appeared to be driven entirely by *Bythotrephes'* presence and, in this scenario, non-consumptive effects were estimated to be up to 10 times greater than lethal effects. Whereas the non-consumptive 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. Krueger, *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 zooplankton prey. Following the introduction of *Bythotrephes* in Lake Michigan, zooplankton vertical distribution deepened (Lehman and Cáceres 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 (Chapter 1).

Because *Bythotrephes* consume prey at higher rates near the surface, we consider if 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 *B. longirostris*) in a manner identical to that reported here (Chapters 1 and 2); (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 (Figure 5.3); (3) analysis of the extensive survey data (Appendix E) 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 non-consumptive 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 (Chapter 3). 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 non-consumptive 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 non-consumptive predator effects at the population level (Nelson et al. 2004; Boeing et al. 2005) if we were 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 non-consumptive effects can strongly influence population-level responses, even exerting greater effect on prey populations than do lethal effects in large-scale, in natural settings.

The results of our study have implications to how 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. Non-consumptive 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, non-consumptive 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 non-consumptive 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 non-consumptive 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 (approximately 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 into changes in non-consumptive effects on Great Lakes zooplankton over the last two decades and further our understanding of the non-consumptive effects of invasive species in general.

CHAPTER 6

INTERACTIONS BETWEEN LAKE MICHIGAN COMPETITORS MEDIATED BY THE BEHAVIOR OF A SHARED PREY

ABSTRACT

We modeled the interactions between *Bythotrephes longimanus*, *Daphnia mendotae*, and age-0 alewife (*Alosa pseudoharengus*) in Lake Michigan to evaluate how consideration of trait-mediated indirect interactions between *Bythotrephes* and alewife would change predictions of the impact *Bythotrephes* has on alewife. We used two models that were linked together and ran simultaneously. The first model estimated the effects of *Bythotrephes* on the population dynamics and vertical distribution of *Daphnia* over the course of a season (June 1 - October 31). The second model estimated consumption and growth of age-0 alewife over the same time period. Daily *Daphnia* density from the first model was added to a pool of prey items in the second model that were available for alewife to encounter and consume. Model predictions depended strongly on whether or not the NCEs of *Bythotrephes* were included. For example, when only CEs of *Bythotrephes* were considered, predicted mean length of alewife entering winter was 110 mm and predicted over-winter survival was 87 %. When NCEs were added, both by including a cost of migration on *Daphnia* population growth rate and considering the reduction in overlap between fish and *Daphnia* resulting from migration, predicted mean length of alewife entering winter was 72 mm and predicted over-winter survival was 19 %. Thus, model results suggest that *Bythotrephes* primarily affects fish growth through trait-mediated indirect effects caused by induced changes in prey behavior. These

findings provide an example in a natural system of how interactions between competitors can be strongly influenced through adaptive behavioral responses of shared prey.

INTRODUCTION

The detrimental effects of human disturbance on ecosystems (Jackson et al. 2001; Essington et al. 2006) combined with the growing demand on ecosystem services (Bennett and Balvanera 2007) have exacerbated the need for sound management of our natural resources. One response has been a paradigm shift within managing from a single species context to managing within a multi-species or ecosystem-based context (Browman et al. 2004; Pikitch et al. 2004). The motivation here is to better account for the complex effects humans may have on ecosystems by considering ecosystem-level processes such as indirect interactions, feedback loops, and shifts between alternative regimes (Curry 2004).

Ecosystem-based management relies heavily on food web models (Christensen and Walters 2004). Food web models link species populations in the ecosystem based on predator-prey interactions. These interactions are typically represented by consumptions rates; however, there is an increasing awareness that predators can affect prey through means other than direct consumption in ways that may profoundly influence food web processes (Abrams 1995; Werner and Peacor 2003). For example, prey may respond adaptively to predators by modifying their traits (reviewed in Harvell 1990; Sih 1997; Lima 1998; Tollrian and Harvell 1999). Trait modifications are important to predator-prey interactions because they generally reduce the vulnerability of prey and because they come at a cost to prey growth rate (Werner et al 1983; Peckarsky et al. 1993; Diehl and

Eklov 1995; Nakaoka 2000; reviewed in Peacor and Werner 2004). Theory indicates that non-consumptive effects of predators may be strong enough to affect prey and predator abundance and dynamics (Ives and Dobson 1987; Abrams 1992, 1995; Bolker et al. 2003). Further, trait modifications may affect how predators and prey interact with other species in an ecosystem, a phenomenon referred to as trait-mediated indirect interactions (Turner and Mittlebach 1990; Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; also termed interaction modifications, Wootton 1994).

Recently, some aspects of predator-induced trait modifications have begun to be incorporated into food web models. Most frequently incorporated are prey vulnerability functions, in which prey become less vulnerable to predators as predation mortality increases (Dill et al. 2003; Christensen and Walters 2004; Garrott et al. 2007). Consideration for prey vulnerability has been shown to improve model predictions of food web dynamics in large, complex ecosystems (Harvey et al. 2003; Araújo et al. 2006). However, in most applied food web models, decreased vulnerability does not come with an associated cost to prey. Further, the vulnerability of a prey to one predator is generally considered independent of the prey's vulnerability to another predator (though see Walters and Christiansen 2007). It is not clear how exclusion of these interactions may affect food web model predictions, but based on ecological theory and experimental findings, the effects may be profound.

Here we present a model of consumptive and non-consumptive interactions occurring in Lake Michigan pelagic ecosystem. We focus specifically on the competitors, age-0 alewife (*Alosa pseudoharengus*) and *Bythotrephes longimanus*, and their shared prey resource, zooplankton. Alewives are a dominant forage fish in Lake Michigan and the primary food resource for salmonids in Lake Michigan (Madenjian et al. 2002). *Bythotrephes* is a predatory cladoceran that was introduced into Lake Michigan via ballast water in the 1980s. *Bythotrephes* has been credited with changing the zooplankton community (Lehman and Cáceres 1993), and is a particular concern to biologists, because its effect on zooplankton may affect the survival of age-0 alewife (Shuter and Mason 2003), whose recruitment into the adult population depends in part on the availability of zooplankton as a food resource (Hook et al. 2007).

In addition to direct consumption of zooplankton, experiments and field observations indicate that *Bythotrephes* induces changes in zooplankton behavior. As *Bythotrephes* density increases, zooplankton migrate to deep-water refugia during the daytime to avoid being eaten. *Bythotrephes*-induced migration may indirectly affect alewife in two ways. First, zooplankton migration causes reductions in zooplankton population growth rate due to inhabiting cooler water temperatures, ultimately leaving less zooplankton for alewife to consume. Second, zooplankton migration reduces zooplankton spatial overlap with alewives, which inhabit shallow regions of the water column during their first year of life.

Here we constructed a food web model that includes the contribution of induced zooplankton migration to the net predicted impact of *Bythotrephes* on age-0 alewife. Our goal was to elucidate the significance of non-consumptive effects to food web predictions by comparing their importance relative to the traditionally considered consumptive effects. This exercise also aids in better understanding the impact of *Bythotrephes* in invaded ecosystems.

