EFFECTS OF LIGHT ON THE FEEDING INTERACTIONS AND SPATIAL DISTRIBUTIONS OF THE OPOSSUM SHRIMP, *MYSIS RELICTA*, AND THE ALEWIFE, *ALOSA PSEUDOHARENGUS*, IN LAKE ONTARIO

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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May 2009

EFFECTS OF LIGHT ON THE FEEDING INTERACTIONS AND SPATIAL DISTRIBUTIONS OF THE OPOSSUM SHRIMP, *MYSIS RELICTA,* AND THE ALEWIFE, *ALOSA PSEUDOHARENGUS,* IN LAKE ONTARIO

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Cornell University 2009

The opossum shrimp, *Mysis relicta,* is a primary predator on zooplankton and both a nutritious prey item for and competitor with planktivorous fish, including the alewife (*Alosa pseudoharengus*), in Lake Ontario. The primary objective of this study is to determine the extent to which spatial overlap and the strength of feeding interactions between mysids and alewife are influenced by the amount of moonlight entering the water column at night. My approach was to study light effects on alewife-mysid feeding dynamics on a variety of different scales – from the absorption of visual pigments in the retina to behavioral experiments in the laboratory to modeling analyses and field distributions in Lake Ontario. A laboratory-based light preference function for adult mysids, in units derived from the spectral sensitivity of the mysid eye, or "mylux" units, was used in combination with an adult mysid temperature preference function to build a model of mysid vertical distribution. This model accurately predicted the vertical distribution of mysids in Lake Ontario on twelve different field sampling occasions between 1995-1996 and 2004-2005. Although laboratory-based temperature and light preferences of juvenile mysids differed from those of adults, the response of adult mysids to temperature and light alone appears to be sufficient to predict mysid vertical distribution across different seasons and moon phases in Lake Ontario.

A series of laboratory and field experiments with alewife and *M. relicta* demonstrated that the light levels associated with the upper edge of the mysid distribution on a full moon night were within the range of those used by alewives to enhance their feeding rates on mysids in the laboratory, but not on a new moon night. Gut content analyses of alewives caught within the mysid layer revealed a greater than 30-fold increase in mysid consumption on the full moon night despite a lower degree of overlap between the two trophic levels, indicating that increased light penetration leads to higher feeding rates of alewives on mysids. These results are significant given that increases in water clarity in Lake Ontario associated with oligotrophication has led to light being more often limiting to mysid distributions than in earlier decades, which, in turn, has led to a better visual foraging environment for alewives. This study is one step towards a better understanding of one of the most central feeding relationships in Lake Ontario and provides insight into how pelagic food web dynamics may be affected by ongoing ecological change.

BIOGRAPHICAL SKETCH

Brent Boscarino was born on November 2, 1979 in the small farming town of Ellington, CT. Nature and the outdoors have always played an important role in Brent's life, whether it was knocking the baseball around at the park down the street, heading up to the Adirondacks for a little R&R on the weekend, or going for a nice long run in some undiscovered neighborhood. He has always preferred a cool breeze and the smell of a fresh cut lawn to the confines of a house. It was always the little things about nature and the outdoors that seemed to spark an interest in Brent, a.k.a. "the man of a million questions". If the first words of his life, "Wha's that?" weren't evidence enough, Brent has always been inquisitive, driven to better understand the world around him.

This passion for the outdoors and thirst for knowledge led him to pursue a career in science education, where he felt that he could balance both his natural interest in the environment with more formal, scientific inquiry. He began teaching biology and environmental science at the Bullis School in Potomac, MD, immediately following graduation from Middlebury College in 2001. These two years at Bullis confirmed what Brent had been thinking for some time at Middlebury– science education was definitely the career path for him. This led him to pursue a Natural Resources Ph.D. at Cornell University, where he was able to combine his love for nature and the outdoors with his passion for teaching and research. While at Cornell, Brent has pursued not only aquatic science research, but has been involved with a variety of different educational opportunities, including teaching a course in Marine Ecology to both graduate and undergraduate students at the State University of New York- Environmental Science and Forestry. He is particularly proud of his volunteer services in science education including his efforts as part of the Oneida Lake Education Initiative and Café Scientifique Jr. held at Syracuse's Museum of Science

and Technology. He believes that encouraging "informal" learning opportunities and the engagement of students, of all ages, to interact with and ask questions about their natural environment are just as important educational tools as formal classroom or research analyses. He is excited to embark on a career that will allow him the flexibility to advance science in both a formal and informal research and teaching capacity. Brent currently resides in Syracuse, NY, where he lives with his wife, Jessica, and newborn son, Wynn.

This dissertation is dedicated to my son, Wynn Joseph Boscarino, born this year January 21, 2009. May your life be full of happiness, love and fulfillment. Here is to starting a new chapter in both of our lives.

ACKNOWLEDGMENTS

This research was funded by New York Sea Grant project R/CE-23 and RFB-19 with additional funding provided by the Cornell University Agricultural Experiment Station federal formula funds, Project NYC147419, received from Cooperative State Research, Education and Extension Service, U.S. Department of Agriculture. The views expressed are those of the author and do not necessarily reflect the views of NOAA or USDA. The U. S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear herein. I also would like to acknowledge both the Canadian Journal of Fisheries and Aquatic Sciences and Aquatic Biology for allowing the reproduction of both Chapters 2 and 3 as part of this dissertation.

I would like to thank Bill Thelen, Brian Young, John Janssen and Howard Riessen for their assistance with the laboratory set-up for the experiments described herein. I extend a special thanks to Gideon Gal, Ora Johannsson, Bob O'Gorman, June Eillenberger, and Kelly Bowen for their important insights into mysid and fish spatial patterns and behaviors, as well as their help with the field and laboratory work. A special thanks should also be extended to the crew aboard the R/V Kaho for all of their help and assistance with the field work as part of this project. This research also would not have been completed without the unbelievable help and encouragement from my student interns, Tyson Buerkle, Christine Chu, Shylene Mata, Emily Freund, Monica Minson and Jill Tirabassi.

I would also like to extend a special thanks to my committee members, Drs. Barbara Knuth, Ellis Loew, Lars Rudstam and Ed Mills, for all of their comments on this dissertation and support and advice throughout the writing process. Special thanks goes to both Lars and Ed for their mentorship, patience and friendship

throughout my tenure here at Cornell. They have allowed me the freedom and flexibility to explore my interests and passions outside of a formal classroom and research atmosphere, while keeping me focused on my development as a scientific scholar. For this I will be forever grateful and the lessons I have learned here under their tutelage I will take with me as I move forward as both an educator and researcher.

I would also like to thank my family- both my parents, Cindy and Tom and my in-laws, Joe and Elaine Widay – who have been so incredibly supportive throughout the time I have spent at Cornell. Without their generosity and spiritual guidance, I would never have made it to this point in my career. Last, but not least, I would like to thank my wife, Jessica, and my new son, Wynn, whose mere presence and unconditional love remind me on a daily basis of the things that are truly important in life. They are a constant source of motivation for me to work hard and to live in the moment. It goes without saying that I would not be at this exciting crossroads in my life without the love and support of my family.

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Lake Ontario: A system in flux

Over the past half-century, Lake Ontario has undergone a series of dramatic ecological changes, spurred on by a host of anthropogenic stresses ranging from overfishing and the proliferation of exotic species to cultural eutrophication and toxic contamination (Mills et al. 2003). This steady stream of human-induced stressors has caused widespread disruption to Lake Ontario's ecosystem function and structure, from algal population dynamics to zooplankton and macroinvertebrate community composition to fish production, posing considerable challenges to managers and policy-makers. Historic milestones such as the Great Lakes Water Quality Agreement (GLWQA) in 1972 and the creation of the Joint Strategic Plan for Management of Great Lakes Fisheries in 1981 have been instrumental in addressing many of the primary human-induced stresses on the Lake Ontario ecosystem, yet significant challenges still remain today. While nutrient concentrations, phosphorus loading and growth of nuisance algae have been significantly reduced since the signing of the GLWQA, the impact of reduced nutrient levels has led to increases in water clarity and a deepening of the euphotic zone, contributing to increased periphyton and submerged aquatic vegetation concentrations in Lake Ontario's nearshore communities (Millard et al 2003).

The establishment of *Dreissena* spp. in the late 1980's further enhanced shifts in Lake Ontario light conditions. Because of *Dreissena's* ability to filter large quantities of algae and other suspended particulates in the water column, the invasion

has caused significant declines in algal abundance and increased water clarity in many of Lake Ontario's nearhsore habitats, beyond what is to be expected from lower nutrient loading rates (Mills et al. 2003). This post-*Dreissena* increase in water clarity has been observed in offshore habitats of Lake Ontario as well. For example, Secchi disk readings at a mid-lake sampling station (Station 41, bottom depth =123 m) increased by over 5 m over a ten-year period from 1993 to 2003 (Holeck et al. 2008). Extinction coefficients have declined, on average, by over 50% of those observed between whole lake cruises in 1990 and 1996 (Millard et al 2003).

Clear water has important implications for Lake Ontario's nearshore and offshore inhabitants and Lake Ontario's food web dynamics, in general. Light can impact feeding relationships between trophic levels through its influence on the behavior, physiology and distribution of organisms, on both a seasonal and daily basis. Most fishes, for example, are active either by day or by night, but typically not both (Loew and McFarland 1990). Visual foragers that are adapted to high spectral sensitivity (degree of brightness) and high visual acuity (detection of objects via. sharpness) are usually most active during the day. In contrast, fishes adapted for nocturnal activity have retinas rich in rods, often have reflective tapeta behind the retina and remain hidden during the day (Muntz 1990; Loew 1995). In addition to these physiological adaptations, many aquatic organisms have evolved complex behavioral responses to light to maximize feeding while minimizing predation risk (Gilliam and Fraser 1987). For example, many organisms perform diel migrations from deeper waters to feed in shallower water at night when detection by visual predators is lowered (Beeton and Bowers 1982; Clark and Levy 1988; Gal et al. 1999).

Given the importance of light in influencing the behaviors and distributions of aquatic organisms, increased light penetration should impact the dynamics of predator-prey interactions, both spatially and temporally, in Lake Ontario. One organism that

may be particularly affected by these recent changes in Lake Ontario is the opossum shrimp, *Mysis relicta* (hereafter, "mysid(s)" unless noted otherwise). Mysids have long been recognized as an important energy link between the benthic and pelagic communities, known for their diel vertical migrations from their daytime benthic habitat to the more food-rich metalimnion and epilimnion to feed at night (see review by Johansson et al. 2003). A review of the different abiotic factors affecting mysid migration patterns suggests that the amount of moonlight entering the water column is a primary factor in regulating vertical distribution and migration patterns of mysids in Lakes Michigan and Ontario, especially in the spring when the water column is isothermal or when the thermocline is very shallow (Beeton and Bowers 1982; Gal et al. 2004). In fact, mysids are so sensitive to light that even differences in moon phase, cloud cover and dimmed ship lights have been shown to affect their vertical distribution in the water column (Janssen and Brandt 1980; Johansson et al. 2003). Consequently, changes in light penetration and water clarity in Lake Ontario have likely altered the migration behaviors and distributions of *Mysis relicta*.

Changing light conditions in Lake Ontario have the potential to not only modify mysid behavior and distribution, but the predators that rely on them as well. Mysids occupy a unique position in Lake Ontario's pelagic food web as both prey for and competitors with the alewife, *Alosa pseudoharengus*, for access to zooplankton prey (see review by Johannsson et al. 2003). This three-way relationship between zooplankton, mysids and alewife in Lake Ontario has commonly been referred to as a "trophic triangle", owing to the interdependence of the three links in this chain (see Johannsson et al. 2003). Maintaining the integrity of this trophic triangle is central to supporting the lake's salmonid fish community, as alewife are the main prey item for chinook salmon, which account for over two-thirds of the lake-wide predator demand for alewives in Lake Ontario (Mills et al. 2003). Hence, alterations to mysid and

alewife distributions and behaviors imposed by increased light penetration may have potentially significant impacts on the sustainability of the Lake Ontario salmonid sport fishery through its effect on these trophic triangle relationships in the lake.

The vast majority of alewife-mysid feeding interactions are thought to occur during the night when mysids migrate into the pelagic realm (Janssen and Brandt 1980; Beeton 1960). The depth at which these interactions occur, however, may vary by moon phase (Beeton 1960; Janssen and Brandt 1980; Beeton and Bowers 1982). On full moon nights, Janssen and Brandt (1980) reported that interactions were occurring much deeper (>35 m depths) in the water column than on a new moon night (<10 m), suggesting the importance of light in dictating where these foraging interactions were taking place. What is not known, however, is how light is affecting the efficiency with which alewife are feeding on mysids at night. Janssen et al. (1995) demonstrated that alewife utilize their lateral line system to feed on *Artemia* (a species of zooplankton which uses metachronal swimming similar to *Mysis relicta)* in complete darkness. Feeding experiments performed by Batty et al. (1990) and Blaxter (1964) on the herring, *Clupea harengus,* suggest that the light level required for visual feeding in clupeids is very close to the threshold determined by Gal et al. (2004) to limit mysid movements and the approximate light levels associated with the peak of the mysid layer on full moon nights in surveys performed by Janssen and Brandt (1980). Thus, increased light penetration is likely to influence the strength of the predator-prey linkage between alewife and mysids in Lake Ontario.

Potential implications of increased light penetration to Lake Ontario's pelagic food web dynamics

The extent to which alewife and mysid behaviors and distributions are influenced by light is the main focus of this dissertation. In the following sections, I provide three hypotheses for how shifting light conditions have affected and may

continue to affect alewife-mysid feeding interactions, behaviors and spatial relationships in Lake Ontario. Implications of increased light penetration for the growth, health and population dynamics of mysids, alewife and, through extension, the salmonid fish community are also discussed. These hypotheses form the main bases for the investigations into how light impacts alewife-mysid feeding dynamics in the chapters to follow.

Hypothesis #1: Alewives do not use vision to feed on mysids at night and do not change their depth distribution in response to increasing light penetration.

If alewives do not use light as a cue to locate and capture mysids, I would expect an increase in light penetration to cause increased spatial separation between mysids and alewife at night and for feeding rates on mysids to decrease. These expectations are predicated on the assumption that mysid migratory ascent would be inhibited at increasingly deeper depths with increased light penetration, as their upper light threshold (Gal et al. 2004) would be penetrating farther into the water column. Alewife typically inhabit the upper waters in the offshore of Lake Ontario during the summer and fall stratified seasons (Olson et al. 1988; Urban and Brandt 1993) and have historically been found several meters shallower in the water column than the depth of the peak mysid density at these times of year (e.g., Gal et al. 2004; 2006). In early spring, alewife migrate from offshore locations along the bottom of the lake to spawn in nearshore habitats (O'Gorman et al. 2000), but by late spring they begin to move offshore and concentrate within the shallowest 20 m of the water column, several meters shallower than the main mysid layer, before the onset of spring turnover (Gal et al. 2004). Thus, alewives are found higher in the water column than mysids for most of the year in Lake Ontario. Alewife predation rates on mysids have historically been highest during the fall and spring months in Lake Ontario, when the lake is isothermal and temperature is not limiting the diurnal ascent of mysids (see

discussion below). During these periods, mysids can contribute up to 40% of an alewife's overall diet (Mills et al. 1992). Recent investigations into the fall diet of alewife have confirmed high predation rates of alewife on mysids at this time of year (Walsh et al. 2008).

