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ENVIRONMENTAL DEPENDENCE OF NON-CONSUMPTIVE EFFECTS IN PREDATOR-PREY INTERACTIONS

By

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ABSTRACT

ENVIRONMENTAL DEPENDENCE OF NON-CONSUMPTIVE EFFECTS IN PREDATOR-PREY INTERACTIONS

By

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Predators affect the population dynamics of their prey in two ways, through direct consumption (consumptive effect) or through inducing trait changes (non-consumptive effect). Studies have shown that the trait changes induced by predators reduce fitness enough to make up a large portion of the total effect of the predator. However, these studies were conducted under a finite set of natural conditions. Little is known about how variation in biotic and abiotic parameters affects trait expression or the importance of non-consumptive effects. I investigated the importance of the non-consumptive effect of *Bythotrephes longimanus* (predator) on *Daphnia mendotae* (prey) in terms of population growth rate (instantaneous measure) and population dynamics (longer-term), using three modeling techniques. *D. mendotae* respond to *B. longimanus*, a visual predator, by migrating down in the water column into cooler, darker water to avoid predation, however, this behavior incurs a reproductive cost associated with the cooler water. I found that the non-consumptive effects are important over a large range of conditions. Interestingly, changes in water temperature and *B. longimanus* density had a large non-linear impact on the importance of non-consumptive effects due to changes in vertical migration behavior. Understanding how *B. longimanus* effects change seasonally will provide better predictions of impacts in the Great Lakes and the many other systems which it has invaded. This approach is also key to predicting species effects in different scenarios, such as those predicted with Global Warming.

To Mom and Dad

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CHAPTER 1
INTRODUCTION

One main area of study within ecology is the interactions between populations of organisms and their environments. Food-webs are a useful model for studying the interactions of populations in ecological communities. Food-webs are graphical representations of the populations in a community and some of the interactions between these populations, in particular, who-eats-whom. Food-webs are built from knowledge of predator-prey interactions. They provide information on how energy flows through a community, as well as information on basic community structure that many scientists use to better understand ecological communities. However, our basic building blocks for food-webs, predator-prey interactions are not entirely understood. There is still much that is not known about how predator induced changes in prey traits might impact prey populations.

Traditionally it has been thought that the only important effect predators have on their prey is through direct consumption. The evidence that predator induced changes in prey traits have important fitness consequences for prey populations has been growing. Examples of prey modifying traits in response to predator risk are ubiquitous in predator-prey relationships (reviewed in Lima and Dill 1990, Lima 1998, Tollrain and Harvell 1999). These trait changes reduce direct consumption, but also reduce the fitness of the prey in other ways (Harvell 1990). Prey face a tradeoff between survival and reproduction in trying to limit the overall effect of a predator: avoid being eaten or produce as many offspring as possible. When prey modify traits (behavioral, morphological, physiological or life-history) in order to simultaneously minimize predation and maximize fitness, the prey population incurs some direct mortality due to predation and some cost to fitness through decreased growth or fecundity. Thus, the total effect of the predator on the prey population can be broken down into multiple components including: the effect due to direct consumption, which is termed the consumptive effect (also density-mediated or lethal effect); and the effect of changes in prey traits on reproduction, which is termed the non-consumptive effect (also trait-mediated or non-lethal effect). Many studies have shown that non-consumptive effects can be very important (reviewed in Peacor and Werner 2004a, Preisser at al. 2005).

Little research has been done to determine how contributions of consumptive effects and non-consumptive effects to predator-prey interactions might vary with changes in the environment. We expect individual trait expression to vary with environmental parameters and if the cost associated with these trait changes is not constant, we would also expect the magnitude of non-consumptive effects to vary with environmental conditions. The goal of this thesis is to explore how trait expression and the magnitude and importance of non-consumptive effects changes with variation in environmental conditions.

State of the field

Importance of non-consumptive effects across systems

Theoretical studies (Abrams 1982, 1984, 1993, Ives & Dobson 1987, Bolker et al. 2003, Peacor & Werner 2004b) and empirical studies (reviewed in Peacor and Werner 2004a, Preisser et al. 2005) have shown that non-consumptive effects are an important component of the net effect of the predator in a number of systems. It is not surprising that increasingly, researchers are finding non-consumptive effects to be important in a wide range of systems given the number of systems where predators induce trait changes in their prey (reviewed in Lima and Dill 1990, Lima 1998, Tollrain and Harvell 1999, Agrawal 2001). These changes in trait expression often have an associated cost in terms of growth and fecundity (Harvell 1990) resulting in large non-consumptive effects (reviewed in Peacor and Werner 2004a and Preisser et al. 2005).

The number of systems where researchers have found large non-consumptive effects of predators on prey fitness surrogates (individual growth, fecundity, population growth, etc.) is growing each year. Recently, several major reviews have been published that summarize how prey trait changes induced by predators effect prey populations (Peacor and Werner 2004a, Preisser et al. 2005, Preisser et al. 2007, Cresswell 2008) and propagate through the community to affect populations of other organisms (Werner and Peacor 2003, Bolker et al. 2003). The majority of these studies have been done in aquatic systems, but there is growing emphasis on terrestrial systems. In a meta-analysis of 49 published studies, Preisser et al. (2005) found a similar strength in consumptive and non-consumptive effects, with particularly strong and sometimes non-intuitive effects documented in aquatic systems. For example, Peacor (2002) found that dragonfly larvae caused a net increase in small bull frog growth through a behavioral response (shift in foraging level). The majority of the terrestrial studies to date have been done on invertebrates. For example, Nelson (2004) found that surgically altered damsel bugs cause a large non-consumptive effect (30% reduction) on pea aphid population growth. There have been few studies on terrestrial vertebrates. Some predator exclusion experiments have been done on mammals and have identified non-consumptive effects of predators on prey body condition or growth rates. For example, Karels et al (2000) found that various predators caused non-consumptive effects on arctic ground squirrels body weight at parturition and litter size. Birds have complicated anti-predator behaviors (Caro 2005), but few studies of the costs of this behavior have documented both consumptive and non-consumptive effects. Thus, the relative importance of non-consumptive effects is not well understood for birds (Cresswell 2008).

The majority of the studies mentioned above have focused on quantifying non-consumptive effects in terms of individual growth (Peacor and Werner 2004a). Recently, researchers have begun attempting to quantify the reproductive cost of modifying traits in terms of population-level responses partially in an effort to quantify non-consumptive effects and consumptive effects in a common currency. The systems where this has been done extend from aquatic zooplankton (Boeing et al. 2005, Pangle et al. 2007) to stream macroinvertebrates (Peckarsky 1993, McPeek and Peckarsky 1998) to insects in agricultural systems (Nelson 2004).

Importance of non-consumptive effects across environmental gradients

The studies mentioned above only give us an understanding of the importance of non-consumptive effects under very specific conditions, a snapshot of the possible biotic and abiotic environmental conditions. We expect plastic traits to change as a result of changes in the environment. If the cost of trait expression is not constant, we would also expect the relative contribution of consumptive and non-consumptive effects to vary across environmental conditions as well. However, few studies have attempted to determine how interactions with the environment and with other species might influence trait expression and the relative importance of non-consumptive effects. A few studies have investigated how predator induced trait changes are influenced by the environment (biotic and abiotic), focusing on exploring the impacts of resource levels (Werner and

Anholt 1996, Fiksen et al 1997, Boscarino et al. 2007), temperature gradients (Boscarino et al. 2007) and density and types of predators (Werner and Anholt 1996, Fiksen, 2006, Boscarino et al. 2007). Boscarino found that the vertical distribution of *Mysis* in the water column depended on food availability, temperature gradient and the level of predator kairomones.

These documented changes in traits suggest we should find that the environment affects the relative contributions of consumptive and non-consumptive effects. Initial studies that have looked for an impact of interactions with other organisms on the relative contributions of consumptive and non-consumptive effects have focused on examining the effect of resource levels (Eklov and Halvarsson 2000, Peacor and Werner 2004b, Turner 2004,) competition (Peacor and Werner 2000, 2004b, 2006, Turner 2004) and predator type (Eklov and Werner 2000, Preisser 2007). These studies found that non-consumptive effects are dependent on resource levels and interactions with other organisms.

These initial studies have shown that changes in the environment (in terms of biotic interactions) can influence the relative contributions of consumptive and non-consumptive effects. However, we as ecologists still do not have a good understanding of how abiotic environmental conditions might affect trait expression or the importance of non-consumptive effects. More work is needed to understand the breadth of conditions over which trait expression changes and non-consumptive effects are important. In order to understand the generality of the importance of including plastic trait expression in our theoretical constructs of ecological communities, we need to investigate how non-consumptive effects and consumptive effects depend on environmental variation.

Needs for further study

Improving our understanding of the generality of the importance of trait-mediated interactions will allow us to determine how influential they may be in community dynamics. We still lack a good understanding of how the importance of non-consumptive effects might change due to environmental variation or in scaling to long-term situations. Bolker et al. 2003 identified scaling from short-term to long-term responses of communities as one of "the most critical needs" to determining whether trait-mediated interactions affect community dynamics at scales that will influence practical management decisions. I attempt to fill this gap in our knowledge by addressing the following questions:

1. Do changes in environmental conditions affect the importance of trait-mediated interactions? Would the ratio of the trait effect to the net effect of the predator change with variation in different environmental conditions (perhaps in a different field, stream or pond or with changes associated with establishment of invasive species, climate change or extreme weather)?

2. How might the importance of non-consumptive effects vary over longer time frames that incorporate variation in environmental conditions?

Thesis research

In this thesis, I use multiple modeling techniques to examine one system extensively, determining the importance of non-consumptive effects under a wide range of environmental conditions. In the second chapter, I determined how environmental conditions influence adaptive behavior and the relative contributions of consumptive and non-consumptive effects, which I measured in terms of prey population growth rate. In the third chapter, I determined how findings of non-consumptive effects on a fitness correlate (population growth rate) translate to longer-term, multi-generational population dynamics. In the final chapter I review my main findings and put them in context of the literature, discussing what data would be necessary to repeat a similar analysis in other systems. I also reviewed the literature to determine if this analysis is currently possible with the available data. The second and third chapters are being prepared for submission with coauthors Scott Peacor and Kevin Pangle.

The second chapter uses modeling techniques to determine adaptive behavior and measure consumptive and non-consumptive effects on a prey fitness correlate, population growth rate. The system I modeled includes an invasive invertebrate predator, *Bythotrephes longimanus* that feeds on zooplankton (small aquatic grazers), in particular *Daphnia mendotae*. This is a well studied system where large non-consumptive effects have been documented (Pangle et al. 2007). Specifically I modeled the decrease in per capita population growth rate of *D. mendotae* due to predation by *B. longimanus* over a range of environmental conditions to examine the generality of the importance of non-consumptive effects. I used two modeling techniques: an optimality model in which I maximized a differential equation for per-capita population growth rate, and a state-dependent dynamic optimality model in which I optimized lifetime reproductive success to determine if the behavioral response of *D. mendotae* to *B. longimanus* is adaptive and to estimate the magnitude and the importance of non-consumptive effects. Using the optimality model and state-dependent dynamic optimality model, I determined whether the behavioral response of *D. mendotae* and the instantaneous importance of non-consumptive effects were general over a range of biotic and abiotic conditions: *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators (including size selective predators), competition, surface light availability, light attenuation and temperature.

The third chapter extends these instantaneous results to the impact of *D. mendotae* trait changes due to *B. longimanus* predation on the population dynamics of *D. mendotae* over an entire season. I used a stochastic simulation model, to understand changes in adaptive behavior and to estimate the magnitude and the importance of the trait effect over the course of an entire season. The stochastic simulation model allowed the extension of these instantaneous results into long-term multi-generational dynamics accounting for seasonal variation in abiotic conditions. I was also able to investigate how changes in abiotic and biotic conditions due to climate change and exotic invasions might influence population dynamics.

The fourth chapter discusses my findings in chapters 2 and 3 and puts them in context of the literature. I also explored whether these results might be expected to extend to other systems. I explored other systems for which researchers have tried to quantify non-consumptive effects. For these systems, I explored the available data for how consumptive and non-consumptive effects might change with biotic and abiotic parameters. I was unable to find any other systems for which sufficient data existed to repeat a similar analysis.

CHAPTER 2

ENVIRONMENTAL FACTORS IMPACT THE RELATIVE IMPORTANCE OF CONSUMPTIVE AND NON-CONSUMPTIVE EFFECTS IN LAKE MICHIGAN ZOOPLANKTON

Abstract

Daphnia mendotae migrate vertically into deeper, cooler regions of Lake Michigan to avoid predation by an invasive planktivore, *Bythotrephes longimanus*. Since *B. longimanus* is a visual predator, *D. mendotae* vertical migration reduces direct consumption of *D. mendotae* by *B. longimanus* (consumptive effect), however, inhabiting the colder and less productive regions of the water column has a reproductive cost for *D. mendotae* (non-consumptive effect). These types of tradeoffs are ubiquitous to predator-prey interactions, and studies of various systems have shown that non-consumptive effects can be important relative to consumptive effects. However, these studies are snapshots, encompassing a small range of the natural variation in biotic and abiotic conditions that might affect prey trait expression and ultimately the importance of non-consumptive effects. Here I evaluated how seasonal changes in the pelagic environment can influence *B. longimanus*'s density and non-consumptive effects on *D. mendotae* using differential equation and dynamic optimization models. Both models were parameterized with data from Lake Michigan and lab experiments. I found that predicted adaptive behavior for *D. mendotae* varies in response to changes in environmental conditions and that some environmental factors can strongly affect the importance of non-consumptive effects. For example, I found that, both, water temperature and *B. longimanus* density had a large non-linear impact on the importance of non-consumptive effects. Under certain conditions, the models predict that *D. mendotae* should remain at the surface.

There are threshold values for surface temperature and *B. longimanus* densities at which point behavior shifts drastically and non-consumptive effects change from being non-existent (no vertical migration) to being very important (vertical migration). An understanding of how *B. longimanus* effects change seasonally will provide better predictions of its impact in the Great Lakes and the many other systems which it has invaded. This approach is also key to predicting species effects in different scenarios, such as those predicted with Global Warming.

Introduction

Predation can have a large impact on prey populations through direct consumption, but also through a suite of phenotypic changes that they induce in individual prey. For many years it was thought that predators affect prey populations primarily through consumptive effects (also lethal or density effects). Ecologists have been aware for some time that prey respond to predation risk by modifying their phenotype to minimize the effect of the predator. It is only recently that ecologists have begun to understand how important a role these phenotypic modifications play in predator prey interactions. In modifying their traits, prey shift the effect of predators on prey fitness from direct mortality to other sources, minimizing the total effect to the predator on prey fitness. Prey incur costs in terms of fitness surrogates such as individual growth, reproduction or population growth rates, this cost is termed the non-consumptive effect (also non-lethal or trait-mediated effect). Prey change their traits in a number of ways in response to predators, including behavioral, morphological and physiological adaptations that make them less likely to be consumed (Lima 1998). These trait changes reduce direct consumption, but can also reduce the reproductive success of the prey

(Harvell 1990). If prey forage less or put resources into growing larger in order to reproduce earlier or into growing defensive features, they have less resources for growth and reproduction or may face mortality from other sources. Thus, prey face a tradeoff in trying to limit the overall effect of a predator: avoid being eaten while maximizing fecundity. Studies have shown that predators induce trait changes in their prey in a large number of systems (reviewed in Dill 1987, Lima and Dill 1990, Lima 1998) and in many of these systems, these trait changes result in large non-consumptive effects (reviewed in Peacor and Werner 2004a, Preisser et al. 2005).

There is reason to believe that the importance of non-consumptive effects will be affected by abiotic environmental parameters and interactions with other organisms. An organisms' phenotype, or level of trait expression is a product of their environment and is affected not only by predation risk, but by environmental parameters and interactions with other species. We know that differing levels of trait expression amount to differing costs in terms of reproduction and that the relationship between trait expression and costs may change with changes in the environment. Thus, it follows that the magnitude of non-consumptive effects might be influenced by environmental parameters and interactions with other species as well. However, very few studies have addressed the question of how levels of trait expression and/or the magnitude of non-consumptive effects are affected by the environment or by interactions with other species. A few studies have investigated how predator induced trait changes are influenced by the environment (biotic and abiotic), focusing on exploring the impacts of resource levels (Werner and Anholt 1996, Fiksen et al 1997, Boscarino et al. 2007), temperature gradients (Boscarino et al. 2007) and density and types of predators (Werner and Anholt

1996, Fiksen, 2006, Boscarino et al. 2007) on trait expression. For example, Boscarino found that the vertical distribution of *Mysis* in the water column depended on food availability, temperature gradient and the level of predator kairomones.