METHODS

We used two models that were linked together and run simultaneously over a simulated growing season (Figure 6.1). The first model predicted seasonal zooplankton population dynamics as a function of abiotic conditions and interactions between zooplankton and *Bythotrephes*. We focused specifically on one zooplankton species, *Daphnia mendotae*, which is the most dominant species during the summer (Barbiero and Tuchman 2001) and thought to be an important food resource to *Bythotrephes* (Lehman and Cáceres) and age-0 alewife (Stewart and Binkowski 1986). The second model estimated the prey consumption and growth of age-0 alewife over the same time period. Daily *Daphnia* density from the first model was added daily to a pool of other prey items in the second model that were available for alewife to encounter and consume. We ran the models under environmental conditions observed in Lake Michigan at a site 20 km offshore of Muskegon, Michigan (Figure 6.2).We chose this location because interactions among *Bythotrephes*, alewife, and *Daphnia* have been observed there, and it is where the off-shore-abundant *Bythotrephes* and the near-shore-abundant alewife have the strongest spatial overlap. In addition, densities of age-0 alewife at this site do not achieve high enough levels to substantially affect the density or behavior of *Daphnia* (K. L. Pangle, unpublished data), thus simplifying the interactions required in the model.

We ran the models under eight different scenarios of indirect effects of *Bythotrephes* on alewife that occur from all possible combinations of the presence and absence of (1) direct consumption of *Daphnia*, (2) reduction in *Daphnia* birth rate due to induced vertical migration, (3) reduction in vertical overlap between *Daphnia* and alewife due to induced vertical migration (Table 6.1). We compared outcomes of the scenarios

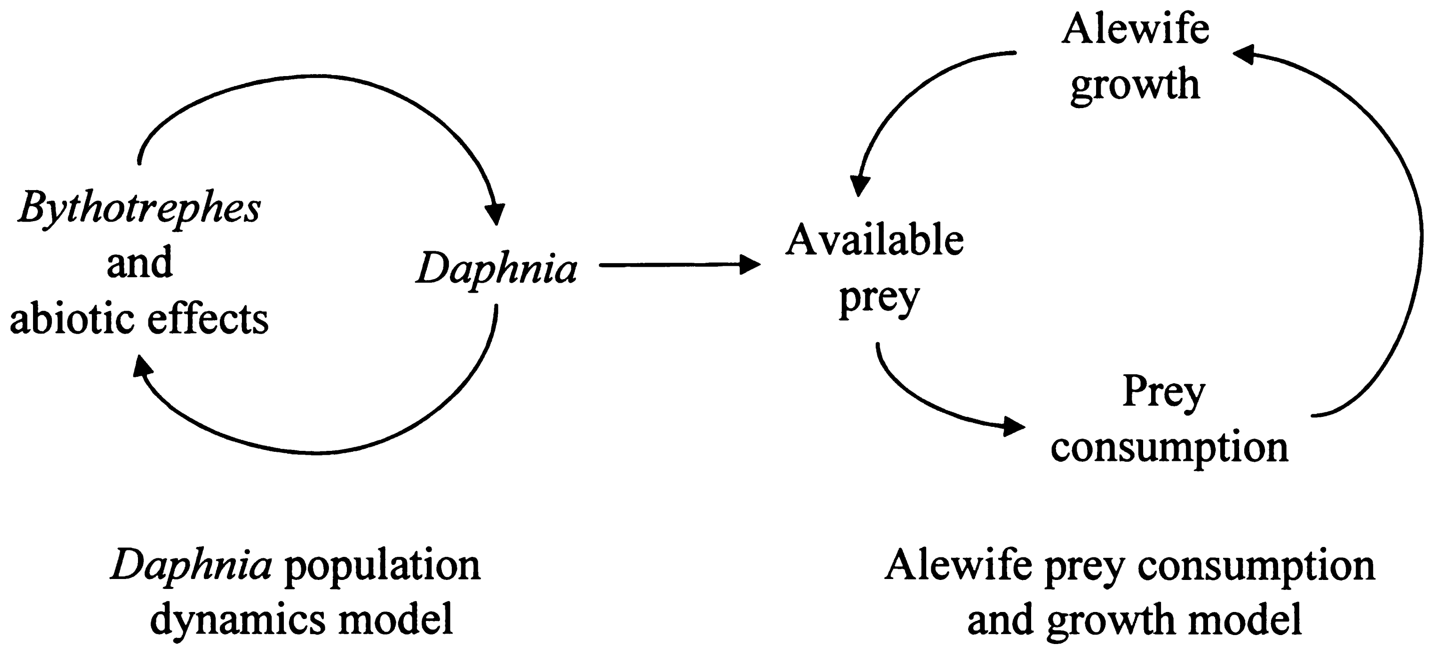

Figure 6.1. Schematic of the two models used in this study and how they are linked to each other.

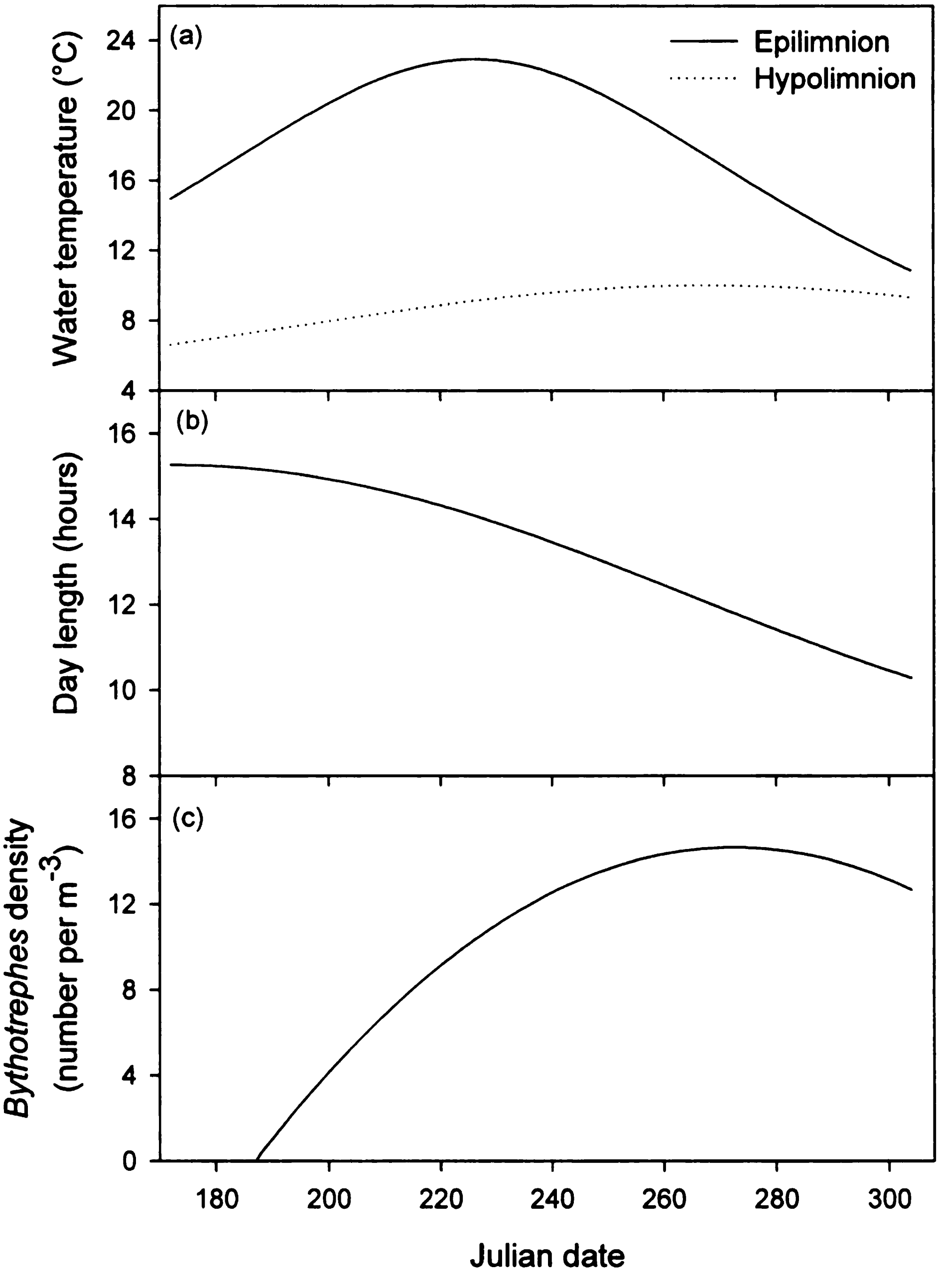

Figure 6.2. Seasonal environmental variables simulated in the model, including water temperature (panel a), day length (panel b), and *Bythotrephes* density (panel c).