If mysids are not venturing as far into upper waters during their migrations and alewives are not following the increased amount of light into deeper depths, the spatial separation between mysids and alewife may be too large for alewives to detect the presence of this food resource, particularly if alewives rely primarily on lateral line sensitivity to locate and capture prey. A decrease in mysid consumption by alewife due to increased spatial separation and lower encounter rates has the potential to impact alewife survival and reproduction. Mysids are rich in highly unsaturated fatty acids (HUFA), which are important in maintaining cell membrane function, executing a proper stress response and contributing to healthy cardiovascular and immune function (Arts 1999). Lake Ontario alewives' lipid levels drop significantly just prior to winter and without the "fatty boost" provided by a mysid-heavy diet in the fall, over-wintering adults will likely not make it through to spring to spawn (Eshenroder and Burnham-Curtis 1999).

In addition to its nutritional content, mysids also are a high-calorie food relative to other zooplankton prey consumed by alewife. Janssen and Brandt (1980) estimate that the energetic benefit per prey item may be 1000 times more for *Mysis relicta* than a typical *Daphnia.* These added calories are significant given that alewife are inefficient at converting available food to growth relative to other Great Lakes prey fish such as rainbow smelt, *Osmerus mordax* and bloater, *Coregonus hoyi* (Eshenroder and Burnham-Curtis 1999). Thus, the ability to exploit mysids is deemed critical to meeting the annual bioenergetic demands of alewives (Johannsson et al. 2003) and to their ability to compete with other planktivores. Larger spatial

segregation of mysids and alewife caused by increased light penetration threatens to disrupt this delicate balance between predator and prey in Lake Ontario's pelagic waters.

Hypothesis # 2: Alewives use vision to feed on mysids at night and adjust their vertical position in the water column to maximize their consumption on mysids

In this scenario, I would expect few changes to alewife-mysid feeding interactions in the lake during the spring and late fall isothermal periods, only that these interactions would occur slightly deeper in the water column. However, under stratified summer and fall conditions, a lower average depth of alewives may result in significant changes in the average temperature experienced by alewife.

Crowder and Magnuson (1982) noted that alewives shifted their distribution to colder, deeper waters in the late 1970's in Lake Michigan (shift from an average temperature experience of 11-16ºC to 4-8ºC from 1977 to 1979), which placed them outside of those temperatures most preferred in the laboratory (Otto et al. 1976), those that maximize growth rate in the laboratory (Kellogg 1982) and those shown to be most preferred by alewife in the field in other deepwater systems (e.g., Gibson 1981). This shift was thought to have occurred due to increased predation from salmonids or possible competition with juvenile bloater, which became very abundant over this period, for access to *Mysis relicta* (Crowder and Magnuson 1982). These shifts in average temperature experience were correlated with decreases in alewife body index values throughout the mid-1980's in Lake Michigan (Rand et al. 1994; Flath and Diana 1985). Small changes in average temperature experience have been shown to have similar bioenergetic consequences in other species of fish (see Kitchell et al. 1977).

Decreases in alewife condition in Lake Michigan have also translated into declines in chinook salmon growth and survival as well as noticeable shifts in feeding

to less preferred prey items like smaller alewife (Stewart and Ibarra 1991). Outbreaks of diseases across the chinook salmon population were also reported shortly after alewife shifts to lower temperatures in Lake Michigan (Stewart and Ibarra 1991), indicating that the salmon population was experiencing high levels of stress. These salmonid predators did not appear to switch to alternative prey species during this time period, showing a certain degree of "prey fidelity" to alewife, despite lower numbers and decreased condition of this prey item (Jude et al. 1987; Rand and Stewart 1998a). An alewife shift to lower temperatures also meant that salmonids were having to forage at lower temperatures to exploit this food resource, which based on bioenergetic modeling and an assumption of a thermal preference of chinook salmon of 11ºC, would cause them to actually lose weight (Stewart and Ibarra 1991). While these shifts in alewife depth distribution occurred just prior to the *Dreissena* invasion, this Lake Michigan example demonstrates how alterations in habitat and average temperature experience can impact the body condition and growth rates of not only alewives, but the predators that rely on them.

Alewife depth distributions also shifted in the early 1990's, following dreissenid-mediated changes to water clarity, which is hypothesized by O'Gorman et al. (2000) to be the main cause for the changes in depth distribution. These depth shifts resulted in fish occupying colder water than they did prior to the arrival of *Dreissena*. For example, O'Gorman et al. (2000) reported that the mean temperature of alewife caught in June trawl surveys changed from 8.3°C to 6.0°C when comparing averages between time periods of 1978-1990 and 1992-1998, respectively. Similarly, alewives were caught at increasingly deeper depths in April bottom trawling for alewives relative to pre-dreissenid years (O'Gorman et al. 2000).

It is important to note, however, that alewife remain primarily epilimnetic in the offshore of Lake Ontario in the summer and a vertical shift to deeper waters due to

increased water clarity has yet to be established. The increased consumption of *Mysis* by alewives in the summer relative to pre-dreissenid years (Mills et al. 1992; Stewart et al., In press) suggests that such a vertical shift during thermally stratified conditions in the lake may be occurring, since mysids are rarely found above temperatures of 10ºC (see discussion below). Thus, alewives would need to dive to increasingly deeper, colder waters to account for this increase in mysid consumption. A thermal shift during the summer would have important implications for alewife growth and production. The spring depth shifts have already been correlated with large fluctuations in alewife growth rate as well as steady decreases in their abundance and body condition (O'Gorman et al. 2008). For example, mean annual alewife biomass estimates by USGS on routine sampling in 2004 was over 40% less than the long term mean (i.e., 1978-2004) (O'Gorman et al. 2004). The numerical abundance index for 2004 was down over 35% from the long term average (O'Gorman et al. 2004). Given the lower primary production in the lake and increased water clarity, the carrying capacity for alewife has been reduced from pre-*Dreissena* years, and adult alewife abundance has been at, or below 2004 levels through to 2006 (O'Gorman et al. 2008). In addition to lower abundance and overall biomass estimates, alewife condition (as measured by the wet weight of a 165 mm alewife) has also been on a downward trend for both fall and spring sampling since 1993, soon after the *Dreissena* colonization and subsequent increases in light penetration (O'Gorman et al. 2004). It has only been in the past six years that body condition indices have shown consistent increases for both the fall and spring sampling surveys (O'Gorman et al. 2008) (see discussion below). O'Gorman et al. (2008) also conclude that the alewife depth shift was the single most influential event in food web disruption as it also coincided with increased inter-annual variation of growth of alewife in the first two years of life and was highly correlated with growth of alewife in years of life two and older. Cumulatively, these

results suggest that changing light conditions in Lake Ontario have, at least in part, already impacted the growth, condition and abundances of alewife in Lake Ontario. Further shifts in vertical distribution and average temperature experience during the thermally stratified summer months may exacerbate these impacts on the alewife population in Lake Ontario.

Reductions in alewife growth, body condition, and abundance have important implications for the salmonid fish community in Lake Ontario. Model results from Rand and Stewart (1998b) suggest that over 100% of the annual production of the alewife population was consumed by the salmon population in 1990, which likely resulted from increased stocking of salmonids in the lake in the 1980's. Similarly, Rand and Stewart (1998a) hypothesized that lake-wide consumption rates of adult alewives by salmonids had tripled in number from 1983 to 1993, while stocking increased salmonid biomass by approximately a factor of two (Jones et al. 1993; Rand and Stewart 1998b). Given a rapidly-depleting prey stock, salmon were forced to feed on smaller alewife over this time period (similar to what was observed in Lake Michigan) and, subsequently, gross conversion efficiencies and production: biomass ratios had decreased considerably in salmonids since the early 1980's (Rand and Stewart 1998b). Rand et al. (1994) suggested that chinook salmon would have had to increase the number of prey fishes consumed per day by over 300% in the early 1990's to maintain the average annual growth rates observed during 1978-1990. Thus, there are a number of factors in addition to increased water clarity that may have contributed to the lower abundances and body condition indices of alewife in the past decade in Lake Ontario, but these results, and also those from Lake Michigan, suggest that even seemingly minor shifts in depth distributions and temperature experiences can disrupt the balance between predators and prey in pelagic waters (e.g., Kitchell et al. 1977), particularly when combined with increased stocking pressure.

Alternatively, a shift to deeper waters to exploit a "deeper" *Mysis* distribution may positively impact the lake's alewife population. The extent of vertical movement in mysids is determined by both light and temperature (e.g., Gal et al. 2004). During periods of strong thermal stratification or periods of the month when the moon is new, temperature is more likely to restrict mysid distributions, and mysids will therefore reside in darker waters than during full moon or isothermal conditions, when mysid distributions are limited by light (e.g., Gal et al. 2004). In an era of increased water clarity, the mysid distribution should more often be limited by light rather than temperature, leading to higher light levels at the mysid layer for more days of the year. This may increase foraging opportunities for alewife on mysids. Evidence is beginning to accumulate that this may be the case in Lake Ontario, as alewives are becoming increasingly reliant on mysids throughout the year (Stewart et al. In press). A switch towards a high calorie mysid diet following increasing light levels may be advantageous to an alewife population already decimated by the high levels of salmonid stocking and lower levels of primary production, as discussed above. The fact that adult alewife condition indices have been on the rise since 2002, suggests the switch to a more mysid-heavy diet is leading to better growth and condition of Lake Ontario alewife (O'Gorman et al. 2008).

A switch to a more mysid-heavy diet by alewife is potentially troublesome for a mysid population which has seen a substantial drop in abundance over the past five years relative to abundances reported in the early to mid- 1990's. Johannsson et al. (2003) reported mysid abundances throughout the mid- to late 1990's as among the highest reported since 1970. However, more recent sampling efforts in 2005 (Rudstam et al. 2008, this study) found abundances at offshore sites in southeastern Lake Ontario to be several times lower than those reported across depth ranges comparable to those reported in Johansson et al. (2003). Similar reports of lower mysid catches have been

noted by several researchers beginning in 2002 (see Walsh et al. 2008; Gideon Gal Kinneret Limnological Laboratory, unpubl.). While there are a number of factors that could be contributing to these lower estimates of mysid abundance, including differences in sampling techniques, sites and interannual variability in recruitment (see discussion in Rudstam et al. 2008), the trend is potentially troubling for mysids, particularly given the increased predation pressure exerted on them by alewife in recent years (Stewart et al. In press). Mysids are a slow-growing species with low fecundity and therefore should be highly sensitive to increased predation pressure (Johannsson et al. 2003). In addition to the increased water clarity which may be contributing to higher consumption rates on mysids, the recent near extinction of the burrowing amphipod, *Diporeia,* may also be increasing predation rates on mysids by benthic fish such as slimy sculpin, *Cottus cognatus,* and the recent invader, the round goby (*Apollonia melanostoma),* which may lead to further declines of mysids in Lake Ontario (see discussion in Walsh et al. 2008; O'Gorman et al. 2008).

Equally troubling for mysids is the effect that a deeper distribution would have on their consumption of zooplankton. If we assume that zooplankton prey do not respond to these changing light conditions in the same manner as mysids (i.e., shifting to deeper depths), *Mysis's* access to the more abundant and nutritive epi- and metalimnetic zooplankton populations would be limited. Gal et al. (2006) estimates that mysid planktivory rates could be up to two orders of magnitude higher than those observed across different seasons in Lake Ontario if they moved to temperatures that maximized their predation rates. Increased light levels would act to separate mysids even more from those temperatures that maximize their consumption on zooplankton prey (Rudstam et al. 1999).

Given that mysid consumption of zooplankton is on par with the zooplankton consumption of Lake Ontario's entire planktivorous fish population (Johannsson et al.

2003), a higher degree of spatial separation between mysids and their prey could increase intraspecific competition for a more limited food resource in deeper waters or force mysids to make more frequent and longer-distance trips to feed in upper waters. Johannsson et al. (1994) and DeGraeve and Reynolds (1975) have both reported that the amount of food available to mysids in the hypolimnetic region may not be sufficient to meet the bioenergetic demands of mysids and that nighttime forays into the warmer regions of the metalimnion and lower epilimnion are necessary to account for observed growth rates. Increased spatial separation therefore has the potential to increase the vulnerability of mysids to predation, as these foraging bouts would have to occur over longer distances, which would increase the amount of time spent outside of the "refuge" of the peak of the main mysid layer (assuming that light levels at the peak of the mysid layer correspond to those that limit visual feeding in alewife- see Chapter 5). This problem of increased spatial separation on mysid foraging would be exacerbated if mysids rely primarily on mechano-reception (see Ramcharan et al. 1985) to sense their prey, as the degree of overlap between the zooplankton and mysid layers would be greatly reduced. If mysids rely primarily on light to feed, a lowered depth distribution in response to light would not necessarily affect their search ability.

A shift to deeper waters may also impact the quality of food ingested by mysids. *Mysis* obtains much of its HUFA from the food it consumes. For example, copepods are rich in two types of critical HUFA fatty acids called DHA (docohexaenoic acid) and EPA (eicosapentaenoic acid) but are more difficult to capture than daphnids which have a much lower concentration of DHA (Ballantyne et al. 2003). Zooplankton biomass in upper hypolimnetic/lower metalimnetic waters in the offshore of Lake Ontario are dominated by calanoid copepods (Johannsson et al. 2008), whereas shallower waters have a substantially higher percentage of *Daphnia.* Thus, a shifting mysid distribution given increased light penetration is likely to change

the types of zooplankton consumed and the fatty acid profiles of mysids (see discussion in Nordin et al. 2007), although the exact ramifications of such a change to both the mysid population and to its predators is still unknown.

Given that an alewife shift towards mysivory and decline in mysid abundance has been noted only recently (alewife predation on mysids had steadily been declining from the mid-1980's to 2002; Johannsson et al. 2003), it is still too early to draw definitive conclusions as to what role increasing water clarity is having on mysid and alewife population and feeding dynamics. This dissertation is a first step towards identifying the extent to which alewife are able to use light to enhance their feeding rates on mysids and the implications for pelagic food web dynamics in Lake Ontario.