Studies that explore the importance of environmental factors and interactions with other organisms in altering the relative contributions of consumptive and non-consumptive effects to predator-prey interactions have focused on examining the effect of resource levels (Eklov and Halvarsson 2000, Peacor and Werner 2004b, Turner 2004,) competition (Peacor and Werner 2000, 2004b, 2006, Turner 2004) and predator type (Eklov and Werner 2000, Preisser 2007). These studies found that non-consumptive effects are dependent on resource levels and interactions with other organisms. However, we still do not have a good understanding of how abiotic environmental conditions might affect trait expression or the importance of non-consumptive effects. More work is needed to understand the breadth of conditions over which non-consumptive effects are important.

Through this study I hope to be able to answer the following questions about the generality of the importance of non-consumptive effects. Would non-consumptive effects be less important in a different field, stream, or pond with slightly different abiotic and biotic conditions? Does inter-annual and intra-annual variability in environmental conditions affect trait expression and/or the importance of non-consumptive effects? Might abiotic and biotic changes associated with establishment of invasive species, climate change or extreme weather events affect trait expression and/or the importance of non-consumptive effects?

In order to answer questions about the generality of the importance of non-consumptive effects I employed different modeling techniques to examine one system extensively, determining the importance of non-consumptive effects under a wide range of conditions spanning intra-annual and inter-annual variability. I used modeling techniques to determine adaptive trait expression and to quantify the instantaneous impact of predation on prey population growth rate in terms of direct consumption (consumptive effect) and decrease in reproduction due to predator induced trait changes in the prey (non-consumptive effect). I used a well studied system, *D. mendotae* and *B. longimanus*, in which non-consumptive effects have been shown to be important (Pangle et al. 2006 & 2007). *D. mendotae* change their vertical migration behavior by migrating deeper in the water column during the day in an attempt to avoid direct predation (consumptive effect) by an invasive predator *B. longimanus* but incur a reproductive cost (non-consumptive effect) from being in colder water. I modeled the decrease in per capita population growth rate of *D. mendotae* due to predation by *B. longimanus* over a range of environmental conditions to examine the generality of the importance of non-consumptive effects.

I used two modeling techniques, differential equations and dynamic optimality modeling to determine if the behavioral response of *D. mendotae* to *B. longimanus* is adaptive and to estimate the magnitude and the importance of non-consumptive effects. Using the differential equation model of per-capita population growth rates I determined whether the behavioral response of *D. mendotae* and the instantaneous importance of non-consumptive effects are general over a range of biotic and abiotic conditions: *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators, competition, surface light availability, light attenuation and temperature. The dynamic optimality model allowed us to add size-selective predation, which is known to be important for gape-limited predators such as young of year fish, which prey on smaller *D. mendotae* (Hansen and Wahl 1981, Mayer and Wahl 1997, Mehner et al. 1998, Graeb et al. 2004, Hulsmann et al. 2004, Gelinas et al. 2007) and may be important for *B. longimanus* predation on larger *D. mendotae* (Schulz and Yurista 1999).

Methods

Description of System:

B. longimanus, a predatory cladoceran, is a recent invader to Great Lakes region and is thought to be having a large impact on the ecological communities of the Great Lakes, particularly on a key prey item of commercially important fish species, the zooplankton *D. mendotae* (Lehman and Caceres 1993; Vanderploeg et al. 2002, Barbiero and Tuchman 2004). *D. mendotae* are small grazers that feed on algae and bacteria and are a main food source for small and young fish. *B. longimanus* is a visual predator, meaning the risk to *D. mendotae* is greatest near the surface where light levels are high (Muirhead & Sprules, 2003). As light attenuates in the water column, *B. longimanus* are less effective predators decreasing the risk to *D. mendotae*. *D. mendotae* reproduce at higher rates in warmer surface waters; their fecundity falls off with the change in temperature of the epilimnion to the hypolimnion (Pangle et al. 2006). *D. mendotae* balance reproductive cost and predation by migrating within the water column to minimize overall fecundity loss due to predation (Lehman & Caceres 1993, Pangle et al. 2006).

The *B. longimanus* – *D. mendotae* system is an ideal system in which to study the dependence of non-consumptive effects on the environment for two reasons. First, the importance of trait-mediated interactions has already been demonstrated in the field for this system. Second, this predator-prey interaction has been studied extensively and field and laboratory studies have been done that give us information on how per-capita birth and death rate change as a function of trait expression and biotic and abiotic environmental parameters.

Overview of modeling techniques

I used two modeling techniques, an optimality model where I maximized per-capita population growth rate (Abrams 1987, Peacor and Werner 2004) and a state-dependent dynamic optimality model where I maximized life-time reproductive success (Mangel and Clark 1988), that together allowed me to determine how environmental parameters and interactions with other organisms influence trait expression and, in turn, the relative contribution of non-consumptive effects. The optimality model which maximized per-capita population growth rate was used to determine how trait expression and the importance of the non-consumptive effects varies over a wide range of biotic and abiotic conditions: *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators, competition, surface light availability, light attenuation and temperature. The state-dependent dynamic optimality model was used to examine the effect of size-selective predation on trait expression, which was not possible with the per-capita population growth rate model. Size-selective predation is known to be important for 1) *B. longimanus* predation on larger *Daphnids* and may be important for larger *D. mendotae* and 2) for predation by young of year fish. I then used the predictions from the state-dependent dynamic optimality model in a per-capita population growth rate model to determine the relative contribution of consumptive and non-consumptive effects.

In the following sections I discuss each of these models in detail. First I describe how I determined adaptive trait expression for the per-capita population growth rate model and the state-dependent dynamic optimality model. Next, I use my results on adaptive trait expression to calculate consumptive and non-consumptive effects. In the third section I describe how each model was parameterized from field surveys and experiments. Finally, I describe how I examined the influence of different environmental factors.

Adaptive Trait Expression

I determined how different biotic and abiotic factors impacted trait expression; in this system the trait in question is vertical migration depth. To find an adaptive vertical migration depth under a set of conditions, I assumed that *D. mendotae* maximize their fitness, which I measured in terms of per capita population growth rate as a function of trait expression (as in Abrams 1984 and 1987) or lifetime reproductive success (as in Mangel and Clark 1988). To determine the effect of *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators, competition, surface light availability, light attenuation and temperature on adaptive vertical migration depth, per capita population growth rate was used as a surrogate for fitness. To determine the effect of size-selective predation on adaptive vertical migration depth, fitness was measured in terms of lifetime reproductive success.

Optimality Model: maximizing population growth rate

Optimality models, where a measure of fitness is optimized, are often used in behavioral ecology to determine adaptive trait expression (Gore and Paranjpe 2001). I used per-capita population growth rate as a measure of fitness, a metric that has been used previously to determine adaptive trait expression (e.g., Abrams 1984, 1987, Peacor and Werner 2004). The general equation for per capita population growth rate, g, is

$$g(z) = \frac{1}{N_D}\frac{dN_D(z)}{dt} = b(z) - d(z) \tag{2.1}$$

where N_D is *D. mendotae* density, z is depth in water column, b is per capita birth rate, d is per capita death rate and t is time. I find the vertical migration depth between 0 and 60 m, that maximizes equation 2.1, by differentiating with respect to z and setting equal to zero and solving to find extrema (as in Abrams 1984, Gore and Paranjpe 2001, Chapter 7). This process is repeated for each hour in a 24 hour period over a variety of different biotic and abiotic parameters (table 1). Thus for a 24 hour period there are 24 values for adaptive migration depth, each for a specific time, which I denote, $z_{p,h}$. The model assumes that *D. mendotae* migrate to each of these adaptive vertical migration depths during a 24 hour period.

In order to determine whether *D. mendotae* behave adaptively (as predicted by my model) in nature, my model predictions were compared to field data. Field data from Pangle et al. (2007, figure 3) for surface light levels, attenuation coefficients and temperature were used to predict adaptive migration depths. I compared model predictions for both mid-day and mid-night to average *D. mendotae* depth from field surveys conducted in Lake Michigan (see Pangle et al. 2007 for details of field surveys).

Dynamic Optimality Model: Maximizing lifetime reproductive success

Dynamic Optimality models can be used to model adaptive traits that are dependant on state variables of the particular organism (Mangle and Clark 1988). This allows us to determine how adaptive behavior should change depending on both state variables (*D. mendotae* size) and the environment (size-selective predation) which was not possible with a non state-dependent model. In this section, we are interested in determining how adaptive vertical migration depth (and non-consumptive effects) will change as a function of *D. mendotae* size when predation risk is size-dependent. I built a dynamic optimality model with *D. mendotae* size as a state variable and predation risk as a function of size.

I found the adaptive vertical migration depth as a function of time, abiotic factors (surface light levels, light attenuation, temperature profile), biotic factors (predation) and state (size) of an individual *D. mendotae* using a recursive formula for a measure of fitness, life-time reproductive success,

$$\Phi(w,z,t) = \max_{0<z<60} \left[b(z) + e^{-d_F(w,z,t) - d_B(w,z,t)} \times \Phi(w + wsg(z), z, t+1) \right]. \quad (2.2)$$

where z is depth, t is time in hours, w is *D. mendotae* size, Φ is lifetime reproductive success, $b(z)$ is birth rate, sg somatic growth, d_B is size-selective predation due to *B. longimanus* and d_F is size-selective predation due to young fish. This equation is used recursively to determine a series of adaptive vertical migration depths (between 0 and 60 m) for each hour, over the course of a 30 day period, an appropirate life-span for *D. mendotae*.

Net Effect, Consumptive Effect and Non-consumptive effect

I calculated the net effect, non-consumptive effect and consumptive effect of *B. longimanus* on *D. mendotae* in the same currency, all in terms of a reduction in *D. mendotae* per capita population growth rate due to predation by *B. longimanus*. I define the net effect of *B. longimanus* on *D. mendotae* as the depression in *D. mendotae* per capita population growth rate due to predation by *B. longimanus*;

$$NE = g_{np}(z) - g_p(z) \qquad (2.3)$$

This equation is equivalent to *D. mendotae* birth rate in predator absence minus birth rate in predator presence, plus the death rate in predator presence.

$$NE = \left[b(z_{np,h}) - b(z_{p,h})\right] + d(z_{p,h}) \qquad (2.4)$$

I then average over 24 hours to account for the effect of diel changes in adaptive vertical migration depth.

$$NE = \frac{\sum_{h=1}^{24}\left[b(z_{np,h}) - b(z_{p,h})\right] + d(z_{p,h})}{24} \qquad (2.5)$$

where NE is the net effect of *B. longimanus* on *D. mendotae*, $z_{np,h}$ is the adaptive migration depth at time h without *B. longimanus* present, $z_{,ph}$ is the adaptive migration depth at time h with *B. longimanus* present, $b(z_{np,h})$ is per capita population birth rate in the absence of *B. longimanus* and $b(z_{p,h})$ and $d(z_{p,h})$ are respectively the per capita population birth rate and death rate at depth $z_{p,h}$ with *B. longimanus* present.

The non-consumptive effect (NCE) is the portion of the net effect of *B. longimanus* predation on *D. mendotae* per capita population growth rate that is due to the reproductive cost of vertical migration, which is the difference of *D. mendotae's* birth rate in the absence and presence of *B. longimanus*.

$$NCE = \frac{\sum_{h=1}^{24} b(z_{np,h}) - b(z_{m,h})}{24} \quad (2.6)$$

where $z_{np,h}$, $z_{p,h}$, $b(z_{np,h})$ and $b(z_{p,h})$ are as above.

The consumptive effect (*CE*) is the portion of the net effect of *B. longimanus* predation on *D. mendotae* per capita population growth rate that is due to direct consumption of *D. mendotae* by *B. longimanus*

$$CE = \frac{\sum_{h=1}^{24} d(z_{p,h})}{24}. \quad (2.7)$$

Parameterizing the models

Population growth rate as a function of depth (no size-selective predation)

The per capita birth rate of *D. mendotae* as a function of daily vertical migration depth, *b(z)*, was estimated using the egg-ratio method (Palheimo 1974).

$$b(z) = \frac{\ln\left(\frac{E}{N_D} + 1\right)}{D} \quad (2.8)$$

This method combines field data on the number of *D. mendotae* eggs *(E)* and *D. mendotae* individuals (N_D) into an egg-ratio (E/N_D), with a relationship for how egg development duration is affected by temperature (*D*). Values for the number of *D. mendotae* eggs and individuals from the field survey of Lake Michigan were combined to give an egg-ratio with an average value of 0.7 but ranged as high as 1.02 (Pangle, KL unpublished data). I used this egg ratio method because it is a surrogate for resource levels. It allowed us to incorporate information on resources without explicitly including resources in the model and allowed us to investigate competition by altering a single parameter, the egg ratio. For *D. mendotae*, the relationship between water temperature and egg developmental duration has been derived from laboratory experiments and can be estimated using the equation:

$$D = \frac{1}{\left[0.00041T^2 + 0.0108T - 0.0163\right]} \tag{2.9}$$

(Edmonson & Litt 1982). Temperature gradients spanning the whole season were obtained from a model developed by researchers at GLERL (Schwab and Bedford 1999), these data were fit (R v2.5.1, nonlinear regression, $p<0.001$) with a sigmoidal equation of the form

$$T = t_{\min} + \frac{t_{dif}}{1 + e^{\frac{z-tc}{ts}}} \tag{2.10}$$

where t_{min}, t_{dif}, tc and ts are parameters of the sigmoidal equation. Here, t_{min} gives a minimum temperature for the hypolimnion, t_{dif} the difference in temperature between the hypolimnion and epilimnion, tc gives the location (depth) of the thermocline and tse the steepness of the thermocline.

Given the temperature dependence of egg development, and how depth affects temperature, I combined equations 2.9 and 2.10 in equation 2.8 to give per capita birth rate, *b(z),* as a function of depth

$$b(z) = \ln\left(\frac{E}{N_D} + 1\right)\left[0.00041\left(t_{\min} + \frac{t_{dif}}{1 + e^{\frac{z-tc}{ts}}}\right)^2 + 0.0108\left(t_{\min} + \frac{t_{dif}}{1 + e^{\frac{z-tc}{ts}}}\right) - 0.0163\right].$$

(2.11)

Per-capita death rate as a function of depth, *d(z),* due to *B. longimanus* predation was determined by combining field data on *B. longimanus* and *D. mendotae* distributions, densities and light gradients with lab data on predator efficiency at different light levels, and the functional response. The predation rate of *B. longimanus* on *D. mendotae* is given by a type II functional response, $F(z)$ which gives an attack rate multiplied by *B. longimanus* density, $N_B(z)$

$$D(z) = N_B(z)F(N_D(z)) \tag{2.12}$$

This predation rate is then modified by a term that accounts for the decrease in predation rate as light levels decrease with depth, $P(z)$

$$D(z) = P(z)N_B(z)F(N_D(z)) \tag{2.13}$$

I then divided by *D. mendotae* density, $N_D(z)$ to get a per capita predation rate

$$d(z) = \frac{P(z)N_B(z)F(N_D(z))}{N_D(z)} \tag{2.14}$$

The functional response of *B. longimanus* is given by (K. L. Pangle unpublished data).

$$F(N_D) = \frac{2.67N_D}{5.31 + N_D} \tag{2.15}$$

I found that the distributions of *B. longimanus* and *D. mendotae* in Lake Michigan (from Pangle et al. 2007) could be well described by a normal distribution (Rv2.5.1, nonlinear regression, $p<0.001$)

$$N_B(z) = \frac{c_B}{\sigma_B\sqrt{2\pi}} e^{-\frac{(z-\mu_B)^2}{2\sigma_B{}^2}} \tag{2.16}$$

$$N_D(z) = \frac{c_D}{\sigma_D\sqrt{2\pi}} e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}} \tag{2.17}$$

where $N_D(z)$ is *D. mendotae* density at depth z, $N_B(z)$ is *B. longimanus* density at depth z, μ_D and σ_D, are mean depth and standard deviations of *D. mendotae* distributions from field surveys, μ_B and σ_B are mean depth and standard deviations of *B. longimanus* distributions from field surveys, and c_D and c_B are scaling constants.