Table 6.1. Eight model scenarios that included (X) and excluded (O) different indirect effects of *Bythotrephes* on alewife.

Scenario	Direct consumption of *Daphnia*	Reduction in *Daphnia* birth rate	Reduction in *Daphnia*-alewife vertical overlap
1	O	O	O
2	X	O	O
3	O	X	O
4	O	O	X
5	O	X	X
6	X	O	X
7	X	X	O
8	X	X	X

based on predicted size of age-0 alewife over the simulated growing season and predicted over-winter survival of age-0 alewife given the size they attained at the start of winter.

Daphnia *population dynamics model*

The dynamics of a *Daphnia* population (N) were modeled using predicted daily per capita birth rate (b) and death rate (d) (i.e., no net immigration or emigration) and the equation:

$$(6.1) \quad \frac{dN}{dt} = (b - d)N$$

Birth and death rates depended on seasonal changes in water temperature, day length, and *Bythotrephes* density (Figure 6.2). These parameters were derived from observations in Lake Michigan, and *Bythotrephes* density was not dynamically linked to *Daphnia* density.

Daphnia birth and death rates vary over the course of the day due to *Daphnia* diel vertical migration, changes in sunlight intensity (Chapter 5), and the density of *Daphnia*. To account for this variation, we estimated birth and death rates for the daytime, crepuscular time, and nighttime, and then averaged the birth and death rates across the different periods, weighted by the portion of time (w_t) represented by each period. In the model, the daytime was the fraction of the day between sunrise and sunset (Figure 6.2), the crepuscular time was the two hours prior to sunrise and the two hours following sunset, and the nighttime was the remaining hours of a 24-hr day.

Daphnia in the model inhabited either the hypolimnion or the epilimnion and the fraction of the *Daphnia* population in each stratum was dependent on *Bythotrephes* density (B) and time of day (Chapter 5). During the daytime period, the fraction of

Daphnia in the hypolimnion ($p_{day,hypo}$) and in the epilimnion ($p_{day,epi}$ or 1- $p_{day,hypo}$) was estimated using the equation:

(6.2) $p_{day,hypo} = \sin(0.04651 + 0.14850 \log_e(3.2\ B+1))$

which was derived from field observations of the change in the fraction of *Daphnia* in the hypolimnion over a gradient of *Bythotrephes* densities (Chapter 5). During the crepuscular period, the relative portion of *Daphnia* in the hypolimnion ($p_{day,hypo}$) was 70 % of the density during the day period, while the other 30 % was added to the density of *Daphnia* in the epilimnion. This change in distribution is based on observations of *Daphnia* migration in Lake Michigan (Chapter 5). During the night period, all *Daphnia* were in the epilimnion.

Daphnia per capita birth rate (b, day^{-1}) was derived by averaging across the different birth rates experienced in a day due to changing temperature using the equation:

$$(6.3)\quad b = \sum_{t} b_t w_t$$

where b_t is the birth rate predicted for time period t and w_t is the time-weighting factor. For each time period, b_t was predicted using the equation:

$$(6.4)\quad b_t = \sum_{z} p_{z,t} b_z \left(1 - \frac{p_{z,t} N}{K}\right)$$

where p_z was the portion of Daphnia in strata z , b_z was the maximum birth rate of *Daphnia* in strata z, and K was carrying capacity (K; 11,000 individuals m^{-3}). Maximum birth rate and carrying capacity was derived from both experimental and observational data (K. L. Pangle, unpublished data). Birth rate of strata *z* was calculated as function of water temperature (*T*, °C) using the equation:

(6.5) $$b_z = 0.0002\ T_z^{\ 2} + 0.0051\ T_z - 0.0077$$

where T_z is the mid-point temperature of strata *z*. The equation was derived experimentally (Edmonson and Litt 1982) and assumed that *Daphnia* fecundity was independent of temperature.

Deaths of *Daphnia* were due solely to predation by *Bythotrephes*, and *Daphnia* were only vulnerable to *Bythotrephes* predation while in the epilimnion. The per capita rate of predation by a single *Bythotrephes* (a_t, individuals consumed m^{-3} *Bythotrephes*$^{-1}$ day^{-1}) during time period *t* was modeled as:

(6.6) $$a_t = \frac{0.008196}{1+\left(\frac{L_t}{24.96}\right)^{-1.034}}$$

where L_t is the light intensity (µmol m^{-2} sec^{-1}) typically observed at the mid-point depth of the epilimnion during time period *t* (Chapter 5). Equation 6 was derived experimentally (Chapter 4). Light intensities used for the daytime, crepuscular time, and nighttime were 600, 60 and 1 µmol m^{-2} sec^{-1}, respectively. Per capita death rate of *Daphnia* for each time period was calculated using the equation:

(6.7) $$d_t = \sum_z p_{z,t}\, a_t B$$

where $p_{z,t}$ was the portion of *Daphnia* in epilimnion during time period t and B is *Bythotrephes* density. Per capita rate of predation for each time period was averaged, weighted by period length, as in equation 3.

The density of *Daphnia* from July 1 to October 31 was solved numerically using the Runge-Kutta (4,5) approximation. The initial density of *Daphnia* (1 individual m^{-3}) was estimated from field observations.

Alewife prey consumption and growth model

The daily consumption and growth of alewife was modeled from its hatch date to the start of winter. The model was adapted from one presented in Fulford et al. (2006), which modeled the same processes for age-0 yellow perch in Lake Michigan, and consisted of a consumption sub-model that determined the number and type of prey eaten and a bioenergetics sub-model that incorporated consumption into an energy budget to determine somatic growth. In this model, alewife consumed seven prey types (Table 6.2) at rates that depended on encounter rates, handling time, and alewife selectivity. Prey types, except for *Daphnia* and *Bythotrephes*, was kept at constant, conservatively high densities that were observed in Lake Michigan during periods in which *Daphnia* was absent (K. L. Pangle, unpublished data). The lengths and weights of prey types were averages observed in Lake Michigan (Fulford et al. 2006).

Consumption sub-model

Encounter rate (E_i, prey sec^{-1}) of each prey type was a product of the swimming speed and reaction area of alewife and the density of the prey type. Swimming speed

Table 6.2. Summary of characteristics of each prey type used in the model.