Hypothesis #3: Mysids do not respond to increased light levels by lowering their distribution in the water column

The two hypotheses outlined above are predicated on the assumption that mysids will respond to increased light by lowering their depth distribution in the water column, presumably to decrease their predation risk in shallow, high-light environments. However, this is not necessarily a foregone conclusion. For example, Boscarino et al. (2007) demonstrated that high prey concentrations may enhance the upward vertical movements of *Mysis relicta* despite adverse light and temperature conditions in shallower waters. Given the importance of zooplankton in the diets of mysids in Lake Ontario (i.e., zooplankton can account for up to 100% of a mysid's diet in mid-summer in Lake Ontario, Johannsson et al. 2003) and that zooplankton densities are several times higher in the more productive meta- and epilimnetic regions of the lake (Gal et al. 2006), the higher prey concentrations in upper waters clearly provide an important impetus for mysid vertical movement. In addition, Boscarino et al. (2007) demonstrated that adult mysids may be maximizing growth at 6-8°C-temperatures typically associated with Lake Ontario's metalimnion in Lake Ontario. It

may be that maintaining a position in the water column within this temperature range confers a higher fitness advantage to mysids than minimizing the predation risk associated with depths at higher light levels at these depths. Therefore, if the nutritional and thermal benefits to staying in the upper metalimnion still outweigh the potentially higher predation risk associated with upper waters despite increased light levels, mysids may not shift to lower depths under conditions of increased light penetration. Under this scenario, I would expect higher predation by alewife on mysids if vision was the primary mechanism for mysid consumption, but minimal differences if alewife lateral line sensitivity was playing the primary role.

Epilogue

Maintaining and managing a healthy Lake Ontario fishery requires a proper balance between predatory demand and prey supply. While much attention has been focused on the predatory demand portion of the equation (i.e., the dynamics of the salmonid community) (see Rand and Stewart 1998a and b), less attention has been paid to the prey side- in particular the alewife-mysid-zooplankton trophic triangle which is central towards supporting the multimillion dollar sport fishery in Lake Ontario. A better understanding of the mechanisms underlying the spatial and behavioral dynamics of alewife-mysid interactions in a changing Lake Ontario ecosystem will be important for maintaining a sustainable sport fishery and therefore important to the surrounding communities that depend on tourism associated with this sport fishery. Recently, the alewife populations in Lake Huron collapsed unexpectedly (see Warner et al. 2005), and the lower abundances and body condition indices reported for alewives in the past decade are signs that Lake Ontario's alewife may be heading in a similar direction. Rand et al.'s (1995) analysis of alewife predation pressure on Lake Ontario zooplankton highlighted our limited understanding of alewife production and feeding rates, as they predicted alewife to consume

approximately twice the amount of zooplankton production available in the lake – which is physically impossible with a prey group like zooplankton without a biomass capital to deplete. It is therefore essential that we begin to understand the mechanisms influencing both the spatial and behavioral dynamics of alewife and their prey across different temporal scales in Lake Ontario, so that managers can make informed decisions on how changes on an abiotic level may impact the growth and production of alewife.

This dissertation takes a multi-dimensional approach to understanding pelagic food web dynamics in a time of ongoing ecological change in Lake Ontario – one that considers not only predator and prey population structures, distributions and behaviors but also considers the variety of environmental factors and underlying biological and physiological mechanisms shaping trophic interactions in Lake Ontario's pelagic food web. The primary focus of this study is how one such mechanism, light, is impacting one of the most central feeding relationships in Lake Ontario's pelagia, that between alewife and mysid shrimp. It is difficult to predict the extent to which changing light conditions in Lake Ontario have and will continue to influence mysid vertical distribution without a firm understanding of the physiological and behavioral responses of mysids to different light levels and wavelengths of light. While a wealth of literature exists which have correlated mysid position in the water column to a particular light level estimated in the field (e.g., Beeton and Bowers 1982; Gal et al. 1999, 2004), there is still no consensus on which light levels are most preferred or avoided by mysids, and even less information is available on the different mechanisms controlling depth selection behavior or how these behaviors may vary by developmental stage or be uniquely shaped by other environmental factors such as temperature and prey and predator distributions. Chapter 2 of this dissertation investigates the behavioral and physiological responses of mysids to different light

levels in the laboratory and to determine the extent to which field distributions can be predicted based on laboratory-derived light preferences during both isothermal and thermally stratified conditions in Lake Ontario. In Chapter 3, I investigate the extent to which these mysid light preferences vary by developmental stage and also explore the degree to which temperature preference may vary between different size classes of mysids. In Chapter 4, I use results from the mysid light experiments to determine the extent to which mysid distribution is influenced by moon phase and whether other environmental factors such as temperature and predator and prey distribution must be invoked to predict distributions of mysids across different seasons in Lake Ontario. Finally, in Chapter 5, I examine the extent to which light enhances the feeding rates of alewife on mysids at night and governs the degree of spatial overlap between the two trophic levels. Throughout the field applications discussed in this dissertation, I use observations of mysid and alewife distributions and feeding rates of alewives under different light conditions (i.e., full moon versus new moon comparisons) and temperature conditions to draw conclusions about how an increase in light penetration in Lake Ontario, commensurate with oligotrophication and increased dreissenid filtering activity, may have impacted the feeding relationships of alewife and mysids. I argue that the results of these investigations may also be used to forecast how future changes in light penetration will continue to impact alewife-mysid feeding dynamics. This dissertation is also significant in that it provides a template for how to study light effects over a range of scales from the absorption of visual pigments in the retina to behavioral experiments in the laboratory to implications at a larger spatial and temporal scale relevant to populations in deepwater ecosystems.

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CHAPTER 2:

PREDICTING THE VERTICAL DISTRIBUTION OF THE OPOSSUM SHRIMP, *MYSIS RELICTA*, IN LAKE ONTARIO: A TEST OF LABORATORY-BASED LIGHT PREFERENCES*

* = A slightly modified version of this chapter appears as: Boscarino, B.T., Rudstam, L.G., Loew, E.R., and Mills, E.L. 2009. Predicting the vertical distribution of the opossum shrimp, *Mysis relicta,* in Lake Ontario: A test of laboratory-based light preferences. Can. J. Fish. Aquat. Sci. 66: 101-113.

ABSTRACT

Light and temperature strongly influence the vertical distribution of the mysid shrimp, *Mysis relicta.* In this study, the vertical movements and depth selection behavior of mysids exposed to different light intensities and light-temperature gradients in the laboratory were monitored and a mysid light preference function in units relevant to mysid vision- "mylux"- was derived. Mysids preferred light levels between 10^{-8} and 10^{-7} mylux (~10^{-6} to 10^{-5} lux) and rarely moved into waters of 10^{-3} mylux (~0.1 lux) and greater. A model that assumed equal weight and independence of mysid light and temperature preference functions successfully predicted the proportion of mysids found in two different temperature-light combinations in the laboratory. This model also predicted the depth of maximum mysid density to within 2 m on two spring nights and within 5 m on two summer nights of varying moon phase and thermal conditions in Lake Ontario. This study provides novel insights into how temperature and light interact to influence the vertical distribution of mysids. The model may be used to predict mysid vertical distribution in any deepwater system inhabited by mysids in which the primary mysid predators are visual feeders.

INTRODUCTION

Zooplankton diel vertical migration (DVM) is a widely occurring and well-documented phenomenon in both marine and freshwater ecosystems (Hamner 1988; Haney 1988). Although a vast literature exists on the different proximate cues (i.e., light, temperature, and chemical cues) influencing zooplankton DVM, there is still no general consensus as to how these different exogenous factors interact to impact a migrating population's vertical distribution. Light is generally considered to be the most important proximate factor influencing zooplankton DVM (Lampert 1991; see reviews by Forward 1988 and Ringelberg 1999); however, whether migrating organisms simply maintain a "preferred" light condition throughout their migration and night/day distribution (the preferendum, or isolume, hypothesis) is still an open question and may be species-dependent.

The opossum shrimp, *Mysis relicta,* (or *M. diluviana* after Audzijonyte and Väinölä 2005- hereafter referred to as "mysids" unless otherwise noted) exhibits diel vertical migration in many deep, freshwater lakes of North America. Mysids are a highly nutritious food item for the planktivorous fish community but are also significant predators of zooplankton in these systems, thereby acting as competitors with the planktivorous fish that eat them (Gal et al. 2006). The availability of mysids as prey to these fish, as well as the degree to which they contribute to pelagic zooplanktivory, is strongly influenced by light (see review by Beeton and Bowers 1982; Gal et al. 2004). For example, mysids are typically found deeper in the water column on full moon versus new moon nights (Janssen and Brandt 1980; Beeton and Bowers 1982). Similar observations of light deterrence have been recorded in other lakes containing mysids (Moen and Langeland 1989). Even dim boat lights and passing clouds can modify mysid vertical distribution in the water column at night (Gal et al. 1999; Johannsson et al. 2003). Since subtle changes in light can impact

where mysids are found in the water column and therefore their overall contribution to the pelagic food web (Gal et al. 2004), the ability to model their response to light and predict their distributions based on ambient light conditions is important for both mysid ecology and food web dynamics in lakes where they occur.

While it is clear that mysids are sensitive to changing light levels, the precise intensities necessary to limit, or enhance, vertical movements are less understood. Teraguchi et al. (1975) reported that the upper edge of the *M. relicta* migratory layer in Green Lake, Wisconsin was associated with a narrow light interval of 0.02 - 0.05 lux, while *Mysis mixta* in the Baltic Sea was shown to avoid light levels of 10^{-4} lux (Rudstam et al. 1989). However, lux is a unit of measure associated with luminosity and is specific for what the human eye perceives; therefore, the "lux" unit does not accurately convey the level of brightness perceived by a mysid eye. Gal et al. (1999) measured the absorbing pigments of mysids from Cayuga Lake, New York using a microspectrophotometer and derived a mysid-specific brightness unit, the "mylux", which accounts for the relative sensitivity of the mysid eye to different wavelengths of light. Using spectral sensitivity curves to derive species-specific brightness units represents the most appropriate way to report the amount of light perceived by an individual organism (Jerlov 1963). In this study, all light levels are reported in the biologically-relevant units of mylux.

The degree to which mysids "prefer" a specific light intensity or range of intensities, as well as how this preference may vary between discrete populations, is also unknown. Gal et al. (2004) generated a mysid light preference function, using the mylux unit, based on acoustic data collected in the eastern portion of Lake Ontario in May, 1996 (Gal et al. 2004). The preference curve indicated that mysids preferred ~10^{-7} mylux, which in Lake Ontario waters on a cloudless, moonlit night is equivalent to ~10^{-5} lux. However, the data used to generate the light preference curve were

collected on the same lake and only one night later than the data used to test the model. Other factors such as chemical cues from predators and prey may affect mysid distribution (Boscarino et al. 2007) and would not have been accounted for in the derivation of the light preference curve. To my knowledge, there have been no studies that have explicitly investigated the responses of mysids to different light levels in the laboratory, to either verify or refute these field-derived light preferences.

Other factors besides light may also serve as controlling mechanisms of mysid vertical distribution. For example, temperature may become increasingly important in determining final depth preferences when the lake is thermally stratified during the summer and fall seasons (Gal et al. 2004; Boscarino et al. 2007). Recently, Boscarino et al. (2007) developed a temperature preference curve, with a peak between 6 - 8°C, based on observations of mysid movements in thermally stratified experimental columns. These authors hypothesized that mysids developed a preference for such a narrow range of relatively low temperatures in response to high predation pressure in shallow waters, or to maximize growth in the strata just below the thermocline (Boscarino et al. 2007). However, mysid temperature preference may be modified by light level; similarly, mysid light preferences may vary with temperature. The interaction between temperature and light has yet to be tested under controlled conditions and therefore the relative importance of light and temperature in determining mysid vertical distribution is not known. In previous models, light and temperature preference functions were assumed to have equal weight and be independent (Gal et al. 2004; Boscarino et al. 2007).

In this study, I test the hypothesis that mysids prefer certain light intensities and will avoid others. The approach was to monitor the behavioral responses of mysids to different manipulations of light in 2 m tall observation columns in the laboratory. I use the results of these light preference experiments to construct a

function describing the relative probabilities of observing a mysid at different light levels. This light function is then combined with a mysid temperature preference function to yield a predictive model of mysid vertical distribution (e.g., Boscarino et al. 2007). I test the ability of this model to predict mysid vertical distribution by comparing model predictions with observed mysid distributions under different light-temperature combinations in the experimental columns. This procedure tests the assumption of Gal et al. (2004) and Boscarino et al. (2007) that temperature and light preference functions are equally important and independent predictors of mysid vertical distribution. The model is also used to predict published field distributions of mysids in Lake Ontario during the spring when light is hypothesized to limit mysid vertical movements and during the summer when temperature and light both influence distribution (see discussion in Johannsson et al. 2003).

METHODS AND MATERIALS

Experimental outline

Three experiments were conducted to determine the effects of light on mysid vertical movement and depth selection behavior as well as investigate the interaction between light and temperature preferences. First, mysid preferences were quantified for different light levels (*Light* experiment). These results and those from the temperature preference experiments performed by Boscarino et al. (2007) were used to evaluate the assumption of Gal et al. (2004) and Boscarino et al. (2007) that temperature and light preference functions are equally important and independent predictors of mysid vertical distribution. To test this assumption, I observed and quantified the distribution of mysids under two light-temperature combinations in the experimental columns: the (1) *Deterring Light/Preferred Temperature (DLPT) combination* experiment in which a preferred temperature (6°C) was combined with a

light level known to elicit an avoidance response (10^{-2} mylux) and the (2) *Preferred Light/Limiting Temperature (PLLT) combination* experiment when a preferred light condition (10^{-8} mylux) was combined with a temperature known to limit mysid vertical ascent (12°C) (Boscarino et al. 2007).

Collection and maintenance of mysids

Mysids used in experiments were collected with vertical net hauls (1-m diameter, 1-mm mesh) on a new moon night in October 2005 at a 100-m deep site in Skaneateles Lake, New York. Skaneateles Lake is a deep, oligotrophic lake in the Finger Lakes region of New York State that drains northward into Lake Ontario. The spectral sensitivity curves of both the Skaneateles Lake and Lake Ontario mysids are very similar and are both best fit by a Vitamin-A_1 template curve (Boscarino, unpubl.). Mysids were placed into 4°C, light-proofed coolers immediately following collection to avoid extended exposure to adverse light and thermal conditions. Mysids were fed *ad libidum* rations of Cyclop-eez®, a food source derived from the subclass Copepoda, on a daily basis. Those mysids selected for use in the experiments were starved for approximately 12 h prior to experimentation to ensure that they would be active when they entered the experiment. Only adult and subadult mysids (>12 mm) were selected for use in this experiment (mean length = 14 mm) and these were selected at random (male or female- although no ovigerous females were used) from the stock tanks. Mysids were euthanized and measured immediately following the experimental trial.

All feeding and handling of mysids were conducted under infrared or near-infrared conditions, as mysids are insensitive to these wavelengths of light (Jokela-Määttä et al. 2005). An opaque blind was placed immediately outside the entrance door of the experimental room to prevent fluorescent light from entering. In addition,

black felt was hung on all four walls of the experimental room to prevent light from reflecting off the walls onto the experimental columns.