Light levels (light level in microeinsteins/m^{2}s) affect predation risk according to the relationship (K. L. Pangle, S. D. Peacor, and H. A. Vanderploeg, unpublished data).

$$P(L) = \frac{L}{11.5 + L} \tag{2.18}$$

Light attenuates as it moves through the water column at a rate K from a surface light level of I_0 (Beers Law) such that the light level is described by

$$L(z) = I_0 e^{-zK}. \tag{2.19}$$

Combining equations 2.18 and 2.19 gives a function for how per capita predation rate is impacted by light attenuation

$$P(z) = \frac{I_0 e^{-zK}}{11.5 + I_0 e^{-zK}} \tag{2.20}$$

Equations 2.15, 2.16, 2.17 and 2.20 were combined into equation 2.14 for per capita predation rate as a function of depth

$$d(z)=\frac{\left[\frac{1.35I_0e^{-zK}}{13.5+I_0e^{-zK}}\right]\left[\frac{c_B}{\sigma_B\sqrt{2\pi}}e^{-\frac{(z-\mu_B)^2}{2\sigma_B{}^2}}\right]\left[\frac{2.27\left(\frac{c_D}{\sigma_D\sqrt{2\pi}}e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}}\right)}{5.31+\left(\frac{c_D}{\sigma_D\sqrt{2\pi}}e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}}\right)}\right]}{\frac{c_D}{\sigma_D\sqrt{2\pi}}e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}}} \tag{2.21}$$

Lifetime reproductive success (size-selective predation)

The parameterization for the first term of equation 2.2, *b(z)*, is described above (equation 9). To parameterize the second term of equation 2.2, we need functions for predation risk due to young of year fish and *B. longimanus*. Predation rate due to *B. longimanus*, $d_B(w,z)$, was estimated using data for *B. longimanus* distribution and density (equation 2.12), typical *D. mendotae* distribution and density (equation 2.13), functional response (equation 2.11) and light levels (equation 2.16) and data from Schulz and Yurista (1999) to account for size preference of *B. longimanus*, *SP(w)*. I used data from experiments conducted by Schulz and Yurista (1999) on the size preferences of *B. longimanus* for *D. pulicaria* (a slightly larger species of *Daphnia*) to estimate *SP(w)* in terms of number of *D. mendotae* eaten per *B. mendotae* per hour

$$SP(w)=0.73w+0.53. \tag{2.22}$$

I modify equation 2.14 from above to incorporate size-selective *B. longimanus* predation by multiplying by a term that describes how per-capita predation rate is modified by *D. mendotae* size

$$d_B(w,z) = \frac{SP(w)P(z)N_B F(N_D)}{N_D} \qquad (2.23)$$

Predation risk due to young of year fish, $d_F(w,z)$, was estimated as in Fiksen 1997 using data from Gelinas et al. (2007). Predation rate was assumed to be proportional to fish density N_F, the area of image of *D. mendotae*, $A(w)$ and light level as a function of depth, $L(z)$ (equation 2.19 from above).

$$d_F(w,z) = \frac{N_F L(z) A(w)}{A(\overline{w})} \qquad (2.24)$$

where $A(\overline{w})$ is the area of an individual *D. mendotae* with median size. The area of image of *D. mendotae* was estimated by assuming spherical body shape.

Population growth rate (size-selective predation)

As described above, I used equations 2.5, 2.6 and 2.7 along with adaptive behavior predicted by the state-dependent dynamic optimality model (equation 2.2) to determine the magnitude of the net, trait-mediated and density-mediated effects of *B. longimanus* predation on *D. mendotae.* I used a modified version of equation 2.1, such that the death rate was dependent on both depth and *D. mendotae* size

$$g(z) = \frac{1}{N_D}\frac{dN_D(z)}{dt} = b(z) - d(z,w) \qquad (2.25)$$

$b(z)$, remained the same (equation 2.9). I modeled predation rate as a function of depth and *D. mendotae* size, as the sum of the predation rate of *B. longimanus*, $d_B(z,w)$ (equation 2.23 from above) and of fish, $d_B(z)$ (equation 2.24 from above).

$$d(z,w) = d_{\mathbf{B}}(w,z) + d_F(w,z)$$
$$d(z,w) = \frac{SP(w)P(z)N_B F(N_D)}{N_D} + \frac{N_F L(z) A(w)}{A(\overline{w})} \qquad (2.26)$$

Examining the effect of the Environment

I determined adaptive levels of trait expression and the net, trait and consumptive effects as described above for a range of different conditions, varying surface light intensity, attenuation rate, water temperature profile, *B. longimanus* distribution and density, functional response, *D. mendotae* density, additional risk of death due to other predators, competition and size-selective predation. Table 1 gives ranges for the different parameters investigated. Predation risk from additional predators was simulated through changing *d(z)* with generic types of predation risk curves with biological rational behind them. The types of curves and rationale are described in the first two columns of Table 2. Interspecific competition was modeled by varying the egg-ratio, which is an indirect measure of resources in the field. Increases in competition would lead to lower egg-ratios and decreases in competition would lead to high egg-ratios. I used my dynamic optimality model of lifetime reproductive success to investigate negative size-selective predation due to young of year fish and positive size-selective predation due to *B.* longimanus. To do this I ran the model described above with no size-selective predation, with only *B. longimanus* size-selective predation (or positive size-selective predation) and with only fish size-selective predation (or negative size-selective predation) and both *B. longimanus* and fish size-selective predation.

I also investigated the impact of adding swimming speed constraints to the model. I limited the range of depths for $z_{m,h}$ over which I maximized equation 2.1 to 5 m ± $z_{m,h-1}$, constraining movement of *D. mendotae* to within 5 m above or below their previous location. I chose a swimming speed constraint of 5m/hr because it represents a biologically relevant constraint to *D. mendotae* vertical migration speeds (Dawidowicz and Loose 1992),

Results

Is vertical migration adaptive?

The model predicts that *D. mendotae* will stay near the top of the water column in *B. longimanus* absence. In *B. longimanus* presence, in contrast, the model predicts that *D. mendotae* will stay near the surface at night, and migrate to deeper waters during the day to avoid *B. longimanus* predation. There was also close quantitative agreement between model and field observations. At mid-day my model predicted an optimal migration depth of 33 m, this agreed with mean *D. mendotae* depths observed in the field, 30.3 m (sd=5.04 m) (Pangle et al. 2007, figure 3). At mid-night the model predicted that *D. mendotae* should remain at the surface, but the field survey showed *D. mendotae* at an average depth of 11.3 m (sd=7.47 m) (Pangle et al. 2007, figure 3).

The discrepancy between model predictions and field observations at night may arise from a combination of two factors, the shape of the fitness landscape and additional cost or constraints not included in the model. The fitness surface is very flat as a function of depth high in the water column; changes in depth have little effect on growth (Figure 2.1 panel A). Above a depth of 12 m the change in per capita population growth rate associated with a decreasing depth is very small, less than 5% (Figure 2.1 panel A). This difference in fitness may be so small that even a very small cost or constraint not included in the model could account for this discrepancy. Constraint on migration speed may be one such factor. Adding this migration constraint makes it necessary for *D. mendotae* to anticipate daybreak and begin migrating early to avoid an area of very high predation risk. The mid-night field data were actually taken at 1 AM, and by this time, *D. mendotae*, have already begun migrating (figure 2.2 panel1b). Panels 1a and 1b of Figure 2.2 are fitness landscapes that show *D. mendotae* per capita population growth rate as a function of time of day on the x-axis and depth of the y-axis. There is a large area of negative fitness between the surface and 25 m down in the water column from 7 hours to 19 hours (Figure 2.2 panels 1a and 1b). With a movement constraint of 5m/hr, *D. mendotae* would have to move through this area of negative fitness (Figure 2.2 panel 1a), and in doing so would incur a large survival cost, such that it is better for *D. mendotae* to remain at the surface in this case (Figure 2.2 panel 2a). However if *D. mendotae* are allowed to anticipate daybreak and begin moving early they can avoid this area of negative fitness (Figure 2.2 panel 1b) and vertical migration is still adaptive (Figure 2.2 panel 2b). This delayed migration means that *D. mendotae* would barely make it to the surface by midnight, combining this with the flatness of the fitness curve gives a plausible reason for the observed discrepancy between the model and field data.

The model predictions were therefore in strong agreement, both qualitatively and quantitatively with field observations. This close match observed between daytime vertical migration in the field and model predictions suggest the vertical migration observed in the field is adaptive.

Impact of environmental variability

General Mechanism

There are two main mechanisms that determine the effect of environmental variability on the relative contributions of consumptive and non-consumptive effects. A change in an environmental variable can change $g(z)$, through changes in either $b(z)$ or

$d(z)$ or both which has two possible effects. First, a change in either $b(z)$ or $d(z)$ or both, can alter the adaptive vertical migration depth, $z_{p,h}$, which leads to changes in non-consumptive effects and consumptive effects. Second, a change in $b(z)$ or $d(z)$ or both, can directly effect the consumptive and non-consumptive effects by changing the factors that affect them, $b(z_{np,h})$, $b(z_{p,h})$ and $d(z_{p,h})$.

Changes in environmental conditions can potentially influence both of these factors, and thereby the contribution of non-consumptive effects. Large changes in the relative contributions of non-consumptive effects due to changes in adaptive vertical migration depth were due to switches between adaptive vertical migration depth being at the surface (no migration) to an adaptive vertical migration depth greater than 22 m. These types of switches resulted in switches from dominance by consumptive effects to non-consumptive effects. Smaller changes in adaptive vertical migration depth (within the range between 22 and 40 m) caused little change in the relative importance of non-consumptive effects, unless there was an accompanying change in $b(z_{p,h})$ or $d(z_{p,h})$. Changes in $b(z_{np,h})$, $b(z_{p,h})$ and $d(z_{p,h})$ without an accompanying change in vertical migration depth also resulted in changes in the relative contributions of consumptive and non-consumptive effects.

Effects of particular environmental variables

Typical levels of variation in environmental parameters experienced by *D. mendotae* were predicted by the model to have a large effect on adaptive behavior and the relative contributions of consumptive and non-consumptive effects. Over the range of environmental conditions I investigated, adaptive vertical migration behavior ranged from staying at the surface to migrating to depths of between 22 m and 40 m. Predation risk during daylight hours creates an area of negative fitness that extends from the surface to 21 m, leading to an absence of adaptive vertical migration depths between 1 and 21 m. The model indicated that the relative importance of non-consumptive effects is strongly dependent on multiple environmental parameters. In particular, temperature, *B. longimanus* density and the presence of additional predators all strongly affected the relative contribution of non-consumptive (nonlethal or trait-mediated) effects to the net effect of *B. longimanus*, while other variables had less pronounced effects (as reviewed below). Importantly, for the majority of the ranges tested for each of these parameters, the magnitude of the non-consumptive effects remained equal to or greater than the magnitude of the consumptive effects.

The absolute value of surface water temperatures had a marked, nonlinear, effect on the contribution of trait-mediated interactions (Figure 2.3). The model indicates that a temperature threshold exists, above which *D. mendotae* do not migrate, but below which it is advantageous for *D. mendotae* to migrate and avoid predation. For high surface temperatures, above a threshold value (of ~25°C) the advantages of staying in the warm water outweigh the risks of direct predation and it is best for *D. mendotae* to stay at the surface. Thus small changes in temperature can have a profound influence on the contribution of non-consumptive effects. The mechanism at work here is a change in $b(z)$ and an alteration in adaptive vertical migration depth. Above the threshold, the net effect of the predator is minimized by remaining at the surface. Since *D. mendotae* do not migrate under these conditions, non-consumptive effects are non-existent. But as temperature falls below the threshold, vertical migration (to a depth of at least 22 m) becomes adaptive and non-consumptive effects dominate.

The model predicts that the threshold temperature described above is dependent on *B. longimanus* density. As *B. longimanus* density increases, the threshold temperature increases as well. As *B. longimanus* density increases *d(z)* increases meaning that the threshold surface temperature must also increase in order for the advantages of staying in the warm water at the surface to outweigh the risks of direct predation.

The density of the predator, *B. longimanus* also had a marked, non-linear effect on the relative contribution of non-consumptive effects (Figure 2.4). For low *B. longimanus* densities, below a threshold of 1 individual/m^3, it was adaptive for *D. mendotae* to remain at the surface because predation risk was not high enough to make vertical migration beneficial (Figure 2.4). At and above that threshold, adaptive behavior shifted to an adaptive vertical migration depth of at least 22 m, predation rates were now high enough at the surface that it was best for *D. mendotae* to migrate. The mechanism here, like above, is a shift in adaptive behavior, however unlike temperature which affect *b(z),* predator density affects *d(z).*

Variation in the temperature profile had a large impact on the magnitude and relative importance of the non-consumptive effects. As the difference in temperature between the epilimnion and hypolimnion decreased the cost of migration also decreased, leading to trait-mediated effects of smaller magnitudes and a decrease in the relative importance of trait-mediated interactions (Figure 2.3). The change in the temperature gradient caused a change in *b(z)* and the difference between $b(z_{np,h})$ and $b(z_{p,h})$ to decrease. However, the depth of the temperature gradient remains fairly constant, except in the extreme case where there is no temperature gradient, so there is very little change in adaptive migration depth, $z_{p,h}$. In the extreme, when there is no temperature gradient, the magnitude of non-consumptive effects is zero and consumptive effects make up the entire net effect of *B. longimanus* predation on *D. mendotae*.

Interestingly, I found that some parameters, such as surface light levels and the light attenuation coefficient had large effects on adaptive vertical behavior, but not much of an impact of the relative importance of non-consumptive effects. Variation in surface light levels and the rate at which light attenuates caused changes in the shape of *d(z),* causing the adaptive vertical migration depths during daylight hours to range from 22 m to 40 m but had very little influence on the magnitude of the non-consumptive effect. These parameters have no influence over *b(z)* and the changes they caused in adaptive vertical migration depth were in a range (below the thermocline) where b(z) varied little and thus had little no impact on non-consumptive effects (see equation 2.6). Both parameters did affect *d(z),* although the change was primarily above a depth of 20 m and since adaptive vertical migration depths were always below 20 m the magnitude of the consumptive effects were barely affected by these changes to *d(z).* Thus, neither, surface light levels or light attenuation had much of an impact on the relative importance of non-consumptive effects.

Variation in predation risk as a function of depth (due to the inclusion of additional predators) influenced the importance of non-consumptive effects, both increasing and decreasing the relative importance of non-consumptive effects depending on the type of predator involved (summarized in table 2). Adding a linear predation curve, constant or increasing/decreasing with depth, led to non-consumptive effects becoming relatively less important, however, only with large predation risk at deeper depths do I see consumptive effects begin to dominate non-consumptive effects. For example, for a constant curve where risk is independent of depth, adaptive vertical migration depth and the magnitude of the non-consumptive effect remained constant, however the magnitude of the consumptive effect increased, decreasing the relative importance of non-consumptive effects. Interestingly, under some conditions such as linear predation risk with a very large negative slope (predation risk increases with depth), staying at the surface is adaptive, and under these conditions there is no trait-mediated effect. Here, the model predicts a similar threshold effect to what I have seen with surface temperature and predator density. As predation rate increases deep in the water column, the relative contribution of consumptive effects increase do to increasing $d(z_{np,h})$, until a threshold above which vertical migration is no longer adaptive and *D. mendotae* do not migrate and consumptive effects make up the entirety of the net effect of *B. longimanus* on *D. mendotae*. Adding a non-linear predation curve, where predation risk decreases as a function of depth (such as for a visual predator or temperature sensitive tactile predator) affects both adaptive migration depth and slightly influences the importance of non-consumptive effects. Adding either an additional visual predator or a tactile (temperature sensitive) predator would either have no impact on adaptive vertical migration depth or would slightly increase adaptive vertical migration depth. The addition of either curve would have no impact on the magnitude of the non-consumptive effect, since $b(z)$ does not change the value of equation 2.4, however, the magnitude of the consumptive effect could increase causing non-consumptive effects to become relatively less important.

Variation in *D. mendotae* densities and competition had little to no effect on adaptive migration depth or the importance of trait-mediated interactions. Variation in *D.*

mendotae densities changed $d(z)$ through the functional response, however, this effect was very small compared to the effect of light attenuation and had very little impact on $z_{p,h}$ or $d(z_{p,h})$. Variation competition changed $b(z)$, but had no impact on the shape and so did not impact $z_{p,h}$. This change in $b(z)$ did impact $b(z_{np,h})$ and $b(z_{p,h})$, but there was still a large cost to migrating and hence a large non-consumptive effect.