Prey type	Density (number per m^{-3})*	length (mm)	dry weight (µg)	selectivity relationships
Rotifers	60000	0.13	0.1	$193{,}449\ \mathrm{TL}^{-7.64}$
Nauplii	4000	0.2	0.19	0.07
Cyclopoid	350	0.43	0.58	$-0.042\ \mathrm{TL}^2 + 0.75\ \mathrm{TL} - 2.6$ for TL<12 0.2 for TL>12
Calanoid	800	0.54	1.85	$0.272\ \ln(\mathrm{TL}) - 0.3834$ for TL<17 mm 0.4 for TL>17 mm
Bosmina	5000	0.3	1.2	$\dfrac{0.4}{\left(1+\left(\dfrac{0.4}{0.09}-1\right)\exp(0.403\ \mathrm{TL})\right)^{1/0.031}}$
Daphnia	*N*	0.9	3.3	$\dfrac{0.445}{\left(1+\left(\dfrac{0.445}{0.092}-1\right)\exp(0.580\ \mathrm{TL})\right)^{1/0.029}}$
Bythotrephes	*B*	10	200	0 for TL<50 mm same as *Daphnia* for TL>50 mm

*prey densities in the model are actually in units, #/m (mm sec^{-1}) was expressed as a function of wet weight (*WW*, g) and water temperature (*T*) using the equation:

$$(6.8)\quad SS_{\mathrm{WW},\,Temp} = 29.3\left(\frac{\mathrm{WW}}{1{,}000{,}000}\right)^{0.274}\exp(0.056\cdot T)$$

derived experimentally for alewife (Klumb et al. 2003). Reaction area ($RA_{i,TL}$) was expressed as a function of prey size and fish size using the equation:

$$(6.9)\quad RA_{i,TL} = \left(\frac{PL_i}{2\tan\left(rad_{TL}/2\right)}\right)^2 \pi\cdot 0.5$$

where PL_i is the length (mm) of prey *i*, and rad_{TL} is the angle (radians) of visual acuity for a larvae of a given TL. This equation is commonly used for age-0 fish (Rose and Cowan 1993, Letcher et al. 1996). We used the relationship between *rad* and TL:

$$(6.10)\quad rad = 0.0167\exp\left(9.14 - 2.4\ln(TL) + 0.229\ln(TL)^2\right)$$

which was found experimentally for bluegill from 10 to 150 mm TL and swimming in clear water (Breck and Gitter 1983) and has been applied to multiple species of fish (Letcher et al. 1996).

The probability that alewife consume an encountered prey ($Q_{i,\mathrm{TL}}$, unitless) is calculated as:

$$(6.11)\quad Q_{i,\mathrm{TL}} = \frac{\alpha_{i,\mathrm{TL}}N_i}{\sum_j \alpha_{j,\mathrm{TL}}N_j}$$

where $\alpha_{i,\mathrm{TL}}$ is the selectivity of a fish of length k for prey type *i* and N_i is the density of prey type *i* (Lockwood 1998). The relationships between α and TL for each prey type are not well known for alewife, so they were derived from experiments using age-0 yellow perch (Fulford et al. 2006, Table 6.2), except for *Bythotrephes*. Yellow perch have similar predatory behavior relative to alewife during early life-history stages (Miller et al. 2007). Alewife are incapable of consuming *Bythotrephes* until they reach approximately 50 mm TL (Branstrator and Lehman 1996), and, after fish reach 50 mm TL, their selectivity on *Bythotrephes* is similar to that on *Daphnia* (Pothoven et al. 2007). Consequently, the α for *Bythotrephes* was kept at 0 for fish < 50 mm TL, and the same as that for *Daphnia* for fish > 50 mm TL.

Handling time (sec) was expressed as a function of *PL* (mm) and TL (mm) using the equation:

$$(6.12)\quad H_{PL,TL} = \exp\left(0.264 \cdot 10^{7.0151 \cdot \left(\frac{PL}{TL}\right)}\right)$$

The equation was derived using yellow perch data from Mills et al. (1984) and Miller et al. (1992). Miller et al. (1992) showed that the relationship between body size and handling time of prey for yellow perch and alewife were very similar.

Consumption rate (C, μg day^{-1}) was calculated as:

$$(6.13)\quad C = \frac{\sum_i E_{i,\mathrm{TL}} Q_{i,\mathrm{TL}} PW_{i,\mathrm{TL}}}{1 + \sum_i E_{i,\mathrm{TL}} Q_{i,\mathrm{TL}} H_{PL,\mathrm{TL}}} \cdot DL$$

where PW_i is the dry weight (μg) of prey i, $H_{PL,\mathrm{TL}}$ is the handling time (sec) for prey of length (PL) for an alewife of a given TL, and DL is day length (sec). Consumption rate (C, μg day^{-1}) could not surpass a maximum level (C_{max}) due to physiological constraints. C_{max} is a function of fish size and water temperature, and this relationship has been specifically derived for alewife (Hanson 1997).

Bioenergetics sub-model

Consumption rate (C) was converted into daily growth using a bioenergetics model developed specifically for alewife (Stewart and Binkowski. 1986; Hewett and Stewart 1989). For positive growth to occur, energy gained through consumption needed to surpass the total loss of mass due to respiration, egestion, excretion, and specific dynamic action. Respiration, the amount of mass used by fish for routine metabolism was a function of water temperature and body size (Post 1990). Egestion, the portion of consumption that is not ingested (e.g., loss to sloppy feeding), is held constant at 16 % of consumption. Excretion, the portion of ingested food that is not assimilated, is held constant at 16 % of ingestion. Specific dynamic action, the portion of ingested food lost to the metabolic demand of assimilation, is held constant at 17.5 % of ingestion. For the calculations, we assumed that the energy density (Calories g^{-1}) of alewife and its prey were equal (Post 1990).

The mass gained (lost) due to consumption and the physiological processes was added (subtracted) to fish's current weight to determine its weight for the next day. If the change was positive, then the new weight was used to determine a new length. Total length was converted to wet weight (WW, μg) using the equations:

$$
(6.14)\quad WW = \begin{cases} \exp\left(-6.7091 + 4.3157 \cdot \ln\left(TL/_{10}\right)\right) \cdot 1{,}000{,}000 & \text{if TL} < 43.4\,\text{mm} \\ \exp\left(-4.72 + 2.96 \cdot \ln\left(TL/_{10}\right)\right) \cdot 1{,}000{,}000 & \text{if TL} \geq 43.4\,\text{mm} \end{cases}
$$

(Stewart and Binkowski 1986). Some functions in the model required the mass of fish in terms of dry weight (DW, µg). The dry-to-wet weight ratio is dependent on fish size, and can be calculated using the equation:

$$(6.15)\quad DW/WW = -0.00001 \cdot TL^2 + 0.0026 \cdot TL + 0.0945$$

derived by fitting data published for alewife (Lantry and O'Gorman. 2007; Hewett and Stewart 1989) using nonlinear least-squares regression.

The model began as alewife hatched over multiple dates. The distribution of hatch dates was based on observations from Lake Michigan (Höök et al. 2007), with mean date of July 1 and the first and last hatches occurring on June 20 and July 31 days, respectively. The initial total length (TL, mm) of alewife on each hatch date was 6 mm. This value represents the size at which alewife typically begin to feed (Heinrich 1981), and was used by Höök et al. (2007) to assign hatch dates in Lake Michigan.

Scenario simulations and comparisons

In order to run the model under the different scenarios, the indirect effects of *Bythotrephes* on alewife were systematically removed (Table 6.1). Direct consumption of *Daphnia* by *Bythotrephes* was removed by setting per capita rate of predation by a single *Bythotrephes* (*a*) to zero. The reduction in *Daphnia* birth rate due to induced vertical migration was removed by setting the water temperature of the hypolimnion equal to that of the epilimnion. The reduction in vertical overlap between *Daphnia* and alewife due to induced vertical migration was removed by allowing alewife to consume *Daphnia* in the epilimnion and hypolimnion.