Experimental columns

The set-up of the observational columns was described by Boscarino et al. (2007). Briefly, experimental columns were 2 m tall Plexiglas® cylinders and held approximately 8 L of dechlorinated, Lake Ontario water (Fig. 2.1). Water temperatures were maintained at 4°C by the temperature of the room. Columns were labeled from 0 cm (bottom of column) to 180 cm (top of column) for mysid depth reference during behavioral observations (Fig. 2.1). Thermal gradients in the *Deterring Light/Preferred Temperature combination* and *Preferred Light/Limiting Temperature combination* experiments were created by lowering a heater down to the 90-110 cm interval of the column and controlling the temperature of the upper portion of the water column by setting an Aqualogic® digital temperature controller to the desired temperature. Temperature varied < 1°C throughout an entire 45-min time interval at each depth that temperature was recorded.

Establishment and measurement of light gradients

The light source for the three experiments was a slide projector (Kodak® Carousel® 5200), which was equipped with a Wiko® 120V, 300W ELH light bulb. The projector was placed approximately 3 m away from the columns and projected light onto the upper portion of the experimental columns (Fig. 2.1). Intensity was controlled by placing a set of neutral density filters (Kodak® Wratten gelatin neutral density filters) in the projector. Different combinations of these neutral density filters (D = 1.0-4.0) were used to achieve the desired light intensity reaching the top portion (i.e., 100 to 180 cm) of the experimental columns. Light was prevented from illuminating the bottom portion of the columns (0 to 40 cm) by placing opaque tape on a portion of a neutral density slide as well as placing an opaque board, which extended

up to the 40 cm line, a few meters away from the column. Each combination of a dark bottom column (Region D) and illuminated upper column (Region L) was considered a treatment. Replicates of each treatment were considered experimental trials. For each treatment, there was also a transition region between the completely dark Region D (0 – 40 cm) and the lighted Region L (100 – 180 cm), which I will hereafter refer to as the transition region, Region T (40 – 100 cm). Region T began when the photometer registered a light level greater than zero and ended when the desired Region L intensity had been reached. Region depth designations remained consistent across all experimental treatments (Fig. 2.1).

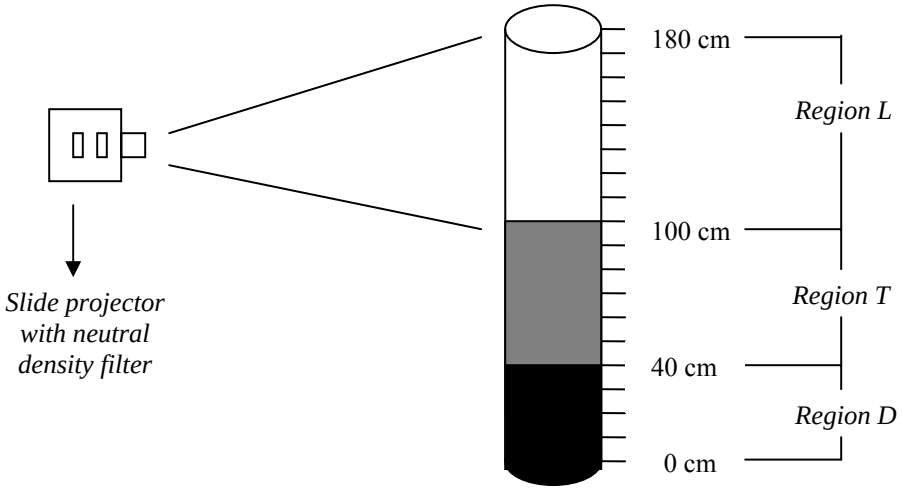

Figure 2.1. Schematic of experimental set-up. Region L represents the portion of the column illuminated with the treatment intensity (100- 180 cm), while Region D (0-40 cm) is completely dark. Region T (40-100 cm) is the transition region between the desired illumination in Region L and complete darkness. Regions are shaded to reflect general differences in light intensities and are not to scale of color. Neutral density filters are inserted into the projector to control overall intensity.

Overall radiance was recorded with an International Light® light meter (Model IL1400A) which had a 5 degree acceptance angle and was calibrated to a Gamma Scientific light source. The light meter has an accuracy of ± 2% of the International

Light calibration transfer standards. The light meter was also fitted with a "mysid filter" (Rosco® Roscolux® filter, #91, peak of filter = 510 nm) selected such that the detector/filter combination closely matched the spectral sensitivity curve of a mysid visual pigment (e.g., Widder and Frank 2001). Thus, this light meter measures radiance relevant to mysid vision (Gal et al. 1999). Light levels were recorded in terms of radiance rather than irradiance because radiance is a more biologically relevant measure of the amount of light reaching a photoreceptor in a mysid eye than irradiance (e.g., Loew and McFarland 1990). Each photoreceptor in a mysid eye has a limited acceptance angle in which to receive incoming light and therefore does not follow the cosine characteristics associated with measures of irradiance. Therefore, a mysid eye acts more like a radiance detector than an irradiance detector. However, all radiance measurements obtained in the laboratory were converted to the irradiance-based "mylux" unit for ease of comparisons with the literature, where light intensity is typically reported in terms of irradiance.

To determine these radiance to irradiance conversions, the total available light was measured during four different nights of varying moon phase (ranging from new moon to full moon) in 2005-2006 with a calibrated archival tag (mk9 Wildlife Computers, Redmond, Washington, USA). This mk9 tag was fitted with the same mysid filter, had the same acceptance angle as that of the International Light® meter used in the *Light* experiments, and was calibrated with the same standard. Therefore, both the mk9 tag and the light meter measured radiance in the same mysid-specific unit. The advantage to using this archival tag versus the International Light® meter directly is that I was able to record light readings at four minute intervals throughout each of these four nights and were therefore able to track changes in light due to moon altitude, as well as phase. The International Light® meter did not have these data-logging capabilities. At each time interval that the mk9 tag logged a light reading, the

corresponding value of moonlight illuminance, in lux, was retrieved from the computer program of Janiczek and DeYoung (1987). Since the Janiczek and DeYoung model is not capable of predicting light levels at new moon, values derived by the moonlight illuminance model of Austin et al. (1976) were used for new moon nights and nights in which the moon was below the horizon. These two models give similar moon illuminance values when zenith angles are approximately the same. These predicted model values in lux were converted to mylux using the conversions of Gal et al. (1999): 1 mylux = 175 lux = 0.51 Watts (W)•m^{-2}. For each four-minute time interval, the ratio between the measured radiance with the mk9 tag (i.e., "mk9 units") and the predicted irradiance in mylux based on the Janiczek and DeYoung and Austin et al. (1976) models was calculated. This ratio was 30.0 mk9 units: 1 mylux (SE of ratio = 1.8; n = 106). All mk9 and International Light® meter readings were converted directly into mylux based on this ratio. All light levels in this study are therefore reported in the same "mylux" values presented in Gal et al. (1999; 2004) and Boscarino et al. (2007).

Note that the conversions between lux, W•m^{-2} and mylux first presented in Gal et al. (1999) will change with depth since the spectral distribution of light changes with depth due to differences in wavelength-specific attenuation. For example, given the measured k_{PAR} and associated wavelength specific attenuation from Jerome et al. (1983), the ratio of lux to mylux increased from 175:1 at the surface to 192:1 at 50 m depth on the two spring nights and decreased from 175:1 to 20: 1 on the two August nights used to test the vertical distribution model. Therefore, all conversions between mylux and lux below the surface are approximate and should be used only as a rough estimate for comparison with other studies that report light in lux rather than more appropriate, species-specific units.

Experiments

Behavioral observations

Three mysids were placed into the bottom portion of the observation column for every trial. Mysid position in the water column was not recorded until at least six minutes after the start of the experiment; this time is needed for the mysids to become randomly distributed in the column during isothermal dark conditions (Boscarino et al. 2007). After this 6-min acclimation period, mysid positions (to the nearest 10 cm) were recorded every three minutes over a period of 45 minutes for a total of 15 observations per mysid using an infrared, digital video camera recorder (Sony® Digital HandyCam®, Model TRV18).

Experiment 1: Light experiment

Three columns were used to monitor mysid movements. Each column was held uniformly at 4°C. One light treatment was administered to all three columns simultaneously and no significant changes in water temperature associated with the illumination of the columns were noted. Light intensity was recorded with the mysid-specific photometer at 10-cm depth intervals throughout each column over a 45-min time period to determine the degree to which light intensity fluctuated over one trial period as well as to what degree intensity levels varied from column to column. The range in light levels varied less than a factor of two for each depth interval throughout the 45-min time period and there was no significant difference in light levels at the same depth among columns (two-way ANOVA, depth-column interaction effect, $p = 0.98$, $n = 21$).

One completely dark condition (control) and ten light gradients were established in the *Light* experiments to monitor the relative light preferences of mysids. Gradients will hereafter be expressed in Region D: Region L light ratios. Region L was varied exactly one order of magnitude for each experimental treatment,

starting at 10^{-10} mylux and continuing up to 10^{-1} mylux (i.e. Treatment 1 = Dark: 10^{-10} mylux gradient, Treatment 2 = Dark: 10^{-9} mylux gradient, etc.). Light level treatments were no higher than 0.1 mylux, as these light levels approximate dawn and dusk light levels on Lake Ontario and, thus, mysids should not experience light levels any higher than this during nighttime migration (Gal et al. 1999).

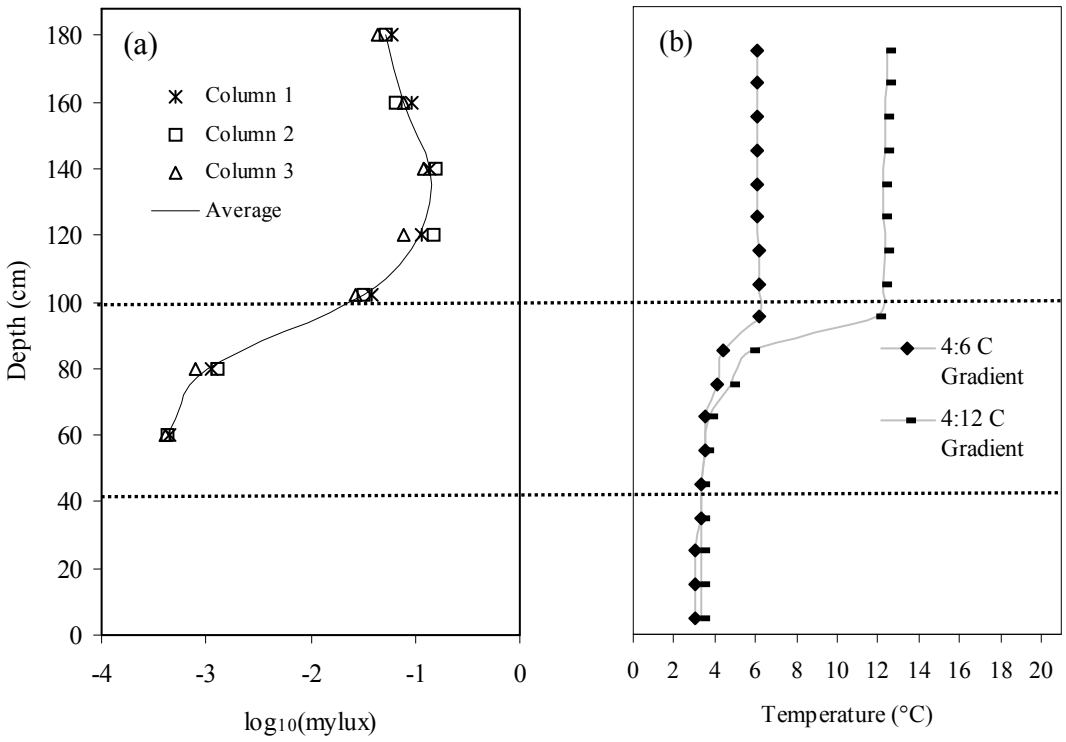

Figure 2.2. Experimental light and temperature gradients. (a) Base light gradient administered in the *Light* experiments. Measurements represent the recorded light intensities, in $\log_{10}$(mylux), at 20-cm intervals in each of the three experimental columns at the highest light level treatment. All other Region L intensity treatments were assumed to follow the same relative gradient, but were dark-shifted exactly one order of magnitude for every neutral density filter placed in the slide. No light intensities are plotted for depths below 40 cm (Region D) because this portion of the column remained less than 10^{-10} mylux for all treatments. (b) Temperature gradients established in the *DLPT combination* and the *PLLT combination* experiments. Dotted lines separate each light region (Region D= 0-40 cm, Region T = 40-100 cm, Region L = 100-180 cm).

The Region L light intensity used to define each treatment was expressed as the mean light intensity experienced by a mysid in Region L (100-180 cm). The range of light levels recorded in Region L varied by less than a factor of five (Fig. 2.2a). The average light gradient experienced by a mysid in all subsequent treatments depended directly on the number of neutral density filters in front of the projector, as each filter decreased light levels by one log unit. The photometer did not detect any light in Region D even at the highest light level treatment. Given that the photometer is sensitive to light levels of 10^{-10} mylux, light levels in Region D were less than 10^{-10} mylux in all treatments. Control (completely dark) trials were conducted separately from the light treatment trials, since a completely dark column could not be ensured while using the projector to generate light gradients in the other columns.

The proportion of observations in Region L relative to Regions L and D in each column was considered an independent data point (Boscarino et al. 2007). Proportions were used as data points since individual observations of position within the water column may not have been independent. Region T observations were excluded from the analysis as Region T light intensities were highly variable between treatments, so direct inter-treatment comparisons were not possible. One-Way ANOVA and Dunnett's t-test ($\alpha = 0.05$) were performed, after arc-sine transformation of the proportions, to test for differences in the proportion of observations at different light intensities relative to control (completely dark) conditions in the *Light* experiments. After arc-sine transformation, no trends in the residuals were noted when regressed on predicted values and no systematic deviations in the normal probability plots, indicating that the parametric ANOVA analyses were appropriate for the transformed data.

Development of light preference curve

A light preference curve (*g(L)*) was generated from the *Light* experiments based on the probability of finding an individual mysid at a particular light intensity relative to complete darkness (see Results section for function derivation). First, the ratio between the mean proportion of mysids observed in Region L and the mean proportion of mysids observed in Region D for each treatment was calculated (i.e, odds of finding a mysid in Region L relative to Region D). Each Region L : D ratio was then divided by a correction factor of 1.6 to account for the 1.6 times as many observations in Region L as in Region D under control (completely dark, 4°C isothermal) conditions. This procedure corrects for mysid preference for the upper region of the columns independent of the light gradient as well as accounts for the larger volume of Region L relative to Region D. A best-fit line was selected which minimized the sums of squares of all observations when fit through each of the Region L : D treatment ratios (see "Results: *Light* experiment and preference function" for derivation). The resulting curve was then scaled between 0 and 1 by dividing each treatment ratio value by the maximum value of the curve. Values on this curve were called "relative probabilities", as each point on the curve represents the *probability* of observing a mysid at that particular light level *relative* to the most preferred light level (where the value of the curve = 1). To calculate the odds of finding a mysid at any one light level (i.e., light level 1) relative to any other light level (i.e., light level 2), the relative probabilities associated with each of the two light levels are simply divided by one another (i.e., value at light level 1•(value at light level 2)$^{-1}$ = odds of finding a mysid in light level 1 relative to light level 2). Note that these relative probabilities are based on the ratio of observations in Region L : Region D and are different from the proportions used in the ANOVA analyses which are based on the ratio of Region L : (Region L + D).