Including size-selective predation caused adaptive migration depth to change over time as *D. mendotae* became larger, increasing for positive size-selective predation and decreasing for negative size-selective predation. Including *B. longimanus* size-selective predation for larger *D. mendotae* led to optimal migration depth becoming deeper over time as size increased. The optimal migration depth for larger *D. mendotae* is deeper than for smaller *D. mendotae* under positive size-selective predation. This is because with increasing size $d(z)$ becomes larger, leading to a deeper adaptive migration depth and a slightly larger consumptive effects. Adding a gape limited predator (such as a small fish) that preferentially feeds on small *D. mendotae* led the opposite effect, adaptive vertical migration depth decreased over time. As *D. mendotae* became larger, the depth to which *D. mendotae* migrated decreased and the magnitude of the consumptive effects decreased slightly. This is because as *D. mendotae* size increased, $d(z)$ became smaller, leading to shallower adaptive migration depths and slightly smaller consumptive effects. Adding both positive size-selective predation and negative size-selective predation increased the vertical migration depth slightly for large and small *D. mendotae,* thus vertical migration depth did not change over time as with only negative or positive size-selective predation.

Increasing migration depth due to size-selective predation had no impact on the magnitude of non-consumptive effects, as *b(z)* did not change with the addition of size-selective predation. The magnitude of the consumptive effect increased slightly with both positive and negative size-selective predation. There was only a slight change because both *B. longimanus and* young of year fish are visual predators and most of the change in *d(z)* was well above the adaptive vertical migration depths. Thus there was very little change in the relative importance of non-consumptive effects with size-selective predation.

Discussion

My results show that trait expression (in this case vertical migration depth) and the importance of trait-mediated interactions are highly dependent on environmental conditions. The model predicts big changes in adaptive vertical migration depth and the relative contributions of consumptive and non-consumptive effects for some variables (surface temperature, temperature gradient, *B.* longimanus density and presence of additional predators) and not others (*D. mendotae* density, competition, surface light levels and light attenuation rate). Some of the changes I observed were gradual, for example, seasonal changes in the temperature gradient caused a gradual decrease in the magnitude of non-consumptive effects. Other variables, such as *B. longimanus* density and surface water temperatures caused strongly nonlinear changes. The variation in impact on the relative importance of non-consumptive effects can be explained by examining how the factors affect birth and death magnitudes as a function of depth, and in turn how this affects the adaptive trait change.

Given the ubiquity of trait changes and the dependence of trait changes on the environment, I expected to find the large effects that I observed. Others have investigated the effect of resource levels (Eklov and Halvarsson 2000, Peacor and Werner 2004b, Turner 2004,) competition (Peacor and Werner 2000, 2004b, 2006, Turner 2004) and predator type (Eklov and Werner 2000, Preisser 2007). These initial studies point to the importance of considering the effects of environmental variation on the relative importance of consumptive and non-consumptive effects. I have expanded on this initial work, showing that environmental variation can have large effects on the relative importance of non-consumptive effects with both gradual and strong, non-linear changes.

The predation curvature results show that different types of predators will have different types of effects. I found that visual and tactile predators, which are very common in Lake Michigan, increase the magnitude of consumptive effects, slightly decreasing the relative importance of non-consumptive effects. Other studies have found that trait expression changes with number of predators present or the type of predator present. In particular, Preisser et al. 2007, found that the importance of non-consumptive effects was highly dependent on predator hunting mode. My results imply that the importance of non-consumptive effects depends on the specific predators present and how predation risk changes as a function of trait expression for the assemblage of predators present.

I found that predation rates were not proportional to predator density. Rather, I observed a marked, non-linearity in this relationship. As predator density increased to above 1 *B. longimanus* per m^3, the model predicts a shift in adaptive behavior from no vertical migration (remaining at the surface) to migrating to a depth of at least 22 m. This behavior shift leads to a shift from dominance of consumptive effects to dominance of non-consumptive effects resulting in a large decrease in the actual predation rate. These results therefore show that if prey modify traits adaptively in response to predation, the death rate of prey due to direct consumption by the predator does not increase proportional to predator density (Abrams 1993), rather there is a strong non-linear decrease in predation risk due to a threshold where adaptive behavior flips, having a huge impact on the relative contribution of non-consumptive effects.

I also found strong nonlinear responses as a function of temperature. As surface temperatures increase there was a gradual increase in the importance of non-consumptive effects, until a threshold, at and above this threshold the model predicts a shift in adaptive behavior similar to the threshold described above. Surface temperatures become so high that it is no longer adaptive for *D. mendotae* to migrate, non-consumptive effects are nonexistent and consumptive effects make up the entirety of the effect of the predator. This has huge implications in terms of climate change. The value of this threshold is dependent on *B. longimanus* density. At natural *B. longimanus* densities, the threshold is at 25°C. Currently, surface temperatures in Lake Michigan during August are typically below this threshold (Pothoven et al. 2001), but with the changes in temperature predicted under climate change, we may see temperatures rising above this threshold on some days during July and August. This would mean a period in late summer when non-consumptive effects are non-existent and consumptive effects dominate, currently non-consumptive effects are at their highest levels during this time period. The implications of climate change are discussed further below. This also has implications across similar systems, implying that we may see large variation in the relative importance of non-consumptive effects depending on lake temperature.

The model predicts that changes in the Great Lakes due to climate change could increase the time period over which non-consumptive effects are important. Climate change scenarios indicate shorter winters with longer periods of thermal stratification with some predictions placing fall turnover up to 2 months later (Brooks and Zastrow, 2002). If stratification were to persist longer into the winter it would add to the period of time that non-consumptive effects dominate. However, if surface water temperatures increase much above current levels (increasing by as little as 2 °C) the model indicates that *D. mendotae* no longer need to migrate. These results, taken together indicate that we may begin to see a brief period during the summer months when density changes dominate due to higher surface temperatures, transitioning to a longer period where non-consumptive effects dominate due to longer periods of stratification. More work is needed to clarify the non-consumptive effects given the simultaneous operation of different mechanisms if we integrate these two results over time.

My findings, that non-consumptive effects are dependent on environmental conditions, have implication for aquatic ecology and community ecology. New studies on the importance of non-consumptive effects in specific systems need to consider how environmental conditions might influence non-consumptive effects based on the biology of the system. Otherwise, they run the risk of under or over-estimating the impact of the predator on the prey. Further, in interpreting the scope of the influence of studies, my results indicate that ecologists need to be careful about interpreting how general finding of the importance of non-consumptive effects are with respect to variation in environmental conditions. For example, consider previous work that has shown non-consumptive effects to be very important for this system in July and August (Pangle et al 2007), to extend these results to other times of the year or other lakes we need to consider how environmental variability might influence adaptive vertical migration and the relative contribution of consumptive and non-consumptive effects. My results indicate that non-consumptive effects are dependent on environmental conditions, but that over the majority of the range of environmental conditions, non-consumptive remained a large and important portion of the net effect of *B. longimanus*. Thus we can make predictions about other lakes surrounding the Great Lakes that have already been invaded by *B. longimanus* or are under risk of invasion. My results indicate the non-consumptive effects will likely dominate the net effect of *B. longimanus* on *D. mendotae* per capita population growth rate, unless the temperature gradient is unusually small or the lake contains a *D. mendotae* predator that is more efficient in cold or dark water or *B. longimanus* densities are very low, below 1 individual per m^3. We can also make predictions about whether non-consumptive effects remain important over a whole season. My results indicate that as the temperature gradient decreases the magnitude and relative importance of non-consumptive effects decreases as well.

Extending the generality of the importance of trait-mediated interactions over a wide range of environmental conditions has implications for community ecology. Theory has shown us that, at least in simple communities, incorporating changes in trait expression and the resulting fitness costs, can stabilize communities, change the relative strengths of direct and indirect interactions (reviewed in Bolker et al. 2003) and even help repel invasion (Peacor et al. 2006). It is unclear how including the effect of the environment on trait expression might impact these results. However, the strong changes I observed in trait expression and the relative contributions of consumptive and non-consumptive effects indicate that considering the effect of environmental variation is important.

Understanding how trait expression and trait-mediated interactions can vary with environmental conditions has implications for ecological communities in terms of trait-mediated indirect interactions. We know that including plastic trait expression and the resulting cost in terms of fitness can change the relative strengths of direct and indirect interactions (Abrams 1995). Knowing that the importance of non-consumptive effects changes as the temperature gradient changes in Lake Michigan or as *B. lonimanus* densities increase could have an impact the rest of the community. *B. longimanus* are having a large impact on the community in Lake Michigan and understanding the mechanisms behind the changes that are occurring in the community is very important (Lehman and Caceres 1993; Vanderploeg et al. 2002, Barbiero and Tuchman 2004). *D. mendotae* are an important food source for young of year piscivorous fish and for planktivorous fish. If non-consumptive effects are important, then the reduction in *D. mendotae* population growth rate is due to lower birth rates rather than consumption by *B. longimanus*. This means that energy is not flowing up the food web into *B. longimanus*, rather the resources that would be consumed by *D. mendotae* may be available to competitors that may or may not be good food sources for fish. Further work should look into the trait-mediated indirect interactions within Lake Michigan and determine what impact variation in trait expression and non-consumptive effects has on other species, particularly important fisheries species such as yellow perch.

Tables

Parameter	Parameter description	Field or lab data range	Parameter space investigated
E/N	Egg-ratio	0.7	0.35 to 1.05
t_{min}	Deep water temperature	4-6°C	4°C - 6°C
t_{dif}	Surface temperature	4°C - 30°C	4°C - 30°C
Tc	Depth of thermocline	18.7 m	14m to 24 m
Ts	Steepness of thermocline	2.8	1 to 6
μ_B	Center of *B. longimanus* Distribution	11.6 m	+/- 5
μ_D	Center of *D. mendotae* Distribution	11.0 m, 31.1 m	+/- 5
c_B	Constant determining height of *B. longimanus* distribution	169	+/- 50
c_D	Constant determining height of *D. mendotae* distribution	26060, 28610	+/- 5000
σ_B	st. dev. of *B. longimanus* distritubion	6.6 m	+/- 3
σ_D	st. dev. of *D. mendotae* distribution	7.2 m, 4.6 m	+/- 3
I_0	Surface Light Levels	0 to 2500 μE	
K	Attenuation Coefficient	0 to 1.5	

Table 2.1. A summary of the Environmental Parameters included in the population growth rate model including Parameter, Parameter description, field or lab data range and parameter space investigated.

Curve type	**Biological rationale**	**Summary of Results**
Constant	Tactile predators where predator movement is independent of temp (endothermic)	DVM to same depth, but consumptive effects become more important as predation risk increases
Linear (risk increases w/ depth)	light or temp dependent but not directly proportional	decreases DVM depth, under some conditions best to stay at surface, consumptive effects become more important
Linear (risk decreases w/ depth)	Somewhat light or temp dependent but not directly proportional	Still best to migrate, increases DVM depth, non-consumptive effects continue to dominate
Non-linear, predation decreasing with depth (following temperature gradient)	Temperature dependent tactile predator	Still best to migrate, increases DVM depth, non-consumptive effects continue to dominate
Non-linear, predation decreasing with depth (following light gradient)	Visual predator	Migration depth remains the same, consumptive effects become gradually more important as the efficiency of the predator increases

Table 2.2. A description of additional predation curves added to the Population Growth Rate model, their biological rationale and summary of the results.

Figures

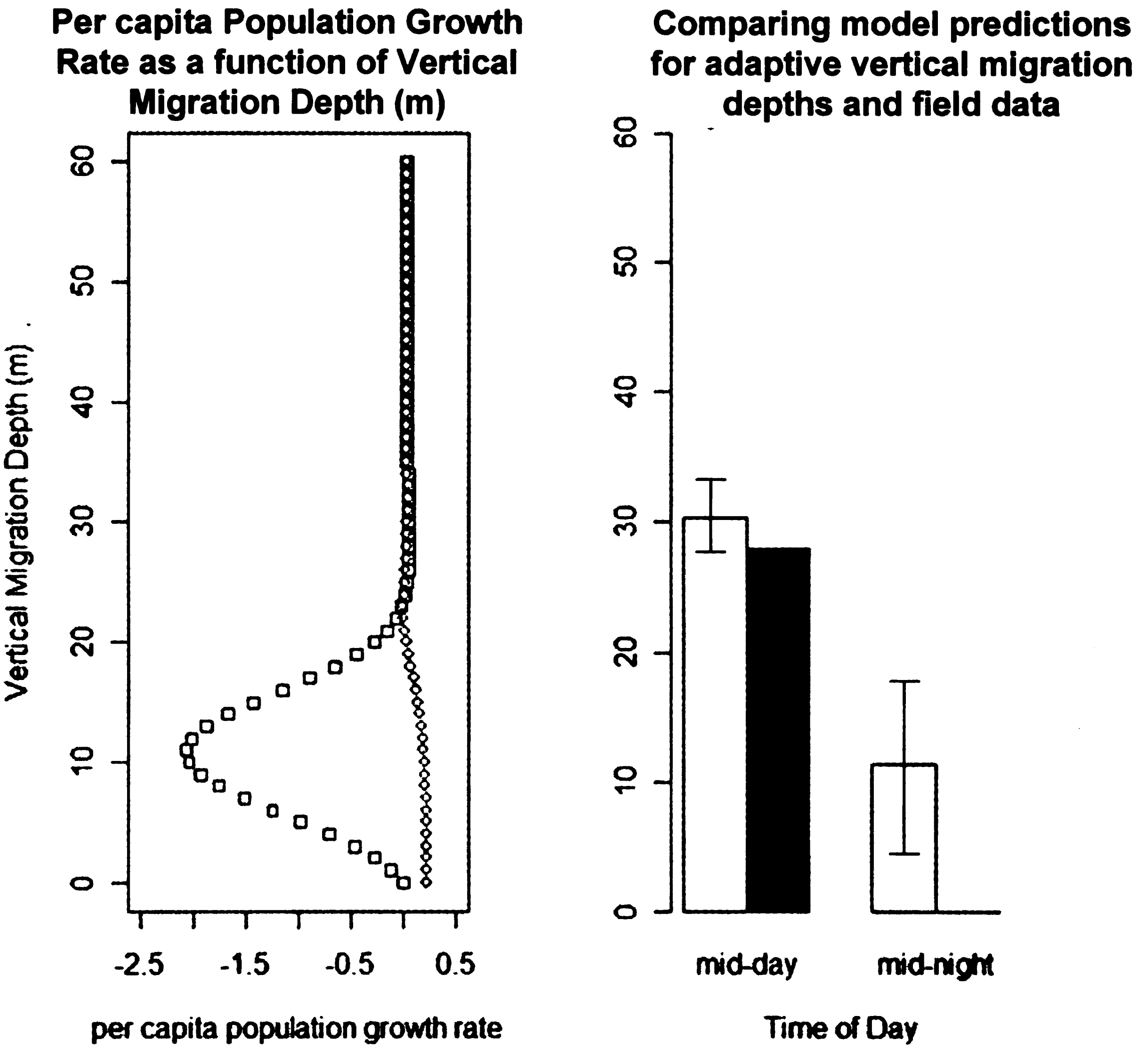

Figure 2.1. Comparing model predictions and field observations.
Per-capita population growth rate as a function of depth for mid-day and mid-night are given in Panel A. This fitness curve (panel A) gives predictions for adaptive vertical migration depth, the depths that maximize per-capita population growth rate (shown in black bars on panel B). Average vertical migration depth from a field survey conducted in Aug. 2005 are shown in panel B (white bars), the mid-day data are from 2pm and the mid-night data are from 1 pm. The error bars represent standard deviations. The model predictions were made for the same light and temperature conditions and times. The mid-day actual depths and predictions agree very well. There is a discrepancy between the mid-night predictions and field data, but this can partially be explained by the flatness of the fitness curve near the surface (between 0 m and 12 m).