Four variables were evaluated to determine the influence of NCEs, including daily *Daphnia* density and the size and growth rate of alewife over the course of the season, and alewife over-winter survival. Alewife overwinter survival was estimated using the distribution of final lengths of alewife at the start of winter and a size-dependent over-winter survival rate observed in Lake Michigan (Hook et al. 2007).

Sensitivity analysis

We evaluated the sensitivity of the model to selected parameter values by varying each parameter by ± 50 % and measuring the effect of this change on predicted over-winter survival of alewife (Christensen and Walters 2004). Sensitivity analysis was only carried out under "full effect" scenario, in which *Bythotrephes* had the largest effect on alewife.

RESULTS

Daphnia densities initially increased in all scenarios, with the greatest rates observed for scenarios in which *Bythotrephes* had no effect on *Daphnia* growth rate, and the lowest for the “full effect” scenario (Figure 6.3a). *Daphnia* densities in the “no effect” scenario were near carrying capacity by day 250, while *Daphnia* densities in scenarios that included direct consumption tended to peak around day 260 and decline thereafter, as the water temperature began to decline and *Bythotrephes* density continued to increase.

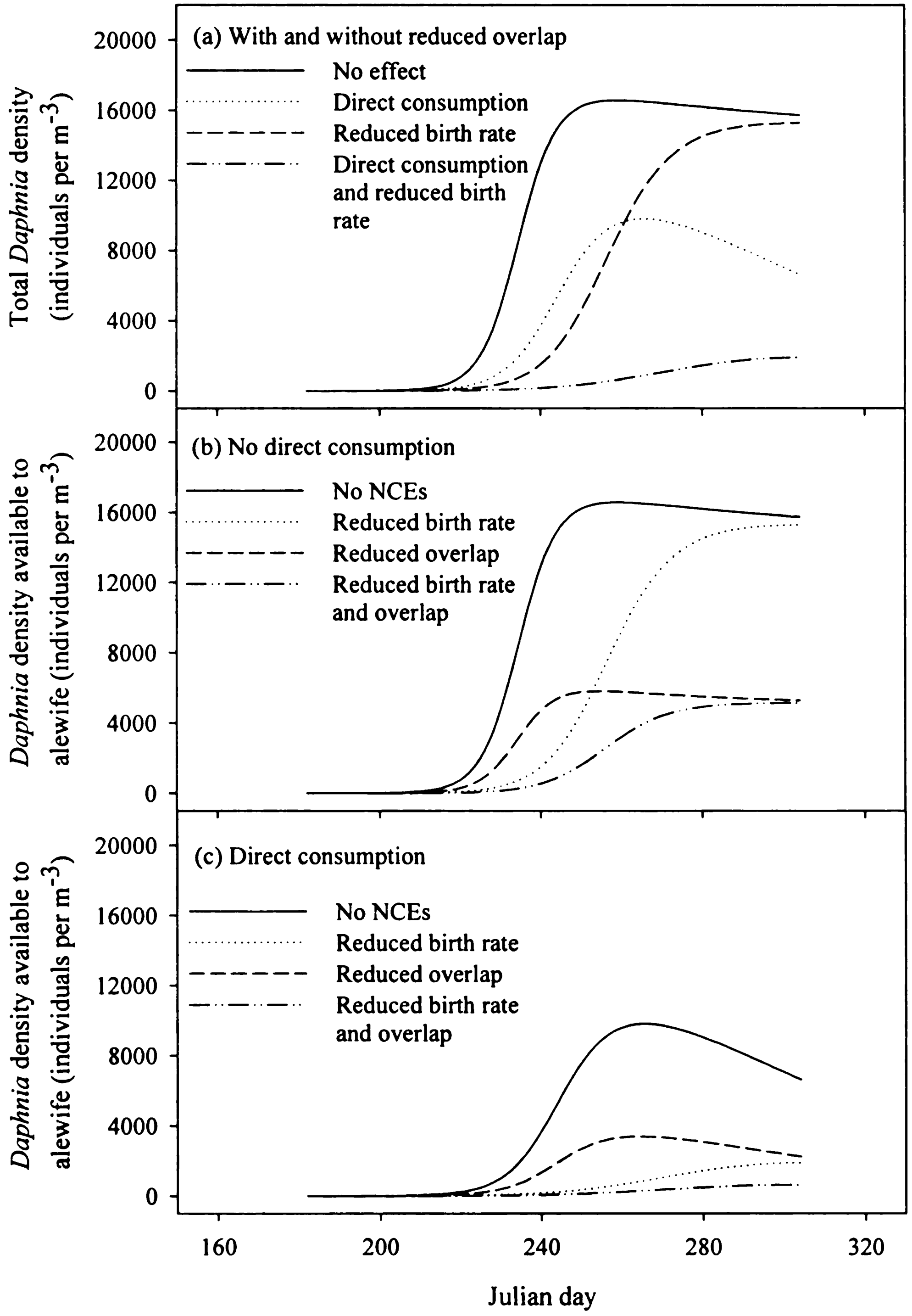

Figure 6.3. Seasonal total density of *Daphnia* (panel a) and density of *Daphnia* available for alewife to consume (panels b, c) under the eight model scenarios. Total *Daphnia* density is not affected by reduced overlap with alewife, thus the eight model scenarios are represented by four lines.

The density of *Daphnia* available from consumption by alewife followed similar trajectories as total Daphnia density (Figure 6.3b and c), with the only differences occurring between scenarios that included the overlap effect.

Alewife growth rate over the simulated season varied considerably among scenarios. The “no effect” scenario had the greatest growth rate (Figure 6.4) with a mean final length of 116 mm. In this scenario, the distribution of alewife sizes tightened as the season progressed, leading to the lowest variation in final alewife length among the scenarios (Figure 6.5). The “full effect” scenario had the lowest growth rate (Figure 6.4) with mean final length with a mean final length of 70 mm. Contrary to the "no effect" scenario, the distribution of alewife sizes remained relatively constant in scenario 8, leading to the highest variation in final alewife length among the scenarios (Figure 6.5).

Over-winter survival rate also varied considerably among the scenarios. As expected, Scenario 1 had the highest over-winter survival at 93.1 %. The inclusion of each indirect effect alone led to relatively small reductions in over-winter survival, with direct consumption having the least effect (Figure 6.4). As effects were combined, over-winter survival dropped steadily, with the lowest value, 18.7 %, obtained when all three effects were included.