Experiments 2 and 3: Deterring Light/Preferred Temperature (DLPT) and the Preferred Light/Limiting Temperature (PLLT) combination experiments

The *DLPT* and *PLLT combination* experiments were performed to test the assumption of Gal et al. (2004) and Boscarino et al. (2007) that temperature and light preference are equally important and independent predictors of mysid vertical distribution. Pairing a deterring condition with a favored condition should provide the best test of independence of the two factors.

In the *DLPT combination* experiment, a deterring light intensity of 10^{-2} mylux was combined with a preferred, 6°C temperature in the upper portion of the column (Fig. 2.2a,b). The Region L light level was set to 10^{-2} mylux because the *Light* experiments indicated that mysids were deterred, but did not completely avoid these light levels. The selection of 6°C as the preferred temperature was based on results from the mysid temperature preference experiments performed by Boscarino et al. (2007). Two sets of control trials were performed for the purpose of statistical comparisons. In the "light control" trials, mysid vertical distribution was observed in a 4°C isothermal, dark: 10^{-2} mylux gradient. In the "temperature control" experiments, mysid position was measured in a completely dark, 4:6°C gradient. Hereafter, these conditions will be referred to as the "Deterring Light Control" and "Preferred Temperature Control", respectively. When a 6°C upper column was combined with the 10^{-2} mylux upper column condition, I defined this as the "Deterring Light/Preferred Temperature (DLPT) Combination" treatment.

In the *Preferred Light/Limiting Temperature (PLLT) combination experiment,* a limiting temperature of 12°C, was combined with a preferred, 10^{-8} mylux intensity, in the upper portion of the column (Region L) (Fig. 2.2 a,b). I used 12°C as the limiting temperature because mysids are limited by, but do not completely avoid, this temperature (Boscarino et al. 2007). The Region L light intensity was set to 10^{-8}

mylux because these light levels were strongly preferred by mysids in the *Light* experiments.

Two sets of control trials were run for the purpose of statistical comparisons. In the "light control" trials, mysid vertical position was observed in a 4°C isothermal, dark: 10^{-8} mylux gradient. In the "temperature control" experiments, mysid position was measured in a dark, 4:12°C gradient. Hereafter, these conditions will be referred to as the "Preferred Light Control" and "Limiting Temperature Control", respectively. When a 12°C upper column was combined with the 10^{-8} mylux upper column condition, I defined this as the "Preferred Light/Limiting Temperature Combination" treatment.

Vertical distribution model

A model was constructed based on the light preference curve derived in this study, (*g(L)),* and the mysid temperature preference curve of Boscarino et al. (2007), *(f(T)),* that predicts the entire vertical distribution of mysids in a water column given ambient light and thermal conditions. The predictions based on light and temperature preferences represent a modification of a model originally created by Gal et al. (2004) and updated by Boscarino et al. (2007) to predict mysid vertical distributions in Lake Ontario. Following these previous studies, I consider the probability of finding a mysid at given depth *z* (P_z) to be proportional to the product of $g(L_z)$ and $f(T_z)$- the preference for light and temperature at depth *z*. The model assumes independence and equal weight of both preferences curves. Therefore, the probability of finding a mysid at any depth z, given all available depths is (1, z_{max}) equals:

$$P_z = \frac{g(L_z) \bullet f(T_z)}{\sum_{1}^{z_{max}} g(L_z) \bullet f(T_z)} \qquad (2.1)$$

This model was used to predict mysid distributions in both the experimental columns and in the field. For comparisons in the laboratory, model predictions were compared to observed proportions of mysids in Region L with two-tailed t-tests (α = 0.05) in the *DLPT* and *PLLT combination* experiments. Predictions of this model were compared to field distribution data from Lake Ontario collected on two nights with an isothermal water column in May 1996 and on two nights in which the water column was thermally stratified in August 1995. The data used in the model applications were collected at sites close, but not identical to the sites published in Gal et al. (2004). All profiles were derived from data collected with a 420 kHz acoustics system (Gal et al. 2004), validated with stratified net tows, and represent sections of the acoustics data where there were no obvious fish targets. Ship lights were turned off during sampling to eliminate effects of artificial light. Comparisons were made between field and predicted distributions using the Czekanowski Index of percent overlap (($\left|$ 1-(0.5 • $\sum$(observed – predicted) $\left|$ •100), Czekanowski Index, Feinsinger et al. 1981) and between observed and predicted peak depth distributions of mysids.

Extinction coefficients on each night were estimated from light profiles measured the previous day with a calibrated LI-193 (Licor®, Inc.) underwater spherical quantum sensor (see Gal et al. 2004). I used the relationship in Jerome et al. (1983) between average k_{PAR} and wavelength specific extinction coefficients to calculate irradiance at depth in mylux, given the normalized spectral sensitivity curve (range of values on curve = 0 to 1) of *Mysis relicta* (see Gal et al. 1999). Moon phase and altitudes, sampling dates and times, and temperature conditions used in the

modeling applications are presented in Table 2.1. Note that the two August and two May profiles include one night in which the moon had not yet risen above the horizon and represented starlight-only conditions and one night in which approximately three-quarters of the moon's disc was illuminated. Surface light levels were estimated with the computer program of Janiczek and DeYoung (1987) for the three-quarters moon nights and with the moonlight illuminance model of Austin et al. (1976) for the starlight-only nights.

RESULTS

Experiment 1: *Light* experiment and preference function

Light strongly affected the proportion of mysids observed in Region L relative to a completely dark Region D (One-Way ANOVA, $F_{10, 59}$, $p < 0.0001$, $n = 70$, Dunnett's t-test) (Fig. 2.3). Mysids displayed strong preferences for the 10^{-8} and 10^{-7} mylux treatments, supporting the hypothesis that mysids are attracted to a certain quantifiable range of light intensities. No significant differences in proportion were observed between dark, 10^{-10}, and 10^{-9} mylux light conditions, indicating that these low light levels are neither preferred nor avoided by mysids (Fig. 2.3). These low light levels may not be detectable by mysids. Significantly fewer mysids were observed in light level treatments of 10^{-3} mylux or greater relative to dark columns and no observations of mysids were recorded for light levels of 10^{-1} mylux.

A Gaussian curve based on the logarithm of light in mylux units was fitted to the experimental data for light intensities $> 10^{-9}$ mylux and $\leq 10^{-1}$ mylux which minimized the sums of squares of differences between observed and predicted Region L: Region D ratios (Non-linear least-squares regression, SAS statistical package

Table 2.1: Light and temperature conditions, sampling depths and times, and comparisons of model predictions and observed mysid distributions. Percent illumination refers to the percent of the moon's disc that is illuminated and moon altitude refers to the angle of the moon above the horizon at the time of sampling. The thermocline depth is defined as the depth at which temperature change per meter is greatest. Difference from peak values were calculated as the difference between model predictions and actual observations (in m) of the depth of maximum mysid density. Predicted values are derived from the vertical distribution model. Percent overlap is based on comparisons between model predictions and observed distributions and was calculated using Czekanowski's Index (Feinsinger et al. 1981).

Date	07 May 1996	06 May 1996	15 Aug 1995	02 Aug 1995
Corresponding Fig. 2.5 panel	a	b	c	d
Moonight conditions (% illumination/moon altitude)	82% / 22°	0% / -16°	69% / 13°	0% / -28°
Bottom depth (m)	120	120	90	130
Time of sampling	02:03	22:00	23:47	01:00
Surface temperature (°C)	2.6	2.6	24.4	23.5
Thermocline depth (m)	N/A	N/A	19	11
Observed depth of peak mysid density (m)	49	36	23	14
Predicted depth of peak mysid density	49	34	24	19
Difference from peak (m)	0	2	1	5
% overlap	70	67	75	79

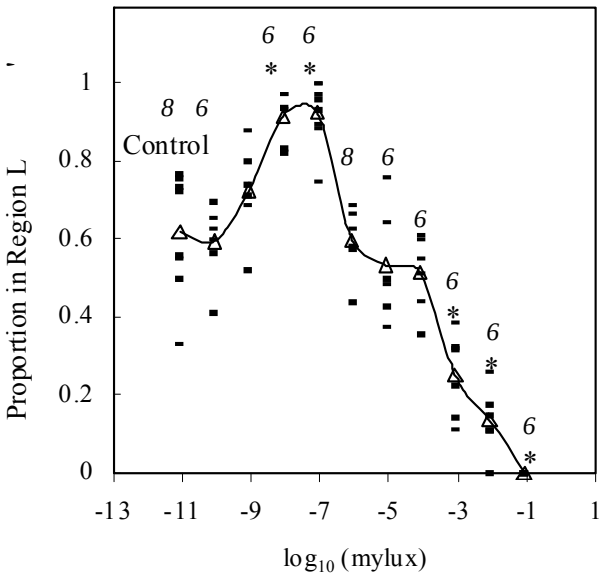

Figure 2.3. Proportion of all Region L and Region D mysid observations that were recorded in Region L in the *Light* experiments. Each replicate is represented by a dash and mean proportions are represented by an open triangle. The solid line delineates a rolling average through the mean proportions. Control distributions are shown on the far left of the graph. Statistical comparisons were made relative to these control distributions. Asterisks above each mean indicate that the treatment was significantly different from the control proportion. Degree of significance was based on One-Way ANOVA of arc-sine transformed data with Dunnett's t-test at an experiment-wise error rate of 0.05. The number of replicates for each treatment is shown in italics above each mean proportion.

version 9.1, $a = 0.76$, $L_{pref} = -7.53$, $r^2 = 0.97$) (Fig. 2.4). The parameter a is the standard deviation of the fitted curve ($a = 0.76$, SE = 0.06) and L_{pref} represents the preferred log light intensity of mysids as predicted by the curve ($L_{pref} = -7.53$, SE = 0.06) (Fig. 2.4). Therefore, the peak of the curve was found at approximately $10^{-7.53}$. The equation for this light preference function, *g(L),* where L equals light intensity in mylux is:

$$g(L) = e^{-0.5\left\{\frac{\log_{10}(L)-(L_{pref})}{a}\right\}^2} = e^{-.5\left\{\frac{\log_{10}(L)-(-7.53)}{0.76}\right\}^2} \quad (2.2)$$

Since there were no significant differences between the 10^{-9} treatment and the dark, control depth distributions in the *Light* experiments, the *g(L)* function was set equal to 0.11 (the function value for 10^{-9} mylux) for all light intensities $\leq 10^{-9}$ mylux . This function was chosen based on the good fit to the observed, experimental data. The upper threshold for mysids was defined as the depth at which 10% of the peak of the mysid distribution is observed or predicted. The cumulative distribution function for Equation 2.2 showed that this threshold corresponded to a light intensity of $2 \cdot 10^{-6}$ mylux (Fig. 2.4).

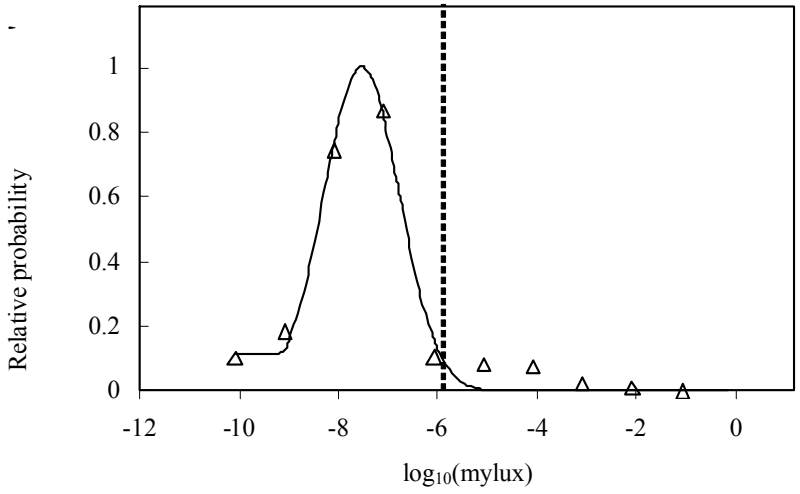

Figure 2.4. Mysid light preference curve from the Light experiments. The Gaussian curve (solid black line) is based on the logarithm of light, in units specific for mysid vision, fit to describe the probability of observing a mysid at a particular light level relative to the most preferred light level. The curve was fit through observed values, which are represented by open triangles. The peak of the curve occurs at $10^{-7.53}$ mylux. The dotted line represents the light level at which 10% of the most preferred light level had been integrated under the curve (assuming a upper light maximum of 10^{-1} mylux), or the upper light threshold for mysids.

Experiments 2 and 3: ***Deterring Light/Preferred Temperature (DLPT) and Preferred Light/Limiting Temperature (PLLT) combination*** **experiments**

The mysid vertical distribution model, based on mysid light and temperature preferences (see Equation 2.1), was used to predict the percent of mysids found in Region L of the experimental columns and to compare model predictions to observed percentages in both the *DLPT* and *PLLT combination* experiments. In the *DLPT combination* experiments, no significant differences were observed between predicted (99%) and observed (96%) percentages of mysids in Region L in the Preferred Temperature Control trials (Two-tailed t-test; $t_{6,\ \alpha=0.05}$; $n = 7$; $p = 0.94$) ; however, a larger percent of mysids were observed in the Deterring Light Control trials (i.e., 13%) than was predicted (< 0.001%) (Two-tailed t-test; $t_{4,\ \alpha=0.05}$; $n = 5$; $p = < 0.0001$) (Table 2.2). I failed to reject the null hypothesis that the percent of observed mysids in Region L of the experimental columns (5%) equals the percent predicted by the model (0.1 %) in the *DLPT Combination* treatment (Two-tailed t-test; $t_{5,\ \alpha=0.05}$; $n = 6$; $p =$ 0.06; Table 2.2).

In the *PLLT Combination* experiments, no significant differences were observed between predicted (39%) and observed (40%) Region L percentages for the Limiting Temperature Control trials (Two-tailed t-test; $t_{7,\ \alpha=0.05}$; $n = 8$; $p = 0.42$) and between predicted (94%) and observed (91%) Region L percentages for the Preferred Light Control trials (Two-tailed t-test; $t_{5,\ \alpha=0.05}$; $n = 6$; $p = 0.80$) (Table 2.2). I also failed to reject the null hypothesis that the percent of observed mysid distributions in Region L of the experimental columns (80%) equals the percent predicted by the model (81 %) in the *PLLT Combination* trials (One-tailed t-test; $t_{5,\ \alpha=0.05}$; $n = 6$; $p =$ 0.47; Table 2.2).

Table 2.2. Observed versus predicted percent of mysids in Region L in the *Deterring Light/Preferred Temperature* (*DLPT*) *Combination* and the *Preferred Light/Limiting Temperature* (*PLLT*) *Combination* experiments. An asterisk next to predicted values indicates that there was a significant difference between predicted and observed percentages. Predicted values are derived from the vertical distribution model. The number of replicates is denoted by "n".