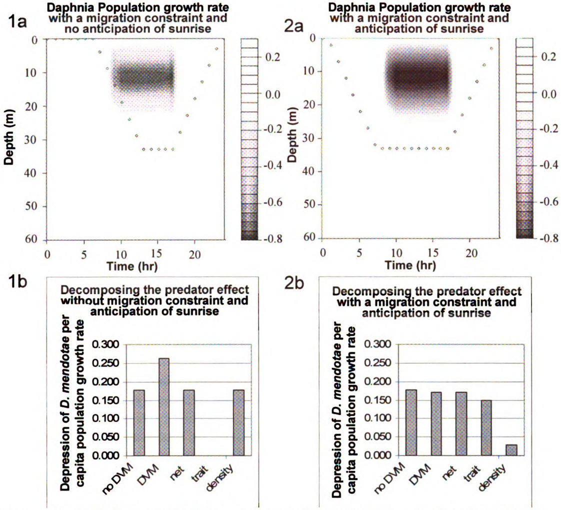

Figure 2.2. Including a migration constraint makes anticipating day-break necessary. 1a and 2a show the same fitness landscape with different migration scenarios. The fitness landscape shows a region of negative population growth rate during daylight hours from 0m to 25m. 1b and 2b compare the net predator effect with and without vertical migration (DVM) and break the net predator effect into non-consumptive and consumptive effects. The impact of *B. longimanus* is measured in terms of the depression of the per capita population growth rate due to the predator, no DVM refers to the total predator effect without *D. mendotae* migration, DVM refers to the total predator effect with migration. The no DVM and DVM bars are compared to determine whether remaining at the surface (no DVM) or migrating (DVM) is adaptive. The net effect is the total effect of *B. longimanus* on *D. mendotae* for the adaptive strategy. 1a assumes a biologically realistic swimming speed constrain, in this scenario, *D. mendotae* would have to migrate through the area of negative fitness incurring a huge mortality cost. 1b shows that the effect of the predator is minimized by remaining at the surface (no DVM). The migration scenario shown in 2a assume the same migration constraint but also assume that *D. mendotae* begin migrating early avoiding the large cost of moving through relatively shallow water with high *B. longimanus* density during daylight. 2b shows that migrating minimizes the total predator effect and that the non-consumptive effect makes up the majority of the total predator effect.

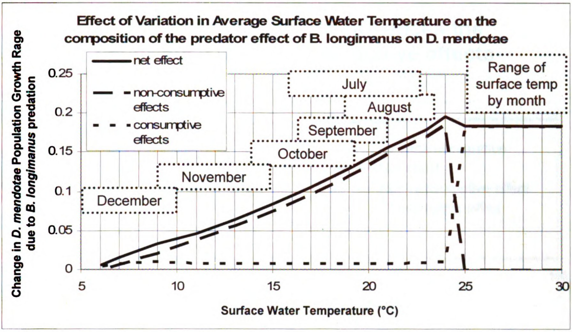

Figure 2.3. The effect of variation in surface temperature on the composition of the predator effect.

The ranges of average surface temperatures for Lake Michigan by month are shown by the amount of the x axis covered by the five boxes near the top of the graph. As the lake transitions into fall and approaches the fall turnover, the relative importance of the non-consumptive effect decreases and the relative importance of the consumptive effect increases, although its magnitude remains fairly constant. There is a strong non-linear effect at higher surface temperatures. Above a threshold temperature of 25 °C, *D. mendotae* do not migrate, non-consumptive effects are zero and consumptive effects make up the entire net effect of the predator.

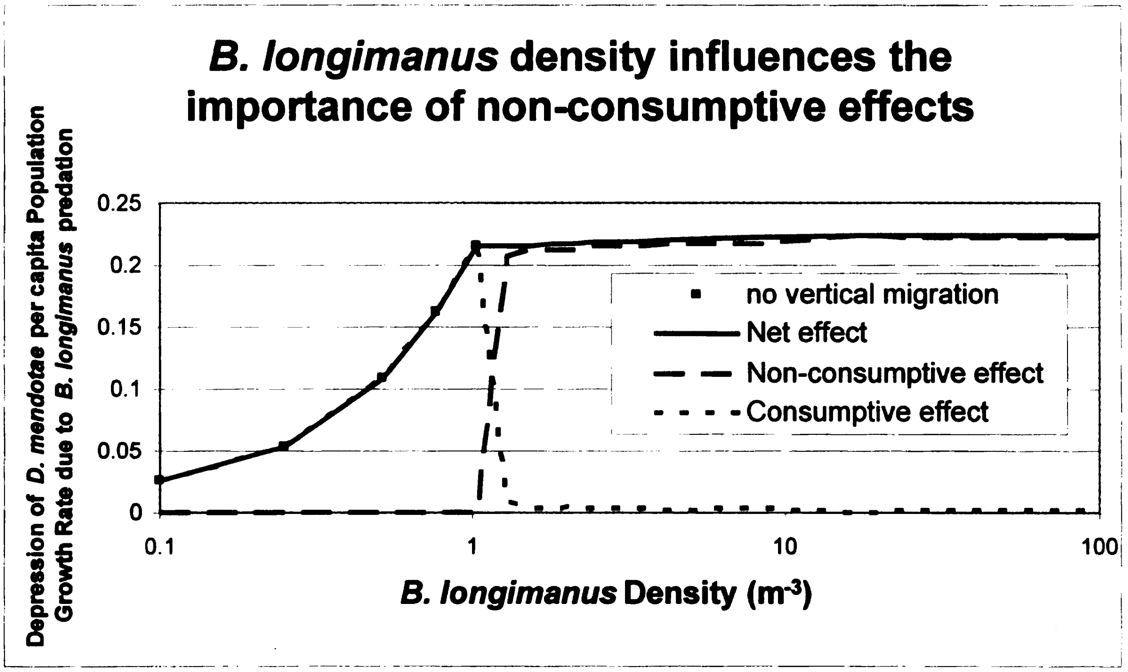

Figure 2.4 The effect of *B. longimanus* density on overall predator effect. At low densities, the predators have very little impact on *D. mendotae* per capita population growth rate and it is best for *D. mendotae* to stay at the surface so consumptive effects make up the entirety of the predator effect since there is no trait change. As *B. longimanus* densities increase, above a level of 1 individual/m^3 vertical migration is the best strategy and the net effect of *B. longimanus* predation on *D. mendotae* is almost entirely made up of the non-consumptive effect.

CHAPTER 3

SEASONAL CHANGES IN THE IMPORTANCE OF NON-CONSUMPTIVE EFFECTS IN LAKE MICHIGAN ZOOPLANKTON

Abstract

Daphnia mendotae migrate vertically into deeper, darker, cooler regions of Lake Michigan to avoid predation by an invasive planktivore, *Bythotrephes longimanus*. Since *B. longimanus* is a visual predator, *D. mendotae* vertical migration reduces direct consumption of *D. mendotae* by *B. longimanus* (consumptive effect), however, inhabiting the colder and less productive regions of the water column has a reproductive cost for *D. mendotae* (non-consumptive effect). These types of tradeoffs are ubiquitous to predator-prey interactions, and studies of various systems have shown that non-consumptive effects can be important relative to consumptive effects. In the *B. longimanus* – *D. mendotae* system, non-consumptive effects are important relative to consumptive effects, but this relative importance is dependent on environmental conditions. Here I translate my previous findings on consumptive and non-consumptive effects into longer-term, multi-generational changes in population dynamics which in this system can be observed with-in a single season. I built a stochastic population dynamics model to explore how changes in the pelagic environment (changes in abiotic conditions such as temperature and light availability along with changes in biotic conditions such as *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators and competition) over the course of a season will influence *D. mendotae* population dynamics. My results show that the importance of non-consumptive effects is large compared to consumptive effects over the course of a season. I also found that predicted changes in the temperature of Lake

Michigan due to climate change impacts the importance of non-consumptive effects. An understanding of how *B. longimanus* effects change seasonally will provide better predictions of its impact in the Great Lakes and the many other systems which it has invaded. Additionally, understanding how previous findings impact population dynamics is key to predicting species effects in different scenarios, such as those predicted with Global Warming

Introduction

Predation can have a large impact on prey populations through direct consumption, but also through a suite of phenotypic changes that they induce in individual prey. For many years it was thought that predators affect prey populations primarily through consumptive effects (also lethal or density-mediated effects). Ecologists have been aware for some time that prey respond to predation risk by modifying their phenotype to minimize the effect of the predator. It is only recently that ecologists have begun to understand how important a role these phenotypic modifications play in predator prey interactions. In modifying their traits, prey incur costs in terms of fitness surrogates such as individual growth, reproduction or population growth rates. This cost is termed the non-consumptive effect (also non-lethal or trait-mediated effect). Prey change their traits in a number of ways in response to predators, including behavioral, morphological and physiological adaptations that make them less likely to be consumed (Lima 1998). These trait changes reduce direct consumption, but also reduce the reproductive success of the prey (Harvell 1990). If prey forage less or put resources into growing larger in order to reproduce earlier or into growing defensive features, they have less resources for growth and reproduction or may face mortality from other sources. Thus, prey face a tradeoff in trying to limit the overall effect of a predator: avoid being eaten while maximizing fecundity. Studies have shown that predators induce trait changes in their prey in a large number of systems (reviewed in Lima and Dill 1990, Lima 1998, Tollrain and Harvell 1999, Agrawal 2001) and in many of these systems, these trait changes result in large non-consumptive effects on prey growth, fecundity, population growth rates, etc. (reviewed in Peacor and Werner 2004a, Preisser et al. 2005).

There is evidence from both empirical work and theory that suggests/predicts non-consumptive effects will be important over long time scales. Empirical studies have been slowly moving towards measuring consumptive and non-consumptive effects on longer-time scales, but researchers are limited in what they can accomplish by the restraints of biological systems, relatively long generation times and funding limits. The question of long-term importance of non-consumptive effects has been addressed in theoretical studies in terms of long-term community stability (Ives and Dodson 1987, Abrams 1995), and community structure. However, these studies are not based on data, rather, they are based on hypothetical relationships between functional responses or trade-offs and the degree of trait expression, rather than relationships supported with data. These studies illuminate the possible long-term implications of important non-consumptive effects. However, it is unclear how these results will apply to real-world scenarios.

The empirical studies mentioned so far measured non-consumptive effects in terms of fitness correlates. There is a gap in our real-world knowledge of how these fitness correlate results will translate into effects on population densities and dynamics. There has been a general progression towards measuring non-consumptive effects in terms of population level measures of fitness, but we do not know the importance of non-consumptive effects in terms of longer-term multigenerational measures, such as population dynamics. Initial studies of non-consumptive effects focused on quantifying costs of trait changes at the level of the individual, for instance individual growth rates, fecundity or mortality (reviewed in Lima 1998). Recently there has been a trend towards measuring non-consumptive effects on population level responses such as population growth rate (r) and geometric population growth rate (λ), these studies extend from aquatic zooplankton (Boeing et al. 2005, Pangle 2007) to stream macro-invertebrates (Peckarsky 1993, McPeek and Peckarsky 1998) to agricultural systems (Nelson 2004). Nelson measured the non-consumptive effects of damsel bug predators on pea aphid population growth in the field in small cages over a single generation and saw large effects (up to 30% decrease in population growth rate). There is a need to determine how changes in trait expression will affect prey population dynamics. Now that we know non-consumptive effects to be important in a large range of predator-prey interactions, what does this mean in terms of population dynamics?

Bolker et al. (2003) reviewed the needs of the field in 2003 and identified scaling from short-term to long-term responses of communities as one of "the most critical needs" to determining whether trait-mediated interactions affect community dynamics at scales that will influence practical management decisions. There is considerable ecological theory predicting that non-consumptive effects are likely to be important in the short term (Abrams 1984, Peacor and Werner 2004b) or to long term population stability (Ives and Dodson 1987, Abrams 1995), and to food web properties such as susceptibility to species invasions (Peacor et al 2006, Sih et al. 1985). These results, while important and interesting, are based on hypothetical curves that relate functional responses or trade-offs to degree of trait expression. The relationship between trait expression and trade-offs is unknown for many systems, thus, it is unclear whether the curves used in these theoretical studies represent real communities. We need to know how non-consumptive effects affect population dynamics at seasonal scales, the scale at which many practical management decisions are made.

Managers and ecologists need to be able to translate previous findings of the relative importance of consumptive and non-consumptive effects into longer-term multigenerational dynamics in order to understand the implications of large non-consumptive effects in ecological communities. In the previous chapter of this thesis I determined that non-consumptive effects were dependent on environmental conditions with a short-term study. In this chapter I translate these results into longer-term multigenerational dynamics. In our system, transitioning from short-term to longer-term time scales means including environmental variability that would be experienced over these longer time scales. The range of parameters I investigated in the previous chapter encompasses all environmental variation that would occur within a season, a time frame that for this system includes multigenerational dynamics. This chapter expands on our previous broad range, short-term results, integrating them in order to study longer-term multi-generational population dynamics of *D. mendotae*. I used a stochastic population dynamics model that allows translation of previous results on consumptive and non-consumptive effects into longer-term, multi-generational population dynamics. With this model I explore how changes in the pelagic environment (changes in abiotic conditions such as temperature and light availability along with changes in biotic conditions such as

B. longimanus density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators and competition) over the course of a season will influence *D. mendotae* population dynamics. This allows us to investigate how changes in abiotic and biotic conditions due to climate change and exotic invasions may influence population dynamics.

Methods

Description of System:

B. longimanus, a predatory cladoceran, is a recent invader to Great Lakes region and is thought to be having a large impact on the ecological communities of the Great Lakes (Lehman and Caceres 1993; Vanderploeg et al. 2002, Barbiero and Tuchman 2004). One of the main prey of *Bythotrephes longimanus* is a zooplankton called *Daphnia mendotae* (Lehman and Caceres 1993; Vanderploeg et al. 2002, Barbiero and Tuchman 2004). *D. mendotae* are small grazers that feed on algae and bacteria, they are a main food source of small and young fish, some of which are important commercially. *B. longimanus* is a visual predator, meaning the risk to *D. mendotae* is greatest near the surface where light levels are high (Muirhead & Sprules, 2003). As light attenuates in the water column, *B. longimanus* are less effective predators decreasing the risk to *D. mendotae*. *D. mendotae* reproduce at higher rates in warmer surface waters, their fecundity decreases with the decrease in temperature from the epilimnion to the hypolimnion (Pangle et al. 2006). *D. mendotae* balance reproductive cost and predation by migrating within the water column to minimize overall fecundity loss due to predation (Lehman & Caceres 1993, Pangle et al. 2006). In the last chapter, it was demonstrated that environmental factors, such as surface temperature, *B. longimanus* density and the presence of additional predators all can have large effects on the relative importance of consumptive and non-consumptive effects. Because these factors change through time, the relative importance of consumptive and non-consumptive effects will likely change over the course of a season and impact *D. mendotae* population dynamics over a season

The *B. longimanus – D. mendotae* system is an ideal system in which to study the importance of non-consumptive effects on longer-term multigenerational population dynamics for several reasons. First, the importance of trait-mediated interactions has already been demonstrated in the field for this system. Second, this predator-prey interaction has been studied extensively and extensive field and laboratory studies have been done that give us information on how per-capita birth and death rate change as a function of trait expression and biotic and abiotic environmental parameters. Third, the effect of environmental variation on the importance of non-consumptive effects has been documented for short-term population level responses. Finally, using a zooplankton based system allows the study of long-term multigenerational population dynamics on relatively short time scales that encompasses seasonal variation in environmental parameters that will influence multiple generations.

D. mendotae Population Dynamics Model

I built a population dynamic model to allow the extension of the instantaneous population growth rate results from the previous chapter to population dynamics, investigating the importance of trait and consumptive effects over a single season, i.e. from June to Nov, which encompass multiple generations of *D. mendotae* and *B. longimanus*. Due to the biology of the *D. mendotae, B. longimanus* system, the changes in population density over multiple generations can be investigated within a single season. With this model I investigate how changes in environmental conditions might affect the importance of non-consumptive effects over the course of a season where abiotic conditions vary naturally, and changes in biotic conditions are controlled by model dynamics.

The model determines how *D. mendotae* population densities change over time and how non-consumptive effects contribute to *D. mendotae* population dynamics. I examine two different scenarios of *B. longimanus* density and dynamics, a responsive *B. longimanus* population scenario and a fixed-data *B. longimanus* scenario. The fixed-data *B. longimanus* scenario uses field data to set *B. longimanus* densities throughout the season. The responsive *B. longimanus* scenario assumes that *B. longimanus* population dynamics are mainly driven by *D. mendotae* since *B. longimanus* has no other prey in the model. I include both types of *B. longimanus* population dynamics to investigate the two extremes of possible predator prey interactions. The first scenario assumes that D. mendotae are the primary prey of *B. longimanus* and drive *B. longimanus* dynamics. The second scenario assumes that *B. longimanus* feed on other prey as well as *D. mendotae* and that with *D. mendotae* migration to avoid *B. longimanus* predation, that other prey primarily drive *B. longimanus* densities. The model also allows no *B. longimanus* predation as a comparison to determine the overall effect of *B. longimanus* predation on *D. mendotae.*

The model is composed of a loop that repeats every time step, determining how *D. mendotae* and *B. longimanus* grow, reproduce and die (Figure 3.1). When the model is run with the data-fixed *B. longimanus* population, only *D. mendotae* grow, reproduce and die, *B. longimanus* population densities are set to natural levels as described below.