Sensitivity analysis showed that model predictions of over-winter survival in scenario 8 were most greatly affected by changes in parameters associated with water temperature, *Daphnia* birth rate, *Bythotrephes* density, and alewife foraging (Table 6.3). For parameters in the *Daphnia* population dynamics model, a 50 % increase in the epilimnetic water temperature led to the greatest increase in over-winter survival. For

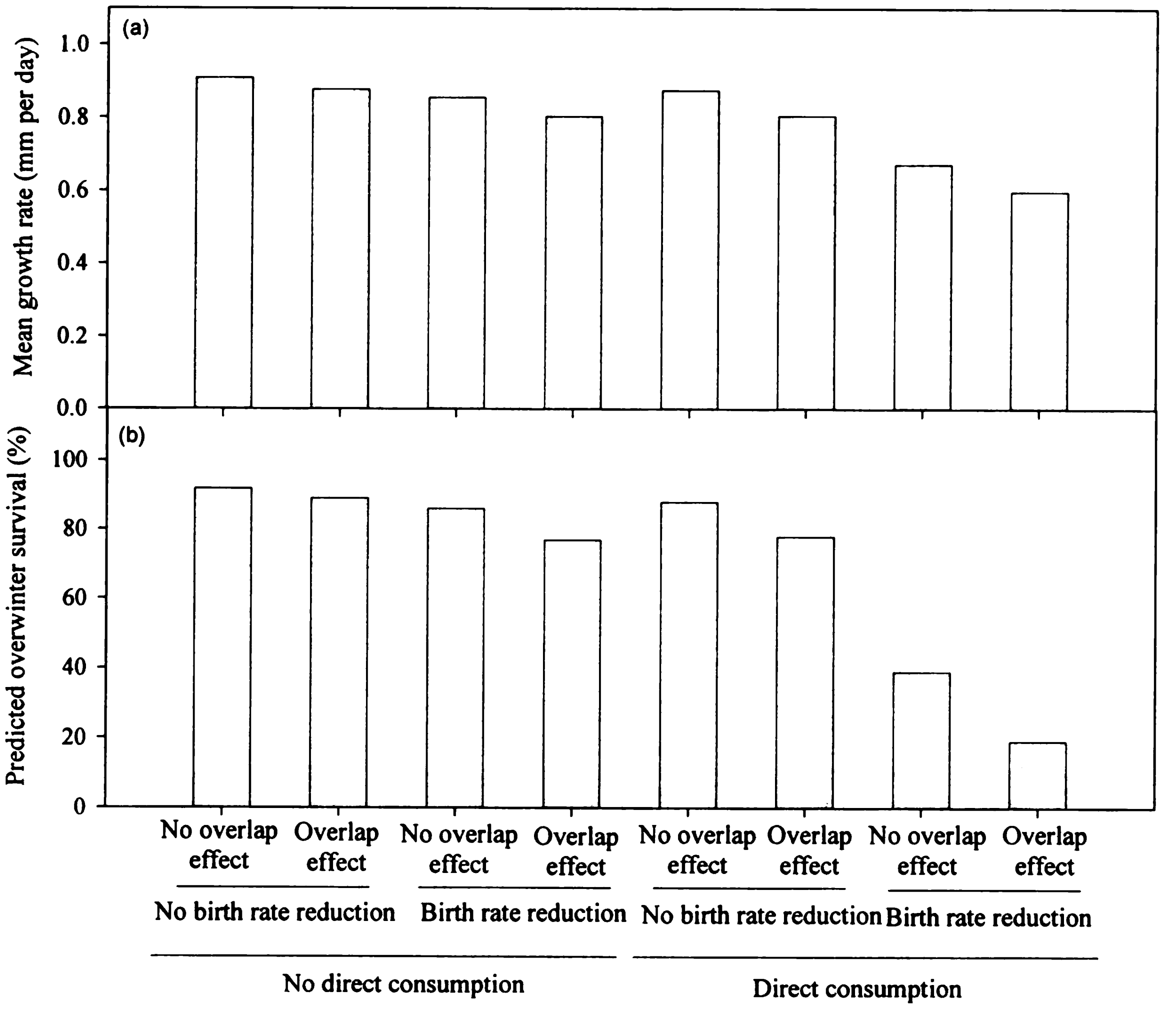

Figure 6.4. Estimated mean growth rate and survival rate for alewife in the eight model scenarios.

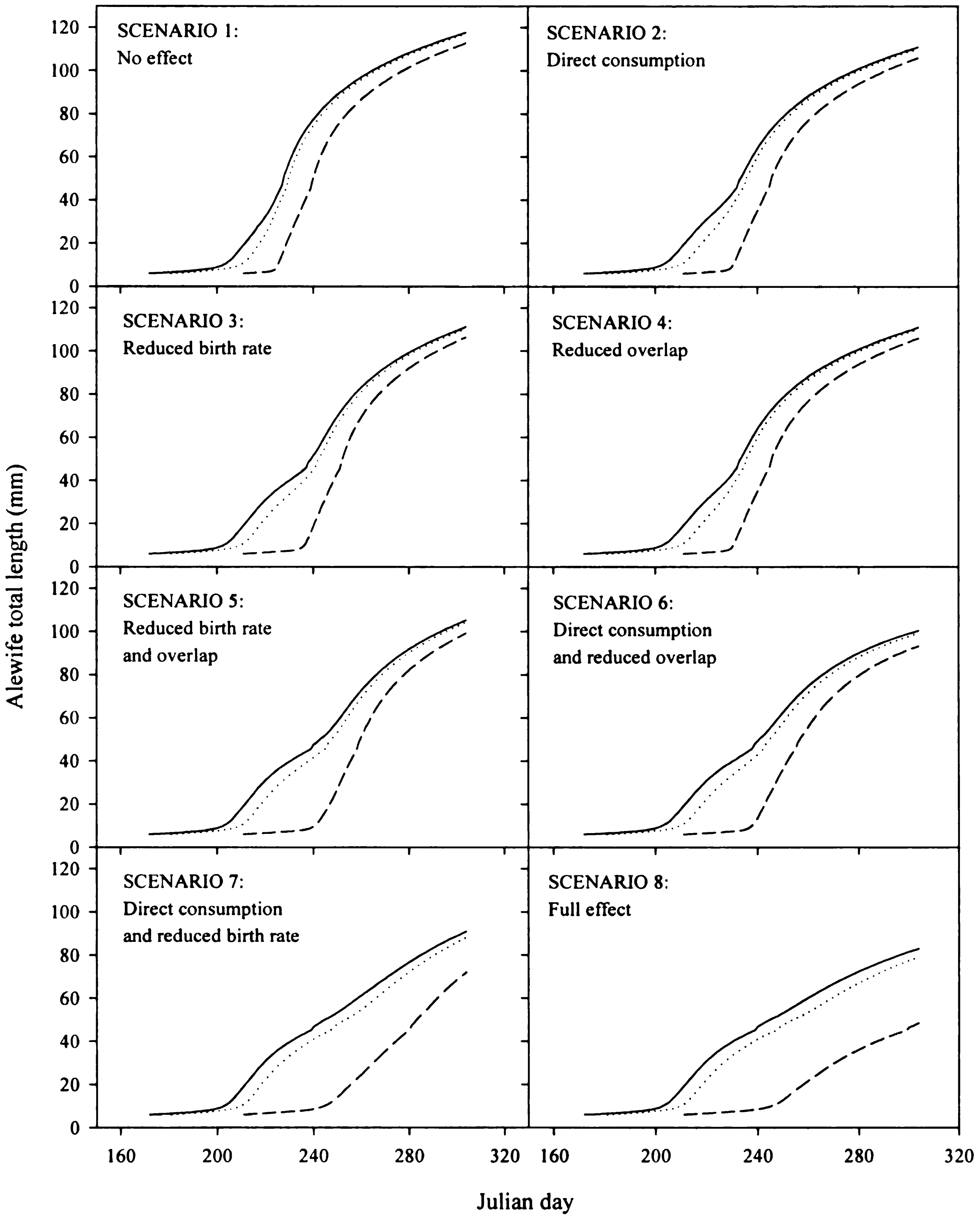

Figure 6.5. Lengths of alewife over the season that were hatched on the first (solid line), mean (dotted line), and last (dashed line) hatch date under the eight model scenarios.

Table 6.3. Results of sensitivity analysis, in which the overwinter survival in the "full effect" (original 18 %) was estimated after a ± 50 % in each parameter.