	Deterring Light/Preferred Temperature Combination experiment		
	Deterring Light Control	Preferred Temperature Control	DLPT Combination
Observed	13%	96%	5%
Predicted	< 0.001%*	99%	0.1%
n	5	7	6
	Preferred Light/Limiting Temperature Combination experiment		
	Preferred Light Control	Limiting Temperature Control	PLLT Combination
Observed	91%	40%	80%
Predicted	94%	39%	81%
n	6	8	6

In summary, these results suggest that giving equal weight and independence to the two preference functions provides reasonable predictions of vertical distribution under different light-temperature combinations in the laboratory.

Comparison of model predictions to field data

The model predicted the depth of the peak mysid density to within 2 m on the spring, starlight-only profile (06 May 1996) and predicted the peak to the exact depth when a three-quarters moon had risen above the horizon (07 May 1996) (Fig. 2.5). The percent overlap was also high for both of these spring night profiles (70% and 67% for the three-quarters moon and starlight night, respectively). The model predicted the depth of the peak mysid density to within 1 m on the 15 August 1995 night and to within 5 m on 02 August 1995 when the water column was thermally

stratified. The percent overlap was also high for both the three-quarters moon and starlight-only profiles in August (75% and 79%, Fig. 2.5c and d, respectively).

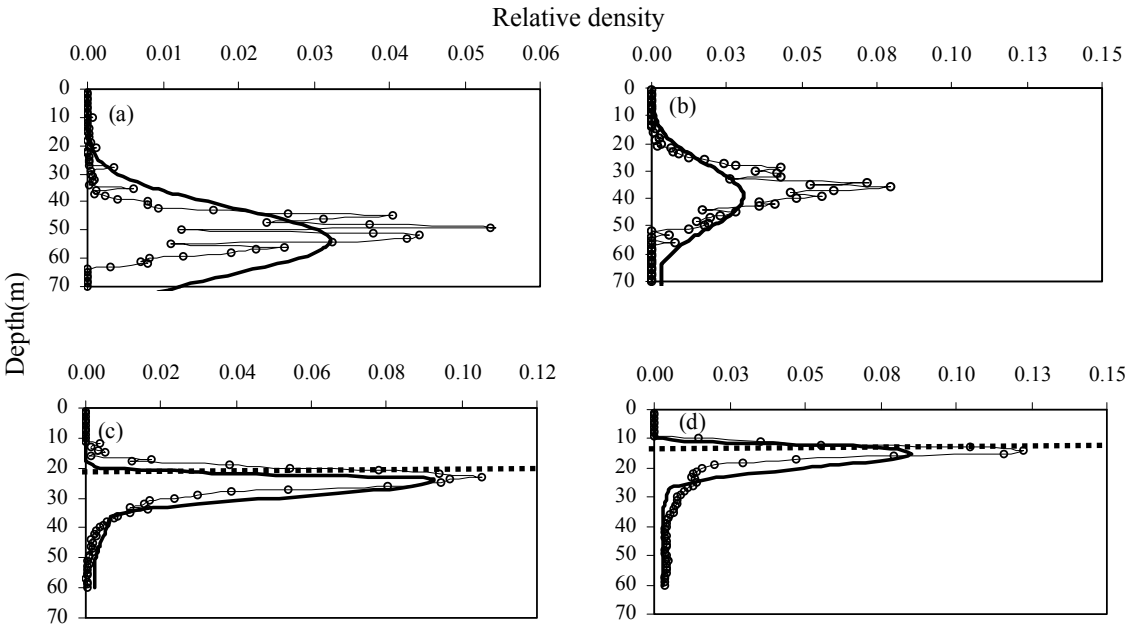

Figure 2.5. The observed and predicted vertical distribution of mysids in Lake Ontario. Acoustic profiles were taken at (a) 2:03 am on 07 May 1996 when a three-quarter moon had risen above the horizon, (b) 22:00 on 06 May 1996 before moonrise, (c) 23:47 on 15 August 1995 when a three-quarter moon had risen above the horizon, and (d) 1:00 on 02 August 1995 after moonset. The distributions are given as relative densities and therefore the total density for a given profile equals one. Model predictions (bold line) were made through application of Equations 2.1 and 2.2 to independently collected acoustic data. Observed distributions are delineated by the solid line with an open circle symbol. The approximate depth of the thermocline on both summer nights is represented by a horizontal, dotted line. Please note the different scales for the relative density axis.

DISCUSSION

The ability to predict a migrating population's vertical distribution from readily measured parameters such as light and temperature has important implications for aquatic food web models. Researchers have relied on temperature and light-based optimization models to predict the depth at which migrating organisms would

maximize either the foraging gain: predation risk ratios (Clark and Levy 1988; Scheurell and Schindler 2003), or overall consumption and growth rates (Levy 1990 a, b). However, migrating populations occupy a range of depths (not just one "optimal" depth) and many of these optimization models do not predict entire distributions. Therefore, they are not able to account for the feeding and behavioral interactions that often take place at the edges of a population's vertical distribution (Stuntz and Magnuson 1976). Other models that build off evolutionary game theory (Iwasa 1982; Gabriel and Thomas 1988), ideal free distribution theory (Larsson 1997; Lampert et al. 2003; Kessler and Lampert 2004) and individual-based-neural network-genetic algorithms (i.e., INGs- Huse and Giske 1998; Huse et al. 1999) do predict entire distributions of organisms. However, these models often rely on idealistic assumptions (e.g., a lack of predators for migrating *Daphnia* to display an ideal free distribution with costs- Kessler and Lampert 2004; Lampert 2005), on complex algorithms that require many parameters with intensive data requirements (e.g., Huse and Giske 1998), or require knowledge of behavioral variability among individuals in the population (e.g. Giske et al. 2003). Therefore, these models are not easily applied to field distributions or to those systems in which these data are not available.

In this study, a model based on two readily measured environmental parameters, light and temperature, provided reasonable predictions of mysids under both thermally stratified and isothermal, as well as new moon and moonlit, conditions. The functions used in the model are based on direct observations of mysid responses to controlled light and temperature conditions in the laboratory. This approach represents an important advance over previous modeling efforts which employed a light preference curve derived from field distributions (see Gal et al. 2004; Boscarino et al. 2007) - a preference curve that may not have been independent of the distribution used to test the model, and did not take into account other potential

influencing factors such as predator and prey densities or distributions. I therefore believe that the light preference curve derived in this study more accurately describes the specific influence of light on habitat selection of mysids.

The experimental procedure used in this study to determine the light preferences of mysids is similar to that used by Swift and Forward (1980, 1982) on the midge larvae, *Chaoborus punctipennis,* and by Forward (1974) and Forward et al. (1984) on the crab larvae, *Rhithropanopeus hariisii*- responses to different light intensities were quantified based on relative proportions of organisms in an illuminated section of an experimental column versus a section furthest from the lighted region. Unlike these previous studies that have focused specifically on the photoresponse mechanisms of migrating zooplankton (see also Forward 1988 and Ringelberg 1999 for good reviews), the results are used to derive a light preference curve capable of predicting field distributions. However, it is important to note that the *Light* experiments were not designed to test actual phototactic responses of mysids. Forward 1988 provides a detailed review of the complications associated with quantifying the "photoresponses" of organisms to a unidirectional source of light. For example, Stearns and Forward (1984a) demonstrate that the marine copepod, *Acartia tonsa,* is positively phototactic (i.e, move towards light) when given a directional light source such as a slide projector, but does not display any phototactic response when a natural, underwater angular distribution of light is simulated (Stearns and Forward 1984b). In this study, a collimated beam of light horizontally was projected onto the experimental columns and I therefore cannot state that mysids are responding phototactically (i.e., either moving towards or away from a source of light). The experiments only reveal the preference for different light levels relative to complete darkness, which is more indicative of mysid light "preference" and "avoidance" rather than providing a direct measure of phototaxis.

I believe that the light and temperature conditions implemented in the experimental columns are comparable to those experienced by mysids in the field. Light level treatments spanned a range of light intensities available to mysids from dusk until dawn. The highest light treatment (10^{-1} mylux, or 1 lux) is comparable to dusk and dawn conditions at the surface of Lake Ontario (Boscarino, pers. obs.) and should represent the highest light level a mysid encounters during vertical ascent. Experimental treatments were also extended to complete darkness to provide control conditions for statistical comparisons, as well as to help determine a lower threshold light level at which mysids do not demonstrate a behavioral response. Additionally, the light meter used to record the intensity of light available to mysids was fitted with a filter that closely matched the relative sensitivity of the mysid eye to different wavelengths of light.

The preferences and deterrences observed for mysids in the laboratory are very similar to those reported for mysids in the field. The peak of the preference curve occurred at $10^{-7.53}$ mylux, which is within a factor of 5 of the peak of the preference curve derived by Gal et al. (2004). The laboratory-derived upper light threshold of $2 \cdot 10^{-6}$ mylux is identical to the light levels associated with the leading edge of *M. relicta* migratory layers in Lake Ontario ($2 \cdot 10^{-6}$ mylux) and closely coincides with that of *M. mixta* in the Baltic Sea (10^{-4} lux, or ~10^{-6} mylux- see Gal et al. 2004 and Rudstam et al. 1989, respectively). Other studies report slightly higher threshold light values (0.3 - 0.03 lux, or 10^{-3} - 10^{-4} mylux in Green Lake, Wisconsin; Teraguchi et al. 1975). However, *in situ* measurements of the water chemistry and/or spectroradiometric data at each depth interval at the time of sampling are rare (but see Gal et al. 1999) and estimates of both the spectral quality and overall intensity of light at depth are typically off by an order of magnitude or more if these factors are not accounted for, as they have in this study (i.e., Widder and Frank 2001).

Light is not the only factor influencing distribution and this study demonstrates the importance of temperature in influencing depth selection of mysids. Previous models of mysid distribution (e.g., Gal et al. 2004 and Boscarino et al. 2007) assumed that temperature and light functions were independent and had equal weight. Although the influences of light and temperature on mysid distribution may indeed be independent as the response may be related to different processes (i.e., predator avoidance and growth maximization), there is no similar *a priori* reason why giving equal weight to the two functions is more likely than another weighing factor. However, the laboratory results in combined light and temperature gradients suggest that these assumptions are at least reasonable. The distributions of mysids in the combined gradients were in most cases not significantly different from model predictions, with the one exception of the Deterring Light Control trials, when a larger proportion of mysids were found in Region L than was predicted. It is possible that the light function may underestimate the number of mysids in these light levels.

Given that the model was constructed based on the preferences of mysids 12 mm or larger, the preference curve may not be applicable to mysids in other size classes. Juvenile mysids, for example, may have different light and temperature preferences than adults. Bowers (1988) demonstrated that the majority of the mysid population between 0-50 m in Lake Superior were less than 7 mm, whereas adults greater than 13 mm were only caught at depths greater than 50 m. Similar vertical separation between adult and juvenile mysids have been reported for *Mysis mixta* in the Baltic Sea (Salemaa et al. 1986; Rudstam et al. 1989) and for *Mysis relicta* in Lake Michigan (Grossnickle and Morgan 1979), suggesting that smaller mysids may have higher light and temperature tolerances than mysids. For example, Morgan and Threlkeld (1982) demonstrated that only juvenile mysids were capable of undergoing horizontal migrations into warmer, nearshore waters in the summer, suggesting

different thermal tolerances of adults and juveniles. Not accounting for juvenile mysids in the vertical distribution model may lead to an underestimation of the upper limit of mysid distribution. This explanation may account for the underestimation of the upper extent of the mysid migratory layer on 15 August 1995. However, I was able to accurately predict both the range and peak of mysid vertical distribution in Lake Ontario for most of the sampling nights that were analyzed, suggesting that either size differences were not playing a large role in structuring the overall distribution, or the acoustic sampling procedure did not accurately detect mysids < 12 mm. Chapter 3 of this dissertation is designed to test the temperature and light preferences of juvenile mysids in an attempt to understand how depth selection behavior may vary by size class.

The low light preferences of mysids obtained in this study may place them tens of meters below a denser epilimnetic zooplankton layer (Reynolds and DeGraeve 1972; Gal et al. 2006). This degree of separation between mysids and zooplankton will vary by moon phase. For example, Rybock (1978) found mysids well below the zooplankton layer in Lake Tahoe on full moon nights, but closer to the zooplankton layer on new moon nights. Beeton and Bowers (1982) hypothesized that full moon conditions should therefore inhibit a mysid's ability to feed on zooplankton and limit their impact on the pelagic food web. In addition to decreased spatial overlap with their prey, lower light levels may decrease capture success. Ramcharan and Sprules (1986) reported significantly higher mysid feeding coefficients at light levels between 1 and 10^{-2} mylux (assuming a conversion factor of 1 mylux = 0.51 W m^{-2}) compared to feeding rates under dark conditions. These results suggest that a mysid's choice of low light habitat inhibits its ability to locate and successfully capture zooplankton. These inhibitory effects of light are likely to be most pronounced during isothermal conditions, when light is the primary abiotic factor influencing distribution (Johansson

et al. 2003; this study). Given that Lake Ontario is isothermal for much of the year (typically from early to mid-November to early June; Schertzer 2003), seasonal changes (i.e., moon phase, algal productivity), as well as long-term shifts in light regime (i.e., oligo- or eutrophication) are likely to play a central role in determining the degree of overlap between mysids, their prey and predators and in structuring Lake Ontario's pelagic food web dynamics, in general.

Given the apparent sacrifice in terms of prey consumption associated with choosing low-light habitats, there must be a strong evolutionary pressure for selecting these types of environment. The most likely reason is that low light preferences of mysids evolved as an adaptation to avoid predation by visual predators like fish. Alewife are a main predator of mysids throughout the Great Lakes and typically remain in epilimnetic waters from late spring to early fall in these systems (Olson et al. 1988; O'Gorman et al. 2000). Although alewife can feed on mysids in the dark (Janssen et al. 1995) feeding rates decline relative to lighted conditions. Batty et al. (1990) offered a mixture of zooplankton to the herring, *Clupea harengus,* which ceased particulate feeding at 0.001 lux (i.e., approximately 10^{-5} mylux) - a light level that is almost 200 times greater than those most preferred by mysids and three times the upper light threshold derived for mysids in this study. However, when fed *Artemia* nauplii, herring ceased particulate feeding at 0.01 lux, or ~10^{-4} mylux, indicating that feeding thresholds for fish can vary depending on the prey item that is used (Batty et al. 1990). Given that mysids are a much larger prey item than the zooplankton used by Batty et al. (1990), mysids may be easier to see under low light conditions, and therefore the light threshold for fish visual feeding may be slightly lower when feeding on mysids. It should also be noted that while alewives have been one of the most abundant planktivores in the Great Lakes system for the past few decades, they are a relatively recent invader (Miller 1957) and mysids have coexisted with coldwater

predators, such as *Coregonus* spp., for a much longer period of time. This coexistence is therefore likely to have had an even greater influence on shaping the habitat preferences and anti-predatory behaviors of mysids than alewife. Little is known about coregonid feeding at low light levels, but Janssen (1980) has shown that lake herring, *Coregonus artedii,* are capable of feeding on *Daphnia* in complete darkness, although they can only do so in a nonselective manner. However, capturing larger, strong-swimming invertebrates such as *Mysis relicta* requires selective particulate feeding, which is thought to be a primarily vision-oriented behavior in coregonids (Janssen 1978). The light threshold required to switch from a nonselective to a particulate feeding mechanism in both coregonids and alewife is still unknown (but see Chapter 5). I cannot, therefore, conclude the precise light levels at which mysids can safely avoid visual predation from coregonids and future investigations would be necessary to provide estimates of coregonid feeding rates in low-light conditions.