Specifically, there are eight steps that determine population dynamics and are repeated each time step (Figure 3.1, each step described in more detail below):

1. determine adaptive vertical migration depth for *D. mendotae*
2. distribute *D. mendotae* around this depth
3. determine how many new *D. mendotae* are born based on distribution and current densities
4. *B. longimanus* catch and eat *D. mendotae*
5. *B. longimanus* grow and reproduce
6. *B. longimanus* die of other causes (background death and old age)
7. *D. mendotae* die of other causes (background death and old age)
8. *B. longimanus* population is redistributed

When the *B. longimanus* population is set to natural densities the densities are treated as a time-dependent model input and read into the model and the main loop consists of steps 1, 2, 3, 4, and 7 from above (Figure 3.1). When there is no predator, the *B. longimanus* population is set to zero and *D. mendotae* die due to other causes, such as background death. Each iteration, the model outputs data on *D. mendotae* and *B. longimanus* population size as well as how many *D. mendotae* are born and eaten by *B. longimanus*, these data are used to quantify the net, non-consumptive and consumptive effect of *B. longimanus* on *D. mendotae* (Figure 3.1). The ongoing model inputs (temperature gradient, light levels, light attenuation and under some conditions, *B. longimanus* density) are based on field data and vary over time, they are read into the model main loop each time step (figure 3.1). The initial model inputs (population densities and distributions) are only entered into the model once, before the first iteration. The initial population densities and distributions are used to populate the model with individual *D. mendotae* and *B. longimanus*. After the first iteration, population densities and distributions are determined by model dynamics (Figure 3.1). All portions of the model will be described in greater detail below.

Describing the different steps of the model

D. mendotae adaptive vertical migration depth

Each time step, the model chooses one adaptive vertical migration depth by maximizing a fitness function that gives projected population growth rates at each depth.

$$g(z) = \frac{1}{N_D}\frac{dN_D(z)}{dt} = b(z) - d(z)$$

As in the previous chapter, *b(z)* (equation 2.11) is per-capita birth rate as a function and *d(z)* (equation 2.21) is per-capita predation rate as a function of depth. The 60 m water column in this model is divided into 1m^3 intervals. Choosing the adaptive vertical migration depth requires calculating g(z) for the center of each interval and comparing to find the highest value.

D. mendotae distribution

After an adaptive depth is chosen, *D. mendotae* are distributed around this depth in a normal distribution with μ = current adaptive migration depth and σ = 4.6 m and 7.2 m for day and night respectively. These values for σ were obtained from non-linear regressions of field data (Rv2.5.1, nonlinear regression, $p<0.001$, data from Pangle et al. 2007) in order to emulate field distributional patterns.

D. mendotae reproduce

Each iteration the model determines how many *D. mendotae* are born and add the new individuals to the population. The per-capita birth rate, *b(z)* is determined for each depth using the egg-ratio method described in chapter 2 (equations 2.8 and 2.9).

$$b(z) = \ln\left(E/N_D + 1\right)\left[0.00041T^2 + 0.0108T - 0.0163\right]$$

Where *b(z)* is per-capita birth rate, *E/N* is the egg-ratio and *T* is water temperature. Information on the birth rate as a function of depth, *b(z)* is combined with the current distribution of *D. mendotae* to determine how many new *D. mendotae* are born

$$B(z) = N_D(z)b(z)$$

Next, *B(z)* is summed over the entire water column to determine how many new *D. mendotae* to add to the population

$$B = \sum_{z=0}^{60} N_D(z)\ln\left(E/N_D + 1\right)\left[0.00041T^2 + 0.0108T - 0.0163\right]$$

The new *D. mendotae* individuals are added to the population, and distributed following a normal distribution with the same mean and variation as the present population.

Predation by _B. longimanus_

The number of *D. mendotae* eaten per iteration by each *B. longimanus* is a function of depth that depends on light levels and the number of *D. mendotae* and *B. longimanus* at a particular depth. For each 1m^3 cell, of depth z, the number of *D. mendotae* eaten, *D(z)*, is determined by an attack rate, which is the number of *D. mendotae* eaten per *B. longimanus*. This attack rate is modified as a function of *D. mendotae* density (type II functional response, equation 2.15) and then multiplied by the number of *B. longimanus* in that particular cell (equation 2.12). This attack rate is modified to decrease as light intensity decreases (equation 2.13). *D(z)* is divide by *D. mendotae* density, $N_D(z)$ to get a per capita predation rate (equation 2.14)

$$d(z) = \frac{\left[\frac{I_0 e^{-zK}}{11.5 + I_0 e^{-zK}}\right] N_B(z) \left[\frac{2.27\left(\frac{c_D}{\sigma_D\sqrt{2\pi}} e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}}\right)}{5.31+\left(\frac{c_D}{\sigma_D\sqrt{2\pi}} e^{-\frac{(z-\mu_D)^2}{2\sigma_D{}^2}}\right)}\right]}{N_D(z)}$$

To determine if an individual *D. mendotae* is eaten, a random number from 0 to 1 is chosen, if it is less than or equal to the predation rate for the current depth of the individual in question, the individual is eaten and removed from the population. For each *D. mendotae* eaten, one individual *B. longimanus* is randomly chosen from the current depth to eat the unlucky *D. mendotae* and this information is stored and used later for *B. longimanus* growth and reproduction.

***B. longimanus* grow and reproduce**

B. longimanus growth and reproduction depends on the number of *D. mendotae* consumed (as determined above). Allocation energy gained from consuming *D. mendotae* towards growth or reproduction is a function of the life history stage (i.e. instar) of each *B. longimanus*. Using a growth model developed by Yurista and Schulz (1999) the *D. mendotae* consumed are converted to growth for instar 1 and 2 individuals and to eggs for instar 3 individuals. The model utilizes consumption, ingestions efficiency, assimilation efficiency, respiration and molting.

B. longimanus and *D. mendotae* die of other causes (background death)

Death due to additional factors was included in the model as a background death rate. Background death is implemented by choosing a random number between 0 and 1 and comparing to the background death rate, if the random number is lower than the background death rate, the individual dies and is removed from the population. The background death rates for both *D. mendotae* and *B. longimanus* were varied between 0 and 0.1 to determine the effect of including additional mortality on population dynamics.

B. longimanus population is redistributed

To mimic natural distributions of *B. longimanus*, the population was redistributed using a normal distribution with $\mu = 11.6$ m and $\sigma = 6.6$ m , these values were obtained from a non-linear regression of field data (Rv2.5.1, nonlinear regression, $p<0.001$, data from Pangle et al. 2007).

Initial Model Inputs

Initial population densities and distributions were based on field data from Pangle et al. 2007 (as described above).

Time-dependent Model Inputs

The model inputs that varied over the course of a season and need to change with each iteration included water temperature, surface light levels, light attenuation rates and *B. longimanus* densities (when *B. longimanus* population densities are set at natural levels). Water temperature data for the entire season were obtained from a GLERL model of temperature profiles for Lake Michigan and data from Pangle et al. 2007. Surface light levels for each hour were obtained from the GLERL real-time meteorological network for the Muskegon site (2005 and 2006 data). Light attenuation rates were obtained from Pangle et al. 2007 and varied stochastically throughout the season. *B. longimanus* natural densities were set following data from Pothoven et al. 2001 with low initial densities that grew to peak between late July and September and then decreased again.

Model Outputs

Each iteration, the model outputs data on *D. mendotae* and *B. longimanus* population size as well as how many *D. mendotae* are born and how many *D. mendotae* are eaten by *B. longimanus*. These data were used to quantify the net, non-consumptive and consumptive effect of *B. longimanus* on *D. mendotae* (Figure 3.1).

Determining how *B. longimanus* predation affects *D. mendotae* population dynamics metrics

The effect of a predator on prey population dynamics can be measured in terms of biomass (standing crop) or energy flow (population turnover). I used both of these methods to determine the effect of *B. longimanus* predation on *D. mendotae* population dynamics. The change in biomass due to predation was determined by taking the difference between *D. mendotae* density in *B. longimanus* absence and *B. longimanus* presence. The change in energy flow due to *B. longimanus* predation was determined by finding the difference between the daily *D. mendotae* population density change in *B. longimanus* absence and presence.

Determining the net effect

The net effect was measured each time step and is called the instantaneous net effect. The instantaneous net effect is determined by calculating how large the population of *D. mendotae* would grow in a single time step without *B. longimanus* predation if they remained at the surface. To determine this value, I take the population density at the beginning of a time step and calculate how many *D. mendotae* would be born if all current *D. mendotae* were to remain at the surface for the time step, I then subtract the actual population density at the end of the time step (after cost of migration and direct predation have been factored in).

Determining the consumptive effect

The consumptive effect is the change in population density due to direct mortality. I isolate the consumptive effect each time step by keeping track of the number of *D. mendotae* that are consumed by *B. longimanus.*

Determining the non-consumptive effect

The non-consumptive effect is the decrease in the number of *D. mendotae* born due to the cost of vertical migration. I isolate the non-consumptive effect each time step by keeping track of the number of *D. mendotae* that are born and comparing that to the number of *D. mendotae* that would have been born if they all were at the surface (i.e. position in *B. longimanus* absence).

Results

B. longimanus predation had a large impact on *D. mendotae* population dynamics (Figure 3.2). When *B. longimanus* densities are fixed at natural densities (figure 3.2a), *B. longimanus* predation substantially decreases *D. mendotae* biomass. Comparing *D. mendotae* density in the presence and absence of *B. longimanus* (figure 3.2b) elucidates the impact of *B. longimanus* predation in terms of changes in *D. mendotae* biomass. The percent decrease in *D. mendotae* biomass due to predation of *B. longimanus* is large, ranging from 90% early in the season to 10% later in the season (figure 3.2c). *B.*

longimanus predation also affects *D. mendotae* population dynamics through the turnover rate of the population, the energy flow (figure 3.2c). The amount of energy flow through the food web due to turnover in *D. mendotae* populations changes over the course of the season, quickly increasing from 10% of the total *D. mendotae* population to 30% of the population and the gradually decreasing over the course of the season (figure 3.2c). The changes *D. mendotae* biomass and energy flow are mainly comprised of non-consumptive effects (Figure 3.2c).

The non-consumptive effect of *B. longimanus* predation on *D. mendotae* population growth rate is very large compared to the consumptive effect (figure 3.2d). Non-consumptive effects make up majority of the net effect of the predator, ranging from 60 to 90 percent of the total effect of *B. longimanus* predation on *D. mendotae* population dynamics (figure 3.3). The model predicts that non-consumptive effects dominate consumptive effects throughout the entire season, although there are seasonal differences in the magnitude of both consumptive and non-consumptive effects. Over the course of the season, both the consumptive and non-consumptive effect change, although the non-consumptive effects changes are much larger than the changes in the consumptive effect.

Seasonal changes had a strong influence on the relative magnitude of non-consumptive effects and a smaller influence in the relative importance of consumptive effects. Generally, the net effect of the predator increases initially and then decreases over the remaining portion of the season (Figure 3.2d). Changes in *B. longimanus* density contribute to the observed changes in the non-consumptive effect. The changes are of small magnitude because the magnitude of the consumptive effects is smaller. Both, changes in surface water temperatures and *B. longimanus* density (figure 3.2a) contribute to the changes in non-consumptive effects. Comparing *B. longimanus* dynamics (figure 3.2a) and non-consumptive effects (figure 3.2d), it is evident that the importance of the non-consumptive effect closely follows *B. longimanus* density. However, during July, August and September, there appears to be another factor influencing *D. mendotae* population dynamics. The non-consumptive effect curve (figure 3.2d) is comparatively less steep than the *B. longimanus* density curve (figure 3.2d) during the earlier portion of the season, however it matches the shape of the temperature curve very well. The model predicts that during the beginning of the season, surface water temperature plays a large role in the interaction between *B. longimanus* and *D. mendotae* and that the influence of *B. longimanus* density increases as the season progresses.

Interestingly, the model predicts two distinct, consistent patterns of population dynamics for both *D. mendotae* and *B. longimanus* densities when a responsive *B. longimanus* population is included. The first pattern of dynamics is remarkably similar to the fixed-data case described above (figure 3.3). After an initial increase, *D. mendotae* density remains fairly constant and gradually begins to decline (figure 3b). *B. longimanus* densities increase gradually for the first month, slowly peak and then begin to decrease (figure 3a) showing very similar dynamics to natural *B. longimanus* density data (figure 3.2a) although with some small fluctuations in density. The second pattern is drastically different, *B. longimanus* densities increase quickly over the first month causing a crash in the *D. mendotae* population (figure 3.4b), which leads to a sharp peak and large decrease in *B. longimanus* densities (figure 3.4a). Interestingly, as *B. longimanus* population density increases and *D. mendotae* population densities begin to fall, consumptive effects become more important that non-consumptive effects for a brief period of time (figure 3.4d). The initial rate at which the *B. longimanus* population grows seems to determine dynamics. Varying both *B. longimanus* and *D. mendotae* background death rates led to these different patterns emerging. For low *B. longimanus* background death rates, or low *D. mendotae* background death rates, initial *B. longimanus* population growth rates were high leading to dynamics that followed the second pattern. For high *B. longimanus* background death rates, or high *D. mendotae* background death rates, where initial *B. longimanus* population growth was much slower, population growth followed the first pattern (similar to fixed-data results).

B. longimanus and *D. mendotae* population dynamics changed drastically with changes in *B. longimanus* background death rate. As *B. longimanus* background death rates decrease *B. longimanus* populations grow at a fast rate until a threshold density (peak in figure 3.4,b) after which the *D. mendotae* population crashes down to refuge levels and then begins to grow again once *B. longimanus* population density has decreased. At lower *B. longimanus* background death rates, where *B. longimanus* has higher growth rates, predation has a drastic effect on *D. mendotae* dynamics that is made up almost entirely of changes in *D. mendotae* population density (with the percentage decreases is density due to predation ranging from 30% to almost 100% under some conditions).

Under climate change predictions water temperatures will increase and fall turnover will occur later (Brooks and Zastrow, 2002), extending the interval for which non-consumptive effects are important (Figure 3.5). We do not see changes in adaptive vertical migration behavior and consequently large non-linear changes in the magnitude of the non-consumptive effect at water temperatures above 25°C, as was predicted in the last chapter (Figure 3.5). This seems to be due to changing *B. longimanus* densities that are tied to *D. mendotae* densities. If *B. longimanus* densities are fixed at natural levels under climate change predictions we see a decrease in non-consumptive effect in July, August and September when there are some days that reach above 25°C (Figure 3.6).

Discussion

My results indicate that non-consumptive effects are an important component of changes in seasonal dynamics. The changes observed at this multigenerational timescale were seen in *D. mendotae* density and turnover rates. Population dynamics were influenced by both *B. longimanus* densities and surface water temperature. Surface water temperature had the greatest impact early in the season and the influence of *B. longimanus* densities increased over time. Non-consumptive effects were very large and made up the majority of the net effect of the predator. As the season progressed and the hypolimnion cooled, non-consumptive effects became less important, but still dominated consumptive effects. Increasing surface temperature and the period of thermal stratification (as is predicted for Lake Michigan under climate change) leads to an increase in the magnitude and importance of non-consumptive effects.

My results point out that non-consumptive effects are very important on seasonal, multigenerational time-scales. Other studies have shown non-consumptive effects to be important in short-term experiments and field studies up to time-frames of a single generation (Nelson 2004, Peckarsky 1993). Theory predicts that non-consumptive effects are likely to be important in the short term (Abrams 1984, Peacor and Werner 2004) or to long term population stability (Ives and Dodson 1987, Abrams 1995), and to food web properties such as susceptibility to species invasions (Peacor et al 2006, Sih et al. 1985). However, these theoretical studies used made up functional responses and so it is difficult to understand how they might apply in real systems. My results build on these previous results by using field and laboratory data to make predictions about the longer-term importance of non-consumptive effects. It may be impractical to attempt to determine if non-consumptive effects are important over longer time scales in many systems through long term experiments since many systems of interest have species with long generation times making long-term experimentation prohibitive. However, as I have shown in this chapter, it is possible to make longer-term predictions of the importance of non-consumptive effects if one understands how biotic and abiotic environmental conditions affect the importance of non-consumptive effects and how these conditions vary naturally over the time frame of interest. Additionally, the *D. mendotae, B. longimanus* system does not have this generational time limitation, thus multi-generational dynamics can be observed in a single season. Further work should test the predictions made in this chapter in the field.