	Overwinter survival (%)	
Parameter	with 50 % decrease	with 50 % increase
Daphnia population dynamics model		
epilimnion temperature (T_{epi})	16	86
hypolimnion temperature (T_{hypo})	16	43
Bythotrephes density (B)	59	16
Intercept of equation 2	19	19
Slope of equation 2	17	23
Daphnia carrying capacity (K)	18	19
epilimnetic birth rate (b_{epi})	16	76
hypolimnetic birth rate (b_{hypo})	16	31
Bythotrephes daytime predation rate (a_{day})	42	16
Bythotrephes crepuscular predation rate(a_{crep})	25	17
Bythotrephes nighttime predation rate(a_{night})	19	18
Alewife consumption and growth model		
Initial size of alewife (TL at hatch date)	0	46
Weight-length conversion (equation 8)	8	100
Dry weight - wet weight conversion (DW/WW)	6	27
Rotifer density	0	35
Rotifer alpha value	23	16
Nauplii density	25	14
Nauplii selectivity coefficient	25	13
Cyclopoid density	21	17
Cyclopoid selectivity coefficient	22	16
Calanoid density	2	38
Calanoid selectivity coefficient	0	33
Bosmina density	3	31
Bosmina selectivity coefficient	18	19
Daphnia selectivity coefficient	17	20
Bythotrephes selectivity coefficient	15	22
Swimming speed (SS)	0	55
Angle of visual acuity (rad)	71	0
Handling time (H)	51	9
Maximum consumption	19	19
Respiration rate	54	0
Egestion	38	2
Excretion	33	5
Specific dynamic action	42	0

parameters in the alewife consumption and growth model, a 50 % decrease in the angle of visual acuity led to the greatest increase in over-winter survival.

DISCUSSION

This study demonstrates the significant role that non-consumptive interactions can play in food webs. Namely, *Bythotrephes* was predicted to have a large effect on alewife only when interactions in addition to direct consumption of a shared prey were considered. In addition, the manner in which survival rate declined with added effects indicates that the effects had complex, synergistic interactions that led to greater reductions in alewife survival than would be predicted by sum of reductions of each effect alone. Such interactions between CEs and NCEs have been shown empirically (Peacor and Werner 2001) and result here due to the non-linearity of alewife growth and survival.

While this model is still a coarse abstraction of the processes occurring in Lake Michigan, evidence suggests that this model produces patterns that are comparable to those observed in Lake Michigan. For example, Pothoven et al. (2001) report several years in which *Daphnia* population in offshore Lake Michigan have a gradual increase in density at the start of the season, which slows or reverses around day 250. In addition, Höök et al. (2007) found that in offshore Lake Michigan the length of age-0 alewife ranged from 35 to 100 mm, with a mean length of 66 mm. These field observations are very similar the distribution of lengths predicted when all three indirect effects of *Bythotrephes* were considered (Figure 6.5).

Results of this study therefore indicate that consideration of NCEs may better capture the nature of food web interactions and thus better inform ecosystem-based management that rely on food-web models. NCEs between competitors, *Bythotrephes* and alewife, have been largely excluded from food web model studies. Existing spatially-explicit models may capture some of the interactions shown to be important here (e.g., Walters et al. 1999); however, these models would only be appropriate for antipredator behaviors involving spatial movement and not for other behaviors, such as vigilance (Lima 1998), or other traits modifications, such as changes in prey morphology and life-history (Tollrian and Harvell 1999), that may also be important to indirect interactions between competitors. One justification for the exclusion of NCEs between competitors in food web models follows an evolutionary argument, in that if two competitors have foraging behaviors that induced a shared prey to modify the same trait, then intense competition between the predators will ensue and natural selection would favor differentiation of their foraging behavior (Walters and Christiansen 2007). Following this argument, consideration for NCEs between competitors in food webs that include invasive species, such as Lake Michigan, may be particularly important given the lack of co-evolution.

Explicitly considering NCEs will likely be a challenging endeavor for ecosystem-based management. Most studies of NCEs have been conducted in controlled laboratory and mesocosm settings, and their applications to large, complex ecosystems will necessarily require novel approaches. The approach we took in this study was to first develop a functional relationship that related predator density with trait induction by prey. Second, we quantified the cost of trait induction at the prey population level. Third, we considered the effect of trait inductions on interactions between the prey and other species in the ecosystem. The third requirement is a particularly severe departure from conventional food web models that are intrinsically based on pair-wise interactions.

In the context of the Great Lakes ecosystem, the results of this study suggest that *Bythotrephes* may be having detrimental effects on alewife recruitment. Indeed, the arrival of *Bythotrephes* has coincided with the declines in alewife populations in Lake Michigan and Lake Huron. It is difficult to ascertain whether these declines were caused by *Bythotrephes* because other dramatic changes have also occurred during this time period, such as the introduction of Dreissenid mussels and increases in salmon populations. In addition, the model presented here is directly applicable only to the offshore regions of Lake Michigan, and it is not well known how recruitment of alewife in the offshore regions contributes to the total alewife population. Consideration of large-scale spatial distribution of age-0 alewife and *Bythotrephes* may thus provide further insights into the impact on *Bythotrephes* on the Lake Michigan food.

APPENDIX A

A list of articles associated with the dissertation chapters. All chapters were collaborative efforts with Scott Peacor. Chapter 5 also represents a collaborative effort with Ora Johannsson.

Chapter one. Pangle, K. L., and S. D. Peacor. 2006. Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. Freshwater Biology 51: 1070-1078.

Chapter two. Pangle, K. L., and S. D. Peacor. Lack of naïveté in Lake Michigan zooplankton prey to risk posed by invasive predators. *In prep.*

Chapter three. Pangle, K. L., and S. D. Peacor. Temperature gradients, but no food resource gradients, affect growth rate of *Daphnia mendotae* in Lake Michigan. *In prep.*

Chapter four. Pangle, K. L., and S. D. Peacor. Light-dependent predation by the invertebrate planktivore, *Bythotrephes longimanus. Submitted* to Canadian Journal of Fisheries and Aquatic Sciences.

Chapter five. Pangle, K. L., S. D. Peacor, and O. E. Johannsson. 2007. Large non-consumptive effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88: 402-412.

Chapter six. Pangle, K. L., and S. D. Peacor. Interactions between Lake Michigan competitors mediated by the behavior of a shared prey. *In prep.*

APPENDIX B

Gerritsen and Strickler (1977) developed a model that predicted how predators encountered prey in aquatic systems, assuming that predator and prey: (1) are randomly distributed; (2) swim in random directions; (3) swim at an average velocity; and (4) encounter each other when prey are within a reaction space around the predator. This reaction space is described by a solid angle (s) using the equation:

(B.1) $s = \sin\theta \, d\theta \, d\phi$

where θ is the polar angle and ϕ is the azimuthal angle. An encounter model was adapted specifically for *Bythotrephes*-prey encounters by Muirhead and Sprules (2003). In this model, the rate of prey encounter (Z, number h^{-1}) by a single *Bythotrephes* is estimated using the equation:

(B.2) $$Z = \frac{R^2 N}{2} \int_0^{2\pi} \int_0^{\frac{\pi}{2}} \sin\theta \sqrt{u^2 + v^2 - 2uv\cos\theta} \, d\theta \, d\phi$$

where R is the reaction distance of the predator (m), N is prey density (number m^{-3}), and u and v are the swimming velocities ($m\ h^{-1}$) of the prey and predator, respectively. Using a series of laboratory experiments, Muirhead and Sprules (2003) related *Bythotrephes* reaction distance (mm) to light intensity (L, $\mu mol\ m^{-2}\ s^{-1}$) according to the set of equations:

(B.3)

$$R = \begin{cases} 6.61, & L < 2 \\ -7.69 + 36.97\log_{10}(L+1) - 21.88\log_{10}(L+1)^2 + 3.93\log_{10}(L+1)^3, & 2 \le L \le 500 \\ 9.995, & L > 500 \end{cases}$$

We estimated difference in the rate of *D. mendotae* encountered between the low and mid-light treatments of Experiment 2 using this model given our experimental conditions. From the literature, we found average swimming velocities (mm s^{-1}) for second instar *Bythotrephes* (16.03; Muirhead and Sprules 2003) and *Daphnia mendotae* (1.2; Gerritsen 1980). Model predictions were compared with difference between encounter rates observed in Experiment 2 calculated using ingestion rates (I) and the equation:

(B.4) $I = N(1 - \exp(-Z(T - hI))$

where T (hours) is the total duration of the experiment and h (hours) is an experimentally-derived estimate of the handling time associated with the consumption of individual *Daphnia* by *Bythotrephes* (K. L. Pangle, unpublished data). This recursive equation allowed us to estimate encounter rate for *Bythotrephes* exposed to a saturating level of prey density (Hassel 1978).

APPENDIX C

A swimming planktivore produces water velocity gradients that can alert zooplankton of its presence. Studies have shown that zooplankton are particularly sensitive to the deformation rate (d, s^{-1}) component of water velocity gradients caused by a predator (Kiørboe and Visser 1999; Kiørboe et al. 1999). Assuming that a planktivore produces water velocity gradients that are similar to that of a sphere, with a radius, r (cm), and a velocity, v (cm s^{-1}), and assuming that zooplankton respond to a planktivore when deformation rate surpasses some critical threshold (Δ, s^{-1}), the distance that zooplankton can detect a planktivore (D, cm) can be calculated using the equation:

$$\text{(C.1)} \quad D = r\sqrt{\frac{3v}{4r\Delta}\left(1+\sqrt{1-\frac{8r\Delta}{3v}}\right)} \quad \text{for } \Delta \le \frac{3v}{8r}$$

Using this model, we estimated the distance that *D. mendotae* could detect *Bythotrephes* using a critical threshold found for *Daphnia* (1.8 s^{-1}, Brewer et al. 1999), *Bythotrephes* swimming velocity (1.6 cm s^{-1}; Muirhead and Sprules 2003), and the mean thoracic radius of *Bythotrephes* used in the experiment (0.15 cm).

APPENDIX D

We used a second method to estimate the non-consumptive effect (Δb) of the predator on prey population growth rate. In this case, we used somatic growth rate as a surrogate for population growth rate. For cladoceran species like *D. mendotae* and *B. longirostris*, somatic growth rate correlates very strongly with population growth rate ($r^2 = 0.99$, Lampert and Trubetskova 1996).We estimated somatic growth rate (SGR, /d) for *D. mendotae* and *B. longirostris* using the equations:

$$\text{(D.1)} \quad SGR = -0.0009\,T^2 + 0.0476\,T - 0.1882$$

and

$$\text{(D.2)} \quad SGR = -0.0002\,T^2 + 0.0020\,T - 0.0506,$$

respectively, where T is water temperature (°C). These equations were derived by fitting nonlinear models to published data on *D. mendotae* (Hall 1964) and *B. longirostris* (Hanasato and Yasuno 1985). The mean somatic growth rate of each sampling profile (SGR_p) was calculated as:

$$\text{(D.3)} \quad SGR_p = \frac{\sum_z SGR_z N_z w_z}{\sum_z N_z w_z}$$

where SGR_z was the estimated somatic growth rate at the depth z given its midpoint temperature, N_z was the prey density (number/m^3) at depth z, and w_z (m) was the height of the water column represented by depth z. SGR_ps were averaged over the entire 24-h period using the same weights as Equation 5 in the main text. The non-consumptive effect of the predator was then calculated as the difference between the estimated somatic growth rate using the vertical distributions of prey when *Bythotrephes* was present and when *Bythotrephes* was absent. The former distributions came from the three intensive surveys, while the latter distributions were the deepest, the average, and the shallowest observed prey distributions in *Bythotrephes* absence from our extensive surveys.

This method yielded qualitatively similar estimates of the non-consumptive effect, relative to the lethal effect, of *Bythotrephes* on prey growth rate that of the more direct method based on life history of organisms collected in the field. For *D. mendotae* in Lake Michigan, the non-consumptive effect on somatic growth rate was estimated as 0, 0.101, and 0.211 /d, respectively, based on our three scenarios in which prey were at the deepest, the average, and the shallowest observed prey distributions in *Bythotrephes* absence from our extensive surveys. For *B. longirostris* in Lake Erie, estimates of non-consumptive effects in the first survey were 0, 0.048, and 0.105 /d, respectively, while estimates were 0, 0.016, and 0.050 /d, respectively, in the second survey.

APPENDIX E

In the extensive field survey, *Bythotrephes* biomass had a negative influence on the percentage of prey in the epilimnion and a positive influence on the percentage of prey in the hypolimnion (Figs. 1 and 2).We interpreted these patterns as reflecting an induced vertical migration that was an adaptive behavioral response to predation risk. Here we evaluate an alternative possibility, namely that the observed changes in prey distribution are due to predation by *Bythotrephes*; i.e. predation by *Bythotrephes*, which was found primarily in the epilimnion, would also cause a reduction (increase) in the percentage of prey in the epilimnion (hypolimnion).

Consider the abundance of prey species in the hypolimnion. If *Bythotrephes* predation, not induced prey migration, were responsible for changes in prey distribution, then *Bythotrephes* would not affect the abundance of prey in the hypolimnion. Therefore, there would not be a correlation between *Bythotrephes* biomass and prey density. In contrast, if changes in prey distribution resulted from induced vertical migration, then we would expect prey abundance in the hypolimnion to be positively correlated with *Bythotrephes* biomass. Therefore a positive correlation would be consistent with our interpretation of induced migration but not predation. Note that these predictions require that there is no correlation between total prey abundance (in the water column) and *Bythotrephes* biomass. Because we expect either consumption or induced vertical migration to negatively affect prey abundance, the inference that a positive correlation between *Bythotrephes* biomass and abundance in the hypolimnion resulted from induced vertical migration is conservative. We used linear regression analysis to examine the relationship between prey abundance in the hypolimnion and *Bythotrephes* biomass. Prior to analysis, absolute prey abundance and *Bythotrephes* biomass were log-transformed to normalize distributions of dependent and independent variables (Zar 1999). There was a positive relationship between *Bythotrephes* biomass and the abundance of *Daphnia mendotae* and *Bosmina longirostris* in the hypolimnion (*D. mendotae*: $t_{12} = 2.02, p = 0.03$; *B. longirostris*: $t_{13} = 1.69, p = 0.05$) in Lake Michigan, and of *B. longirostris* and *D. retrocurva* abundance in the hypolimnion (*B. longirostris*: $t_{52} = 2.37, p = 0.01$; *D. retrocurva*: $t_{40} = 2.42, p = 0.01$) in Lake Erie. Therefore, analysis of the absolute abundance of *Bythotrephes* prey are consistent with our interpretation that the prey relative abundance at different levels was affected by *Bythotrephes*-induced changes in vertical migration rather than predation.

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