This study extends previous efforts by Gal et al. (2004) and Boscarino et al. (2007) to describe and model the responses of mysids to light and temperature gradients. These previous modeling efforts have relied on extrapolation from field distributions to predict the effect of light on vertical distribution and did not test for "preference" under controlled conditions. I argue that the derivation of a function that is based on laboratory observations of mysid depth selection behavior given known light gradients is a more accurate method of determining light preference than field extrapolations, which may be sensitive to errors in acoustic estimates and/or light estimation. Successful application of the laboratory-derived model to predict independently-collected field distributions further supports the light preferences observed for mysids in the laboratory.

Given recent increases in water clarity associated with oligotrophication and the dreissenid mussel invasions of many of the ecosystems inhabited by mysids (e.g.,

Mills et al. 2003), as well as the potential impacts of global climate change on the thermal structure of deepwater lakes of North America (Magnuson et al. 2000; Schindler et al. 2005), it is important that we begin to understand how such long-term shifts in environmental conditions may be impacting the distributions and behaviors of the biotic community inhabiting these systems, including mysids. Similar models to those derived in this study have been used to forecast impacts of climate change on the vertical and horizontal distributions of migrating organisms (e.g., DeStasio et al. 1996; McDonald et al. 1996; Schindler et al. 2005). The model can also be used to predict how global-warming-mediated thermal changes and shifts in light regime may impact food web dynamics via. alteration of habitat use by *Mysis relicta.* These predictions may be made in any deepwater ecosystem that mysids inhabit where the main mysid predators are primarily visual-feeding fish.

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CHAPTER 3: LABORATORY-DERIVED LIGHT AND TEMPERATURE PREFERENCES OF JUVENILE MYSID SHRIMP, *MYSIS RELICTA*

ABSTRACT

Light and temperature both play an important role in governing the vertical movements and distribution patterns of the opossum shrimp, *Mysis relicta;* however, these factors likely do not influence the depth selection behavior of mysids in the same way for all members of the population. In this chapter, the depth selection behaviors of different size classes of mysids exposed to different temperature and light gradients in the laboratory are compared to determine whether mysid light and temperature preferences have an ontogenetic component. Juvenile mysids were attracted to temperatures between 10-12ºC, which is 4-6ºC higher than those most preferred by adults and subadults. All size classes of mysids, including adults, completely avoided temperatures of 16ºC and preferred light levels between ~10^{-7} to 10^{-8} "mylux"- a unit of brightness specific for mysid vision that is equivalent to approximately 175 lux (Gal et al. 1999). However, juveniles were less sensitive to higher light levels than adults and subadults and were frequently observed in waters up to $10^{-1.6}$ mylux (~$10^{0.6}$ lux). Adults are rarely observed in waters brighter than 10^{-6} mylux (~10^{-4} lux) in the field. Lower sensitivity to high light levels, combined with higher temperature preferences, should enable smaller mysids to inhabit upper portions of the water column that are largely avoided by adult mysids.

INTRODUCTION

The opossum shrimp, *Mysis relicta* (also *M. diluviana* after Audzijonyte and Väinölä 2005- hereafter referred to as "mysids" unless otherwise noted), is a member of a group of freshwater crustaceans found in deep, oligotrophic lakes throughout North America and Eurasia (Mauchline 1980). *M. relicta* exhibit dramatic diel vertical migration (DVM), ascending from the deep dark waters they inhabit during the day into the pelagic realm to feed at dusk and throughout the night (Johannsson et al. 2003; Gal et al. 2004). It is during these dusk to dawn hours that mysids become an important food resource for planktivorous fish and are thought to be essential to the over-winter survival of fish due to their high caloric density and fatty acid content (Arts 1999). Mysids can also be the dominant zooplanktivore in the offshore waters of the deepwater ecosystems they inhabit (Spencer et al. 1991; Johannsson et al. 2003) and will compete for access to zooplankton with the same predators that eat them.

The nighttime vertical distribution of mysids is strongly influenced by both light and temperature (e.g., Gal et al. 2004; Boscarino et al. 2007; Chapter 2). Adult mysids prefer light levels between 10^{-8} and 10^{-7} mylux (a mysid-specific unit of brightness equivalent to 175 lux; e.g., Gal et al. 1999) in the laboratory and tend to select depths that fall within this narrow band of light in the field at night (see Chapter 2); however, mysid vertical ascent is also restricted by temperatures above 12ºC and the night-time distribution is a function of thermocline depth as well (Gal et al. 2004; Boscarino et al. 2007). For example, on full moon nights and periods of the year when a deep thermocline is present, mysids are typically found deeper in the water column than on new moon and isothermal nights, respectively (Janssen and Brandt 1980; Rybock 1978). These deeper distributions place mysids further away from more abundant food resources in shallower waters (Gal et al. 2006) and also increase the degree of spatial separation between mysids and their fish predators (Gal et al. 2006;

see Chapters 4, 5). Thus, seasonal and monthly changes in temperature and light can strongly influence the degree to which mysids overlap with and interact with both their predators and prey at night.

However, temperature and light may not elicit the same depth selection responses for all members of a migrating population. Size class segregation of migrating crustaceans is a common phenomenon in both freshwater and marine systems (Angeli et al. 1995; Hays 1995; Ghan et al. 1998). The most frequently observed pattern is for smaller individuals to select for warmer, higher light habitats than larger adults, particularly in those systems in which the largest members of the population are at the highest risk of planktivorous fish predation (Lythgoe 1979). Smaller individuals also typically maximize growth rates at higher temperatures than their adult counterparts (e.g., Fiksen and Giske 1995); thus, the ratio between mortality risk and growth gains in juveniles tends to be minimized at depths nearer to the surface than adults (e.g., Clark and Levy 1988). Even if predation risk is higher for juveniles than adults in near-surface waters, juveniles may still select waters nearer to the surface despite the increased risk to maximize food intake and outgrow this predation pressure as quickly as possible (Fiksen and Giske 1995).

While predator avoidance is likely to be the main ultimate cause for size-dependent aggregations, the relative importance of temperature versus light as the primary proximate factor controlling the depth selection behavior of different size classes of migrating invertebrates is still not well understood. Forward et al. (1984) observed that later-stage larvae of the crab, *Rhithropanopeus harrisii,* were found deeper in the water column than smaller, early-stage larvae and demonstrated that these size-dependent aggregations resulted from differences in photoresponses. Size class segregation has been linked to differences in photoresponses of other migrating invertebrates as well (e.g., Swift and Forward 1980; Miller and Hadfield 1986;

Johnson and Forward 2003); however, I am not aware of any studies that have explicitly investigated the differences in the photoresponses or light sensitivities of different size classes of mysids. Beeton (1960) hypothesized that juvenile mysids (which I hereafter define as mysids < 12 mm since *M. relicta* in the Great Lakes are not sexually mature at this size - Reynolds and DeGraeve 1972; Johannsson et al. 2008) have lower light sensitivities than adults (hereafter defined as individuals >12 mm that can be reliably sexed) as they were observed at light intensities in which no adult mysids were ever caught. Similar observations been reported for *Mysis mixta* (Rudstam et al. 1989) in the Baltic Sea.

Although juvenile mysid distributions have been associated with higher light levels than adults in the field, these associations are often constrained by a high degree of correlation between temperature and light levels with depth. Thus, it is not easy to untangle the influence of temperature and light on depth selection behaviors of different size groups of mysids through field studies alone. Morgan and Threlkeld (1982) demonstrated that only juvenile mysids were capable of undergoing horizontal migrations into warmer, nearshore waters in the summer, indicating higher thermal tolerances of juveniles relative to adults. Similarly, only juvenile mysids were caught at temperatures above 12ºC in Lake Michigan (Beeton 1960) and above 14 ºC in Lake Superior (Bowers 1988) during periods of similar moon phase. It is a common phenomenon in bony fish for both larvae and juveniles to both prefer and tolerate higher temperatures than adults (see review in McCauley and Huggins 1979), and their growth is typically optimized at higher temperatures than adults (e.g., Imsland et al. 2006; Otto et al. 1976). Similarly, individual juvenile mysids maximize their growth at higher temperatures than adults when reared under laboratory conditions (Johannsson et al. 2008).

It is therefore unclear whether depth selection behavior of different size classes of mysids is driven primarily by a preference for or lower sensitivity to higher temperatures, light, or some combination of both of these factors. This study is the first to explicitly investigate the differences in both light and temperature preferences and thresholds of juvenile *M. relicta* relative to adult mysids in the laboratory. The underlying hypothesis is that juvenile mysids will express a preference for and lower sensitivity to higher light intensities and temperatures than adult mysids. The approach is the same as was introduced in Chapter 2 and in Boscarino et al. (2007) in that temperature and light preferences are determined by monitoring the behavioral responses of mysids to different manipulations of light and temperature in 2 m tall observation columns in the laboratory. Results from the light and temperature preference experiments were used to construct functions describing the probability of observing a mysid at different light and temperature levels and compare these functions to those derived for adult mysids (Boscarino et al. 2007; Chapter 2).

METHODS AND MATERIALS

I conducted two experiments to determine the temperature and light preferences of juvenile *M. relicta.* These experiments will hereafter be referred to as the *Temperature* and *Light* experiments, respectively.

Collection and maintenance of mysids

All mysids used in both experiments were collected with vertical net hauls (1-m diameter, 1-mm mesh net) from a 70-m deep site in Skaneateles Lake-a dimictic and oligotrophic lake in the Finger Lakes Region of New York State. Mysids used in the *Temperature* experiments were collected on several occasions from June and August 2006, between the hours of 2100 to 2300 and mysids used in the *Light*

experiments were collected on several occasions from June to July of 2008 between the hours of 2130 and 2400.

Immediately following collection, live mysids were placed into light-proofed coolers filled with 4°C water. The coolers were transported to the Cornell Biological Field Station in Bridgeport, NY where they were transferred to 50-L aquaria in a light-tight, 4ºC temperature-controlled room. Juvenile mysids (5-10 mm), subadults (10-12 mm) and adults (> 12 mm) were separated less than 15 hours after arrival to the experimental facility. Size class has been shown to be a reasonable proxy for maturity (DeGraeve and Reynolds 1972; Johannsson et al. 2008). Only one size class (juveniles) was used in the *Light* experiment. Size estimations were confirmed by measuring mysid length (tip of the rostrum to the cleft of the telson, e.g., Boscarino et al. 2007) after the mysids were euthanized at the end of the experiment.

Mysids were fed *ad libitum* densities of Cyclop-eez® (a food source derived from the subclass Copepoda and closely resembles *Artemia* nauplii in nutritional value). To minimize exposure to light, all feeding and handling of mysids and cleaning of tanks was done in far-red or infrared light, as mysids are insensitive to these wavelengths (Jokela-Määttä et al. 2005). Black felt was hung on all four walls of the experimental room to prevent light from reflecting off the walls onto the experimental columns. In addition, an opaque blind was placed immediately outside the entrance door of the experimental room to prevent fluorescent light from entering.

Temperature experiment

Experimental set-up

Temperature gradients were established in four, 2-m tall Plexiglas columns hung from the ceiling of the experimental room and were labeled from 0 - 180 cm from the bottom to the top of the columns, respectively. Gradients were created by lowering a heater approximately half-way down each of the columns so that only the

upper portion of the column would be heated. We hereafter refer to the heated portion of the columns as Region E, for "experimental" (depths 125-180 cm). The heater was set to and maintained at a desired temperature in Region E through the use of an Aqualogic® digital temperature controller. The lower portions of the columns were maintained by the temperature of the room (4ºC) and will hereafter be referred to as Region C, for "control" (depths 0-100 cm). There was also a "transition" region, Region T (100-125 cm), which began when a 0.05°C cm^{-1} change was observed and ended when the set upper column temperature in Region E was reached. Region designations remained consistent regardless of the Region E temperature and all experimental gradients will hereafter be expressed as the ratio between Region C to Region E temperatures. The experimental set-up is described in further detail and diagrammed in Fig. 1 of Boscarino et al. (2007).

Six different temperature gradients and one control, 4ºC isothermal condition were established in total for each of the size classes (Table 3.1). Each of these gradients was considered an experimental "treatment", which consisted of a 4ºC bottom and a heated Region E that were set to vary at 2ºC intervals (i.e., Treatment 1=4:6°C, Treatment 2=4:8°C, Treatment 3=4:10 °C, etc.) up to a 4:16°C gradient. Please note that while the temperature controller was set to vary at 2ºC intervals, I used the actual recorded temperatures in Region E to derive the preference curve (Table 3.1). To determine the actual temperatures in Region E, I measured the temperature at 10-cm intervals throughout the column at the beginning and end of the experiments with a temperature probe (Yellow Springs Instrument Company, Inc., Model 95 temperature probe). This method also ensured that temperatures remained the same throughout the course of the experiment. Temperatures varied less than 1°C at each 10-cm depth interval for all treatments. Region E and C temperatures are hereafter reported as the mean of all 10-cm interval temperatures recorded in the

Table 3.1: Experimental conditions for both juveniles and subadults in the *Temperature* experiments. "*n*" represents the number of replicates, or trials, run for each temperature treatment. Differences in sizes between treatments are denoted by different letter superscripts. Relative probabilities represent the probability of observing a mysid at a particular temperature relative to the most preferred temperature. All relative probabilities were scaled so that the value at the most preferred temperature (see Results: *Development of light and temperature preference curves)* was equal to one. One asterisk indicates a preference for that particular temperature and two asterisks indicate an avoidance (see text for definition). Note that there were no size differences between treatments in the subadult trials.

	Mean Region C temp. (ºC)	Mean Region E Temp. (ºC)	Mean size (mm)	Proportion in Region E (± 1SE)	Relative probability	*n*
Juveniles	4.50	4.51	$6.0^{b, c}$	0.16 ± 0.08	0.31	15
	4.30	6.08	5.1^{c}	0.22 ± 0.14	0.47	6
	4.45	7.17	6.9^{a}	0.28 ± 0.14	0.65	6
	4.57	9.71	5.2^{c}	0.31 ± 0.12	0.74	6
	4.43	11.07	6.1^{b}	0.37 ± 0.06	0.97^{*}	6
	4.96	13.58	$5.7^{b,c}$	0.05 ± 0.02	0.08^{**}	6
	4.67	15.20	6^{b}	0.00	0.00^{**}	6
Subadults	4.60	4.55	10.8	0.37 ± 0.12	0.04	6
	4.44	5.88	11.2	0.92 ± 0.08	0.73^{*}	3
	4.49	6.98	11.4	0.76 ± 0.07	0.21^{*}	3
	4.52	10.34	11.1	0.06 ± 0.06	0.0043^{**}	3
	4.69	11.19	10.8	0.18 ± 0.12	0.015^{**}	6
	4.50	13.74	11.4	0.02 ± 0.01	0.0011^{**}	3
	4.40	16.28	10.4	0.00	0.00^{**}	3

respective regions (Table 3.1). Mysids were acclimated to 4ºC for at least one week prior to the commencement of the experimental observation period, the same temperature they experience during the day in Skaneateles Lake.