Previous empirical studies have shown non-consumptive effects to be important relative to consumptive effects (reviewed in Peacor and Werner 2004 and Preisser et al. 2005) and theoretical work has shown non-consumptive effects to have important implications for long-term community stability (Abrams 1995, Ives and Dobson 1987). These studies have helped to answer questions about the importance of non-consumptive effects. However, these are not the scales at which management decisions are made. For managers to understand that non-consumptive effects are very likely to be important in their systems, it is necessary to show that non-consumptive effects are important on scales at which practical management decisions are made, on seasonal dynamics. Our results show that non-consumptive effects have more of an impact on seasonal dynamics than consumptive effects.

Results from this model support some of the predictions made in the last chapter. Results reported in the previous chapter show a strong non-linear relationship between surface temperature and non-consumptive effects for high temperatures that is affected by *B. longimanus* density. As *B. longimanus* density increases, the threshold temperature increases to a level above what is predicted with climate change and we no longer see a shift in behavior; non-consumptive effects dominate for the whole summer and fall. Our model probably over estimates the dependence of *B. longimanus* on *D. mendotae* since it dose not include any other prey. In natural communities, *B. longimanus* prey on other species and fluctuations in their population density do not follow *D. mendotae* population density fluctuation as closely. Thus, it still might be possible for the temperature threshold to fall within climate change predictions. Whether we see days in July and August in the future where non-consumptive effects are non-existent because *D. mendotae* do not migrate will depend on *B. longimanus* densities as well as surface temperature.

Our model predicts that changes in the Great Lakes due to climate change could increase the time period over which non-consumptive effects are important. Climate change scenarios indicate shorter winters with longer periods of thermal stratification with some predictions placing fall turnover up to 2 months later than current dates (Brooks and Zastrow, 2002). If stratification were to persist longer into the winter it would add to the period of time that non-consumptive effects dominate. Increasing temperatures over the season also increase the magnitude of the non-consumptive effects for later months. It is still unclear what might happen in July and August. If temperatures are consistently above the temperature threshold, then *D. mendotae* should remain at the surface and non-consumptive effect will be non-existent. It is unclear if this will happen, since the threshold value depends on *B. longimanus* density as *B. longimanus* density increases, the threshold for the behavior shift also increases. My model indicates that observing this behavioral transition in the field will likely depend on how quickly *B. longimanus* densities respond to increases in *D. mendotae* densities. If there are days with low *B. longimanus* densities and high temperatures then we expect to see *D. mendotae* remain at the surface and non-existent non-consumptive effects. Since this behavior shift is dependent on *B. longimanus* densities, we might expect to see particular days where *D. mendotae* do not migrate, however, we probably will not observe long periods where *D. mendotae* do not migrate. This would lead to non-consumptive effects being less important overall during late summer but still dominating consumptive effects, transitioning to a longer period where non-consumptive effects dominate due to longer periods of stratification but become increasing less important. However, I am making an assumption here that the mechanism by which *D. mendotae* respond to *B. longimanus* presence is also attuned to temperature and predator density. This is probably not the case so we probably will not see *D. mendotae* remaining at the surface on hot August days. More work is needed to clarify the non-consumptive effects given the simultaneous operation of different mechanisms if we integrate these temperature results over time.

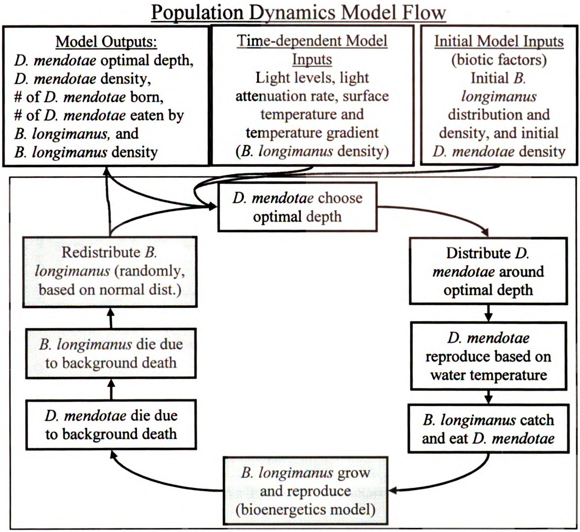

Figure 3.1: Flow diagram for Population Dynamic Model
The general flow for the Population Dynamic Model describing the model inputs (green), the basic model loop (blue) and the outputs (red). The main loop for the model version that includes a *B. longimanus* population that is dynamically tied to *D. mendotae* follows the black arrows and includes the rectangles with white and gray backgrounds. The main loop for the model version where *B. longimanus* densities are fixed at natural levels includes only the rectangles with white backgrounds (skip over the gray backgrounds). Initial model inputs include *D. mendotae* density, *D. mendotae* distribution, *B. longimanus* density and distribution, these are parameters that are initially supplied to the model, but for all subsequent model loops are provided by the previous iteration. Time-dependent model inputs are abiotic parameters that are used each iteration and may vary with time, such as surface light levels, light attenuation, temperature profile and with the fixed *B. longimanus* populations, *B. longimanus* density. Each iteration of the model the main loop of the model runs and *D. mendotae* and *B. longimanus* grow and reproduce and *B. longimanus* density, *D. mendotae* density, optimal depth, and number of *D. mendotae* births and deaths are outputted.

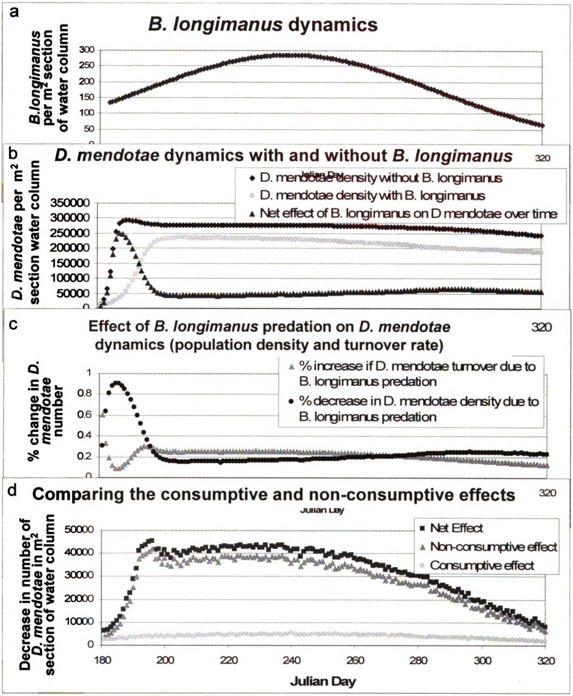

Figure 3.2: *D. mendotae* population dynamics with fixed *B. longimanus* population based on field data.

Figure 3.2a shows *B. longimanus* population densities. Figure 3.2b shows *D. mendotae* population dynamics with and without *B. longimanus* predation and the cumulative net effect of *B. longimanus* predation on *D. mendotae* population density. Figure 3.2c shows the effect of *B. longimanus* predation on *D. mendotae* density and turnover rate. Figure 3.2d shows the instantaneous net effect of the predator, the non-consumptive effect and the consumptive effect.

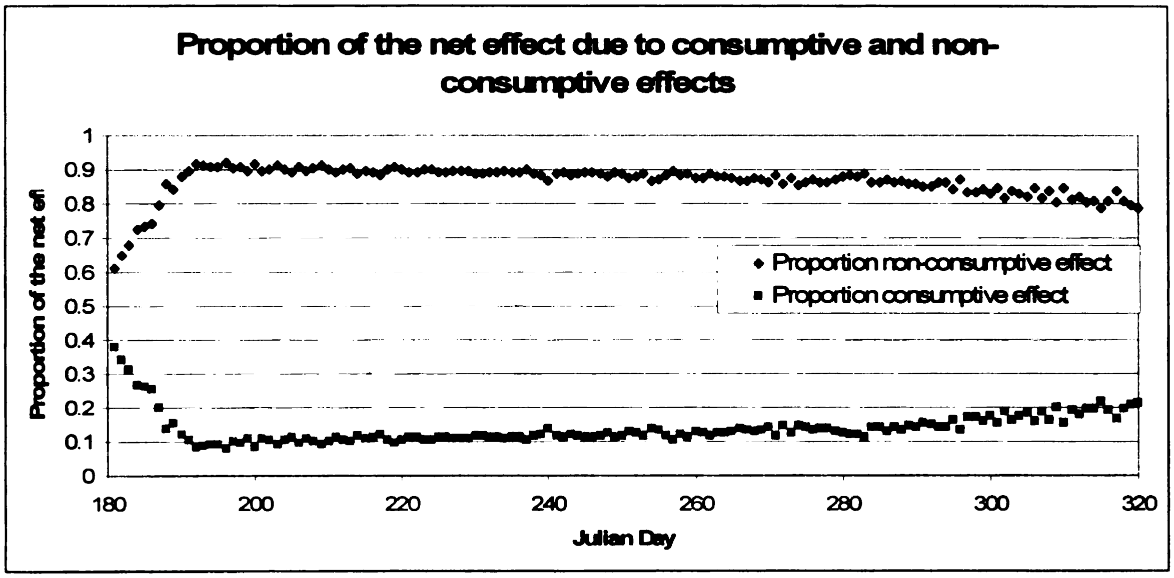

Figure 3.3: Breaking down the net effect of the predator into the proportion due to non-consumptive effects and the proportion due to consumptive effects.

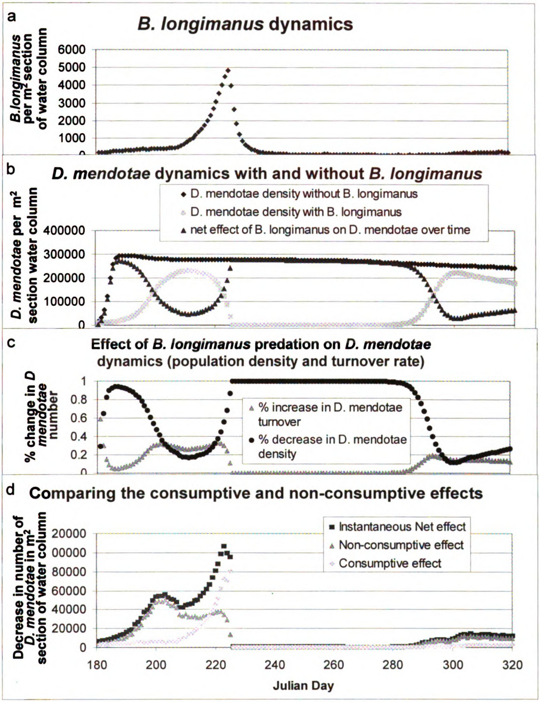

Figure 3.4: *D. mendotae* population dynamics with a responsive, slow growing, *B. longimanus* population.
Fiugre 4a shows *B. longimanus* population dynamics. Figure 3.4b shows *D. mendotae* population dynamics with and without *B. longimanus* predation and the cumulative net effect of *B. longimanus* predation on *D. mendotae* population. Figure 3.4c shows the effect of *B. longimanus* predation on *D. mendotae* density and turnover rate. Figure 3.4d shows the instantaneous net effect of the predator, the consumptive effect and the non-consumptive effect.

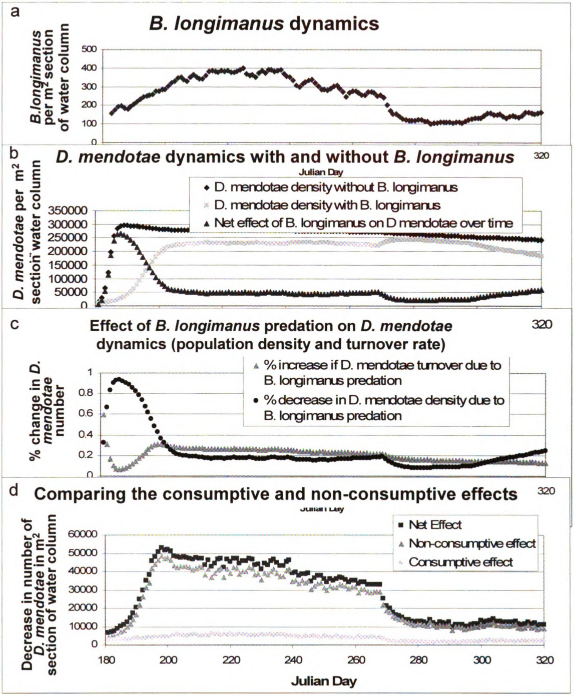

Figure 3.5: *D. mendotae* population dynamics with a responsive, fast growing, *B. longimanus* population.

Figure 3.5a shows *B. longimanus* population dynamics. Figure 3.5b shows *D. mendotae* population dynamics with and without *B. longimanus* predation and the cumulative net effect of *B. longimanus* predation on *D. mendotae* population density. Figure 3.5c shows the effect of *B. longimanus* predation on *D. mendotae* density and turnover rate. Figure 3.5d shows the instantaneous net effect of the predator, the consumptive effect and the non-consumptive effect.

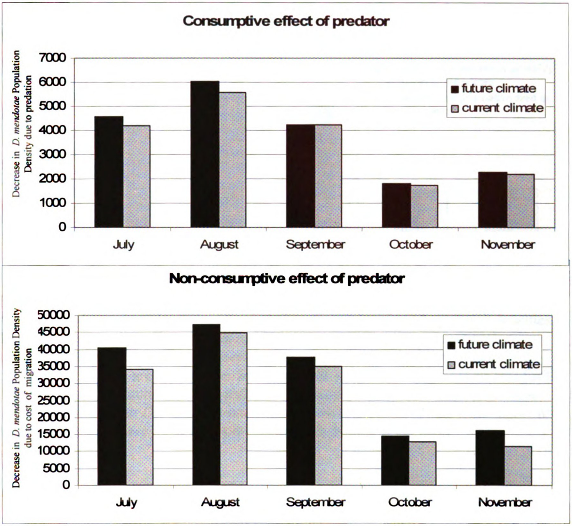

Figure 3.6: Comparing consumptive and non-consumptive effects for present and future climate over a season.
Both the consumptive and non-consumptive effects are measured in terms of decrease in *D. mendotae* population density. Each bar represents an average value for the month. Non-consumptive effects are much larger than consumptive effects, although the magnitude of consumptive effects decreases over time.

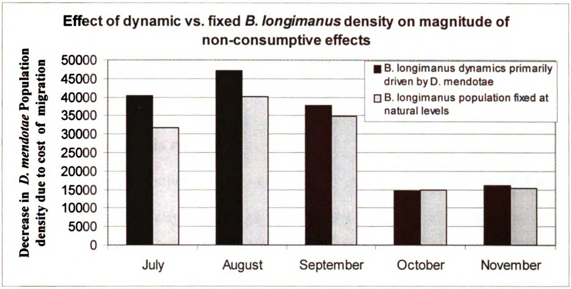

Figure 3.7: Comparing the non-consumptive effect for future climate conditions over a season with dynamic *B. longimanus* population densities or forced at natural densities. The non-consumptive effects are measured in terms of decrease in *D. mendotae* population density. Each bar represents an average value for the month. Non-consumptive effects are much larger for dynamic *B. longimanus* populations that for the populations set at natural densities and not dynamically tied to *D. mendotae*. These differences are due to *D. mendotae* not migrating on some days in July and August when temperatures are above 25°C and non-consumptive effects being zero.

CHAPTER 4

SUMMARY AND IMPLICATIONS

Summary of thesis

Motivation for thesis research

As I began my thesis, there was a substantial body of research showing that a large variety of prey modify their phenotypes in an attempt to minimize predation (reviewed in Lima and Dill 1990, Lima 1998, Tollrain and Harvell 1999, Agrawal 2001). A growing number of studies have shown that when prey modify their phenotype, they incur a cost that effects their fitness through changes in growth rate, fecundity, etc. and that these costs can be as large or larger than the fitness cost of direct mortality (reviewed in Peacor and Werner 2004a and Preisser et al. 2005). These trait modifications, while maximizing overall fitness, shift the cost from mortality due to predation (consumptive effect) to other costs (non-consumptive effects) such as growth and fecundity. Many studies have quantified these costs on fitness correlates (such as individual growth, fecundity, population growth rate) and found non-consumptive effects to be large in a variety of systems (both aquatic and terrestrial).

Ecologists have made great strides towards understanding the importance of non-consumptive effects, but many questions still remain regarding the general importance of non-consumptive effects. Particularly, little is know about how interactions with the environment and with other species might influence trait expression and the relative importance of non-consumptive effects. We expect plastic traits to change as a result of changes in the environment. If the cost of trait expression is not constant, we would also expect the relative contribution of consumptive and non-consumptive effects to vary across environmental conditions as well. However, very few studies have attempted to determine how environmental variability affects the relative importance of consumptive and non-consumptive effects.

The majority of studies that have quantified non-consumptive effects so far, have measured them in terms of fitness correlates. We know that prey trait modification in response to predators has a large impact on prey growth and fecundity and in some more recent studies, population growth rates. However, we do not know how these instantaneous effects translate into longer-term, multi-generational population dynamics. These longer-term dynamics are the scales at which management decisions are made. If we truly want to understand how much of an impact prey trait modification has on communities, we need to understand how these instantaneous results translate to longer time scales.

The effect of environmental variation

I used the models presented in chapter 2 to determine how environmental conditions affect trait expression and the relative importance of consumptive and non-consumptive effects. This required a thorough knowledge of how birth and death rates depend on trait expression, and how this relationship is affected by changes in both biotic and abiotic environmental parameters. I used a zooplankton predator-prey system (*B. longimanus* and *D. mendotae*). In this system the trait in question was vertical migration. The environmental conditions I investigated are *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators, competition, surface light availability, light attenuation, surface water temperature and the thermal profile of Lake Michigan.

My results show that trait expression and the importance of trait-mediated interactions are highly dependent on environmental conditions. The models predict large changes in adaptive vertical migration depth and the relative contributions of consumptive and non-consumptive effects for some variables (surface temperature, temperature gradient, *B.* longimanus density and presence of additional predators) and not others (*D. mendotae* density, competition, surface light levels and light attenuation rate). Some of the changes we observed were gradual. For example, seasonal changes in the temperature gradient caused a gradual decrease in the magnitude of non-consumptive effects. Other variables, such as *B. longimanus* density and surface water temperatures caused strong, nonlinear changes. The variation in impact on the relative importance of non-consumptive effects can be explained when we examine how the factor affects birth and death magnitudes as a function of depth, and in turn how this affects the adaptive trait change.

Translating fitness correlate results to seasonal population dynamics

To translate previous findings on consumptive and non-consumptive effects into longer-term, multigenerational changes in population dynamics, I used a population dynamic model presented in chapter 3. I used the *Daphnia mendotae, Bythotrephes longimanus* system to explore how changes in the pelagic environment (i.e., changes in abiotic conditions such as temperature and light availability along with changes in biotic conditions such as *B. longimanus* density, *D. mendotae* density, *B. longimanus* distribution, *D. mendotae* distribution, predation risk from additional predators and competition) over the course of a season influence *D. mendotae* population dynamics. The focus was on seasonal dynamics because it is a scale at which management decisions are made and in this system a season incorporates environmental variability and encompasses many generations of both *D. mendotae* and *B. longimanus.*

My results indicate that non-consumptive effects are an important component of changes in seasonal dynamics. The changes we observed at this multi-generational timescale were mostly due to seasonal changes in water temperature and *B. longimanus* densities. As the season progressed and the hypolimnion cools, non-consumptive effects became less important. As the season progressed, the influence of *B. longimanus* densities on *D. mendotae* dynamics increased. As *B. longimanus* densities decrease and surface temperature decreases later in the season, the effect of *B. longimanus* densities becomes more important. This study shows that it is possible to make longer-term predictions on the importance of non-consumptive effects if one understands how biotic and abiotic environmental conditions affect the importance of non-consumptive effects and how these conditions vary naturally over the time frame of interest.

Needs for further study

The apparent universality of prey modifying their phenotype to minimize the effect of predators and the dependence of expression of phenotypic traits on environmental conditions, suggests that the relative importance of consumptive and non-consumptive effects will generally depend on the environment. However, aside from some preliminary studies and this in depth study of the *B. longimanus, D. mendotae* system, there is not a lot of evidence to support this idea. Therefore, the analysis performed in my study needs to be repeated in additional systems. I put a large effort into applying my approach to additional systems. However, was unable to find the system in which sufficient data were available, even when combining data from multiple laboratories and contacting authors for unpublished data. This suggests that whereas many researchers are demonstrating the short term effects of non-consumptive effects, they are not collecting the information required to make longer term inferences. In order to apply the analysis performed in my study to other systems the following information is required

1. birth and death rate dependence on trait expression
2. how these birth and death rate functions vary with changes in environmental conditions
3. extensive data on how environmental conditions vary over time

I reviewed studies that have looked at the impact of some environmental conditions (predators, resources and competitors) and studies that attempted to measure both consumptive and non-consumptive effects in an attempt to repeat this study and determine if my main result, the dependence of the relative importance of non-consumptive and consumptive effects on the environment, is true for other systems. Through this literature search, I learned that the necessary data are not available for many systems and was unable to find the data needed to repeat such a study. In particular, there is little understanding of how birth and death rates change as a function of trait expression.

My study indicates that further work on the *B. longimanus, D. mendotae* system would improve our understanding of the impact variation in trait expression and non-consumptive effects has on other species, particularly important fisheries species. Theory predicts that including plastic trait expression and the resulting cost in terms of fitness can change the relative strengths of direct and indirect interactions (Abrams 1995) and many empirical studies have shown trait-mediated indirect interactions to be important (reviewed in Werner and Peacor 2003). Previous studies have shown that *B. longimanus* are having a large impact on the community in Lake Michigan and understanding the mechanisms behind the changes that are occurring in the community is very important (Lehman and Caceres 1993; Vanderploeg et al. 2002, Barbiero and Tuchman 2004). *D. mendotae* are an important food source for young piscivorous fish and for planktivorous fish. If non-consumptive effects are important as my study indicates, then the reduction in *D. mendotae* population growth rate is due to lower birth rates rather than consumption by *B. longimanus*. This means that energy is not flowing up the food web into *B. longimanus*, rather the resources that would be consumed by *D. mendotae* may be available to competitors that may or may not be good food sources for fish. We need to understand how these large non-consumptive effects propagate through the Lake Michigan community. We also need to understand that these non-consumptive effects are large, but change over the course of the season and that this can influence the rest of the community.

Implications of thesis work

The implications of the work presented in this thesis are far reaching. It is now clear that changes in phenotypic trait expression due to environmental conditions have a large impact on predator-prey interactions, including prey population dynamics. This work has implications for community ecology, aquatic ecology, particularly understanding the Lake Michigan pelagic community and understanding how climate change and invasive predators will likely impact aquatic communities.

It is clear that researchers need to consider that the importance of non-consumptive effects depends on environmental conditions when deciding whether results from specific systems regarding the importance of non-consumptive effects will hold for their particular set of conditions. The work presented in this thesis has implications for generalizing from empirical studies that show important non-consumptive effects. My work has shown that the relative importance of consumptive and non-consumptive effects depends on environment conditions making it clear that environmental conditions should be considered when trying to extend results within a system to different environmental conditions (temporally or spatially) or between similar systems. An understanding of the effects of the environment will be particularly important when considering past and future changes to ecosystems from invasive species and climate change.

Understanding how trait expression and non-consumptive effects can vary with environmental conditions has implications for ecological communities in terms of trait-mediated indirect interactions. Theory indicates that including plastic trait expression and the resulting cost in terms of fitness can change the relative strengths of direct and indirect interactions (Abrams 1995), indicating that changes in trait expression due to changes in environmental conditions may be very important. Explicitly including environmental factors in addition to predation risk may change how we understand communities. These observed changes in consumptive and non-consumptive effects as a function of the environment do not only affect the predator and prey populations, but also propagate through the community, as indirect interactions, affecting additional prey, competitors and predators of our two focal species. Thus, plastic traits and non-consumptive effects may have large impacts on biological communities.

My results indicate that these large instantaneous non-consumptive effects are important on longer time scales and do affect population dynamics. In fact, non-consumptive effects make up a large portion of the effect of *B. longimanus* on *D. mendotae* population dynamics. The contribution of non-consumptive effects to changes in prey dynamics indicates that managers need to seriously consider the importance of changes in trait expression and the resulting non-consumptive effects in interactions between species. Non-consumptive effects are large enough that they have a substantial impact on prey population dynamics through both changes in prey biomass and energy flow. Potentially, non-consumptive effects on prey population dynamics could drastically impact the community through trait-mediated indirect interactions.

Lastly, the work I have presented in my thesis adds to the growing understanding that adaptive behavior needs to be included in a general understanding of biological communities. Specifically, this thesis adds to a growing body of research that shows that adaptive changes in trait expression have a profound effect on communities. We, as ecologists, cannot hope to understand ecological communities without including dynamic traits. It is becoming clear that in order to understand biological communities, the fields of ecology, evolution and behavior must come together. The body of research on the importance of adaptive trait expression and non-consumptive effects indicates that ecological models need to include plastic traits or risk severely underestimating the importance of species interactions and the mechanisms that underlie these interactions.

LITERATURE CITED

Abrams, P. A. 1982. Functional responses of optimal foragers. American Naturalist 120:382-390.

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80-96.

Abrams, P. A. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. Pp. 38-54. in Kerfoot, W.C. and A. Sih, eds. Predation: direct and indirect impacts on aquatic communities. University Press of New England. Hanover.

Abrams, P.A. 1993. Why predation rate should not be proportional to predator density. Ecology, 74:726-733.

Abrams, P.A. 1995. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. American Naturalist, 146:112-134.

Abrams, P.A. 1997. Variability and adaptive behavior: implications for interactions between stream organisms. Journal of the North American Benthological Society, 16:358-374.

Agrawal, A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294: 321–326.

Barbiero R.P. and M.L. Tuchman. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran Bythotrephes longimanus. Canadian Journal of Fisheries and Aquatic Sciences, 61, 2111–2125.

Boeing, W.J., Wissel, B. and C. W. Ramcharan. 2005. Costs and benefits of Daphnia defense against Chaoborus in nature. Canadian Journal of Fisheries and Aquatic Sciences, 62:1286–1294.

Bolker, B., Holyoak, M., Krivan, V., Rowe, L., and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology, 84:1101-1114.

Boscarino, B.T., Rudstam, L.G., Mata, S., Gal, G., Johannsson, O.E., and E.L. Mills. 2007. The effects of temperature and predator-prey interactions on the migration behavior and vertical distribution of Mysis relicta. Limnology and Oceanography, 52:1599-1623.

Brooks, A.S., and J.C. Zastrow. 2002. The Potential Influence of Climate Change on Offshore Primary Production in Lake Michigan. Journal of Great Lake Resources, 28:597-607.

Caro, T.M. 2005. Antipredator Defenses in Birds and Mammals. Chicago: University of Chicago Press.

Cresswell, W. 2008. Non-lethal effects of predation on birds. Ibis, 150:3-17.

Dawidowicz, P., and C. J. Loose. 1992. Cost of swimming by Daphnia during diel vertical migration. Limnology and Oceanography 37:665–669.

Dawidowicz, P. and M. Wielanier. 2004. Cost of predator avoidance reduce competitive ability of Daphnia. Hydobiologia 526:165-169.

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. Canadian Journal of Zoology, 65:803–811

Edmonson, W.T., and A.H. Litt. 1982. *Daphnia* in Lake Washington. Limnology and Oceanography. 27:272-293.

Eklov, P., and E.E. Werner. 1999. Multiple predator effects on size-dependent behavior and mortality in two anuran species. Oikos, 88:250-258.

Eklov, P., and C. Halvarsson. 2000. The trade-offs between foraging activity and predation risk for Rana temporaria in different food environments. Canadian Journal of Zoology, 78:734-739.

Fiksen, O., 1997. Allocation patterns and diel vertical migration: modeling the optimal Daphnia. Ecology 78:1446-1456.

Fiksen, O., Eliassen, S., and J. Titleman. 2005. Multiple predators in the pelagic: modeling behavioural cascades. Journal of Anmical Ecology 74:423-429.

Gelinas, M., Pinel-Alloul B., and M. Slusarczyk. 2007. Alternative antipredator responses of two coexisting Daphnia species to negative size selection by YOY perch. Journal of Plankton Research 29:775-789.

Gore, A., and S. Paranjpe. 2001. A course in mathematical and statistical ecology. Kluwer Academic Publishers.

Harvell, C.D. 1990. The ecology and evolution of inducible defenses. Quarterly Review of Biology, 65:323–340.

Ives, A. R., and A. P. Dobson. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. American Naturalist 130:431-447.

Karels, T.J., Byrom, A.E., Boonstra, R. and C.J. Krebs. 2000. The interactive effects of food and predators on reproduction and overwinter survival of Arctic Ground Squirrels. Journal of Animal Ecology, 69: 235–247.

Lehman, J.T. & Caceres C.E. 1993. Food-webs response to species invasion by a predatory invertebrate: *B. longimanus* in Lake Michigan. Limnology and Oceanography, 38, 879–891.

Lima, S.L. (1998) Non-lethal effects in the ecology of predator–prey interactions: What are the ecological effects of anti-predator decision-making? Bioscience, 48, 25–34.

Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation. Canadian Journal of Zoology 68:619-640

Mangel M, Clark C (1988) Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, NJ

McPeek, M.A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: Combining mortality, growth and fecundity effect. Ecology 79:867–879.

Muirhead J. and W.G. Sprules. 2003. Reaction distance of *B. longimanus* longimanus, encounter rate and index of prey risk for Harp Lake, Ontario. Freshwater Biology, 48:135–146.

Nelson, E. H., C. E. Matthews, and J. A. Rosenheim. 2004. Predators reduce prey populations growth by inducing changes in prey behavior. Ecology 85:1853–1858.

Nelson, E. H. 2007. Predator avoidance behavior in the pea aphid: costs, frequency and population consequences. Oecologia. 151: 22-32.

Palheimo, J.E. 1974. Calculations of instantaneous birth rate. Limnology and Oceanography. 19:692-694.

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

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

Peacor, S.D., and E.E. Werner. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. Ecology, 81:1998-2010.

Peacor, S.D., and E. E. Werner. 2004a. How dependent are species-pair interaction strengths on other species in the food web? Ecology 85(10):2754-2763.

Peacor, S.D., and E. E. Werner. 2004b. Context dependence of non-lethal effects of a predator on prey growth. Israel Journal of Zoology, 50:139-167.

Peacor, S.D. and E.E. Werner. 2006. Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. Ecology, 87: 347-361.

Peacor S.D., Allesina S., Riolo R.L., and M. Pascual. 2006. Phenotypic plasticity opposes species invasions by altering fitness surface. PLoS Biology,4:2112-2120.

Pekarsky, B.L., Cowar, C.A., Penton, M.A. and C. Anderson. 1993. Sublethal Consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology, 74:1836-1846.

Pothoven, S.A., Fahnenstiel, G.L., and H.A. Vanderploeg. 2001. Population dynamics of Bythotrephes cederstroemii in south-east Lake Michigan 1995-1998. Freshwater Biology, 46:1491-1501.

Preisser, E.L., Orrock, J.L., and O.J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology, 88:2744-2751.

Preisser, E.L., Bolnick, D.I., and M.F. Benard. 2005. Scared to death? The effects of intimidation in predator-prey interactions. Ecology, 501-509.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and K. Strohmeier. 1985. Predation, competition and prey communities – a review of field experiments. Annual Review of Ecology and Systematics. 16: 269–311.

Schulz, KL., and P.M. Yurista. 1999. Implication of an invertebrate predator's (Bythotprehes cederstroemi) atypical effects on a pelagic zooplankton community. Hydobiologia 380:179-193.

Schwab, D. J., and K. W. Bedford. 1999. The Great Lakes Forecasting System. In Coastal Ocean Prediction, Coastal and Estuarine Studies 56, C.N.K. Mooers (Ed.), American Geophysical Union, Washington, DC, pp. 157-173.

Tollrain, R. and C.D. Harvell. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, N. J.

Trussell, G. C. 2000. Predator-induced morphological tradeoffs in latitudinally-separated populations of Littorina obtusata. Evolutionary Ecology Research 2:803–822.

Turner, A.M. 2004. Non-lethal effects of predators on prey growth rates depend on prey density and nutrient additions. Oikos 104:561-569.

Vanderploeg H.A., Nalepa T.F., Jude D.J., Mills E.L., Holeck K.T., Liebig J.R., Grigorovich I.A. and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 59:1209–1228.

Werner, E.E. and B.R. Anholt. 1993. Ecological consequences of the tradeoff between growth and mortality rates mediated by foraging activity. American Naturalist 142:242-272.

Werner, E.E., and S.D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities, Ecology 84:1083–1100.

Yurista, P.M. and K.L. Schulz. 1995. Bioenergetics analysis of prey consumption by Bythotrephes cederstroemi in Lake Michigan. Candian Journal of Fisheries and Aquatic Sciences, 52:141-150.