Behavioral observations

Five mysids were placed into the bottom half of each of the four columns and restricted from entering the upper column by closing a gate valve (7.62-cm diameter Valterra® gate valve) that was fitted to the middle of the column. Gate valves remained closed until the observation period commenced to ensure that all mysids began in Region C and were not opened until the desired temperature in Region E was reached. I then allowed a half hour acclimation period before recording mysid position in the columns (see Boscarino et al. 2007). Boscarino et al. (2007) demonstrated that neither the placement nor presence of the heater or the gate valve significantly influenced mysid position in the water column.

After the half-hour acclimation period, I recorded mysid position (as either in Region E, T, or C) through the use of an infrared, digital video camera recorder (Sony® Digital Handycam®, Model TRV18). The experimental room was otherwise kept in complete darkness throughout the behavioral observation period. Mysid positions were recorded at regular 3-min. intervals for a trial period of 45 min., as three minutes provides sufficient time for mysids to move from one end of the column to the other (Boscarino et al. 2007). This procedure was repeated for each temperature treatment and for each size class (juvenile and subadults).

I consider each 45-min. observation period in each column an independent, experimental trial. A minimum of three trials was performed for each temperature gradient-size class combination. At the end of each trial, mysid size and sex was determined to confirm that each of the individuals used in the experiments fell into the expected size range (5-10 mm for juveniles and 10-12 mm for subadults). The

proportion of all observations (excluding Region T) in a given trial that was recorded in Region E was considered an independent data point for statistical analysis. Proportions were used because individual observations of position within the column at 3-min intervals may not have been independent. Region T observations were excluded from the analysis as Region T temperatures were highly variable between treatments. I used the relative probability of finding a mysid at each temperature (see *Development of light and temperature preference curves* section below for discussion of relative probabilities) to determine whether an experimental temperature was either "preferred" or "avoided" by mysids, relative to control, isothermal conditions. I define a temperature as preferred if the relative probability of finding a mysid in Region E was at least three times higher than under control, isothermal conditions. Similarly, I define a response as an "avoidance" behavior if the relative probability of a mysid being found in Region E was at least three times less than under control, isothermal conditions.

Light experiment

Experimental set-up

The experimental design for the *Light* experiment is described in detail in Chapter 2. Briefly, the upper portion of each experimental column (depths 100 – 180 cm, Region E) was illuminated with a slide projector (Kodak Carousel 5200). The intensity of light reaching Region E was controlled by placing neutral density filters in the projector.

A control portion of the column (depths 0-40 cm, hereafter referred to as Region C) was kept completely dark by placing an opaque table in front of the columns, which prevented light from reaching the column. There was also a transition region (Region T, depths 40-100 cm) between the completely dark Region C and the illuminated Region E, which began when the photometer registered a light level

greater than zero and ended when the desired Region E intensity had been achieved. Region depth designations remained consistent regardless of the light gradient that was established.

Light levels were recorded with an International Light light meter (model IL1400A) equipped with a filter (Rosco Roscolux filter, #91, peak of filter = 510 nm) which mimicked the spectral sensitivity of the mysid eye (see Chapter 2 for details). This light meter therefore measured light in units relevant to mysid vision. These units have been termed "mylux" (e.g., Gal et al. 1999). One mylux unit is approximately equivalent to 175 lux or 0.51 $W \cdot m^{-2}$ given a moonlight spectrum at the Earth's surface. Further discussion on the derivation of the mylux unit and the conversion between these units can be found in Chapter 2.

Nine different light gradients and one control, dark condition were established in total. Each different combination of a completely dark Region C and illuminated Region E was considered an experimental treatment. Treatments will hereafter be referred to by the mean light intensity recorded in Region E. The range of light levels recorded at 10-cm intervals in Region E in each treatment varied less than a factor of five for all treatments. The highest light level treatment administered was $10^{-0.6}$ mylux. Each subsequent light intensity treatment was varied exactly one order of magnitude, down to $10^{-8.6}$ mylux, by placing the appropriate number of neutral density filters in the projector (each filter decreased light levels by exactly one log unit). The photometer did not record any light in the highest light level treatment, indicating that Region C remained less than 10^{-10} mylux (the lower sensitivity threshold for the photometer) for all light treatments.

Behavioral observations

Five mysids were placed into the bottom half of each of the four columns at the start of each trial. After a 6-min. acclimation period, mysid position (recorded as

either Region C, T, or E) was noted every 3-min. over a 45-min. trial period through the use of the Sony Handycam®.

Only one size class (juvenile mysids, 5-10 mm) was used in the *Light* experiment. A minimum of six trials (defined by a 45-min. observation period at a certain Region E intensity) was performed for each treatment. Mysids were sized at the end of the experiment to confirm that all experimental animals fell within the expected 5-10 mm size class.

The proportion of all observations (excluding Region T) in a given column that was recorded in Region E was considered an independent data point for statistical analysis. Preference and avoidance behaviors were quantified in the same manner as in the *Temperature* experiment.

Development of light and temperature preference curves

Two temperature preference curves, $(f_j(T)$ and $f_s(T)$, for juvenile and subadult mysids, respectively), and a light preference curve, $(g_j(L))$ was generated based on the probability of finding an individual mysid at a particular temperature or light intensity (See Results section for function derivations for both experiments). The probabilities used to derive these curves are based on the ratio of the mean proportion of mysids observed in the experimental portion of the column (Region E) relative to the observed proportion in the control portion of the column (Region C). Each ratio therefore represents the odds of finding a mysid at that experimental light or temperature condition relative to the control condition. A best fit curve was selected that minimized the sums of squares of all observations when fit through each Region E: Region C ratio. The resulting curves were then scaled between 0 and 1 by dividing each ratio measure by the maximum value of the curves (for derivation of each curve, see Results Section). I call values on each of these curves relative probabilities, as each point on the curve represents the probability of observing a mysid at that

particular light level or temperature relative to the most preferred condition (where the value of the curve equals 1). A more detailed discussion of relative probabilities can be found in Chapter 2.

RESULTS

Temperature experiment

A response was defined as "preferred" if the relative probability of observing a mysid in Region E was at least three times that found under control conditions. Juveniles most strongly preferred 12 ºC, although the mean proportion of mysids found at both the 10 and 12 ºC treatments was higher than the mean proportion found under control, isothermal conditions, suggesting that mysids are attracted to temperatures between 10-12 ºC (Table 3.1). Subadults preferred temperatures between 6-8ºC, which is similar to those preferred by adults (6-8 ºC) (Boscarino et al. 2007) (Fig. 3.1).

A response was defined as an avoidance behavior if the relative probability of observing a mysid in Region E was at least three times that found under control conditions. Juvenile mysids did not display avoidance behaviors until 14ºC, whereas subadults avoided temperatures of 10ºC. By comparison, avoidance behaviors for adult mysids begin at 12ºC (Boscarino et al. 2007). All size classes of mysids, including adults, completely avoid temperatures of 16ºC in the laboratory (Boscarino et al. 2007, this study).

Although mean mysid size varied slightly between treatments in the juvenile mysid trials (one-way ANOVA, $F_{6, 136, \alpha=0.05,}$ F-stat = 7.3, p <0.001, Table 3.1), size was not highly correlated with the proportion of mysids found in Region E (Pearson's r = .080, p = 0.89). There were no significant differences in mysid size in the subadult trials (one-way ANOVA, $F_{6, 29, \alpha=0.05,}$ F-stat = 0.76, p = 0.78). In addition, mean

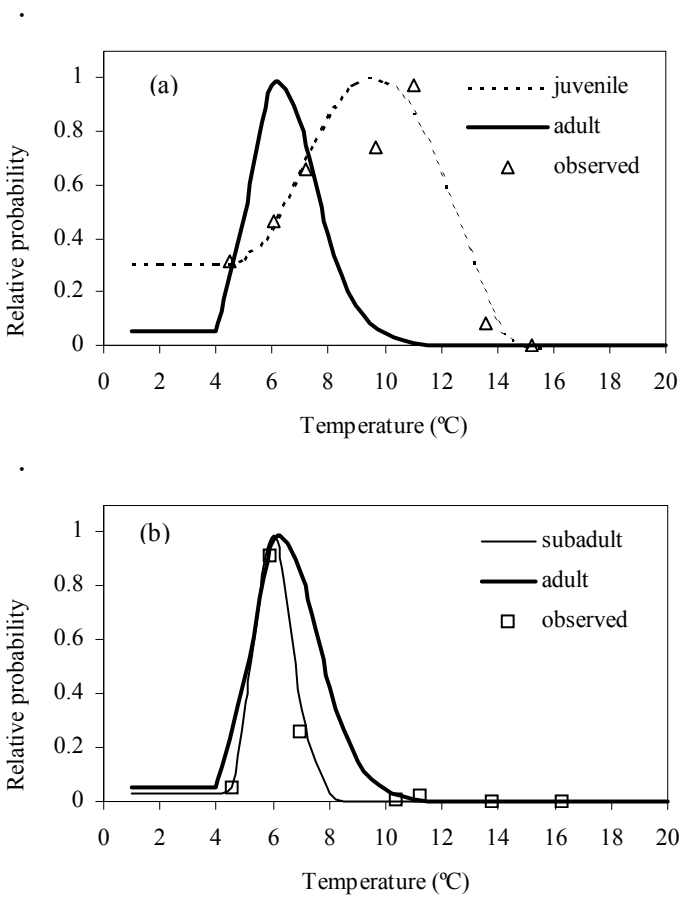

Figure 3.1: Juvenile (a) and subadult (b) temperature preference curves derived from the *Temperature* experiments in comparison to adult mysid temperature preference (courtesy of Boscarino et al. 2007). The juvenile preference curve is a fourth order polynomial and the subadult preference curve is a Gaussian curve based on the logarithm of temperature fit to the observed probability of finding a mysid in a particular temperature relative to the most preferred temperature (see *Development of the light and temperature preference curves* section for further details). The peak of the juvenile curve occurs at 10ºC and the peak of the subadult and the adult curves occur at 5.9ºC and 6.1 ºC, respectively.

Region C temperatures were maintained within a narrow range (4.30ºC to 4.96ºC) regardless of Region E temperature in both the juvenile and subadult trials. I therefore assumed that any depth selection behavior differences between treatments were not due to mysid size, maturity differences, or Region C temperatures, but were instead due to differences in response to Region E temperatures.

***Light* experiment**

Juveniles preferred both the $10^{-7.6}$ and $10^{-6.6}$ mylux treatments. These light preferences are similar to those levels most preferred by adult mysids (Chapter 2). However, juvenile mysids displayed lower sensitivities to higher light levels than adults. For example, juvenile mysids showed neither a strong preference for nor avoidance of light levels of $10^{-5.6}$ to $10^{-1.6}$ mylux, but completely avoided $10^{-0.6}$ mylux indicating that this light level represents an intensity of light juvenile mysids will not to enter in the absence of other cues (Fig. 3.2). By comparison, adult mysids avoid light levels of 10^{-3} mylux and greater (light levels over two orders of magnitude lower than those avoided by juveniles) and will completely avoid light levels of 10^{-1} mylux and higher (Chapter 2).

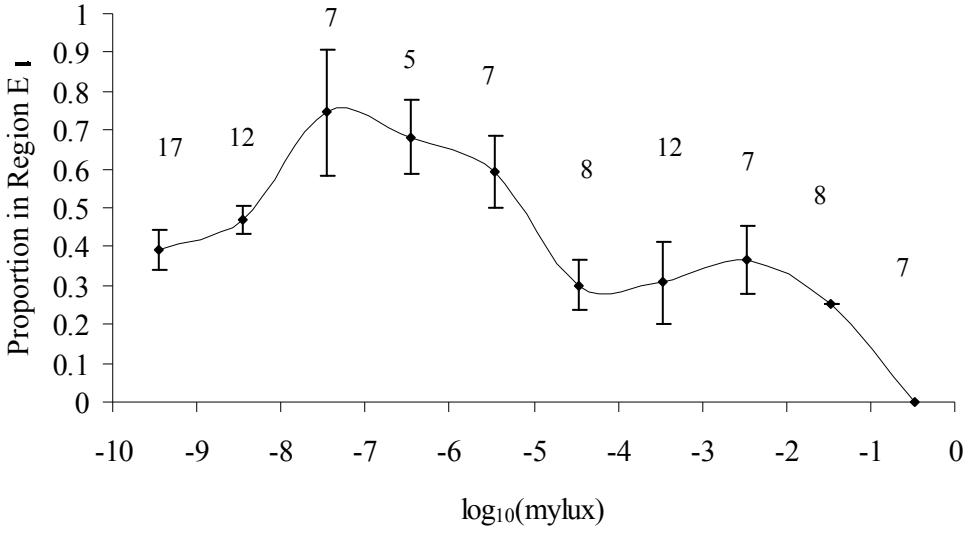

Figure 3.2: Mean proportion (± 1 SE) of all Region E and C mysid observations that were recorded in Region E for the *Light* experiments. Mean proportions are represented by solid circles and the solid line delineates a moving average through these means. The number of replicates for each treatment is shown above each mean proportion.

Mean mysid size (one-way ANOVA, $F_{7, 187, \alpha=0.05,}$ F-stat = 0.55, p = 0.80) did not change throughout the course of the experiment. The photometer did not detect any light in Region C even at the highest light level treatment. Given that the photometer is sensitive to light levels of 10^{-10} mylux, light levels in Region C were less than 10^{-10} mylux in all treatments. I therefore assumed that any differences in depth selection behavior between treatments were not due to mysid size differences, the date at which the experiment was conducted or Region C light levels, but to differences in response to Region E intensities.

Development of the light and temperature preference curves

Temperature experiment

A temperature preference function was constructed for both the juvenile ($f_j(T)$) and subadult ($f_s(T)$) mysids for all temperatures > 4ºC which minimized the sums of squares of differences between observed and predicted relative probabilities. For $f_j(T)$), the best fit was obtained with a fourth order polynomial and for $f_s(T)$, the best fit was obtained with a Gaussian curve based on the logarithm of temperature. The equations for these temperature preference functions are:

$$f_j(T) = 0.00126 \bullet T^4 - 0.0496 \bullet T^3 + 0.666 \bullet T^2 - 3.54 \bullet T + 6.78 \quad (3.1)$$

Microsoft Excel Version 12.0; $r^2 = 0.87$

$$f_S(T) = e^{-.5\left\{\frac{\ln(T)-\ln(5.90)}{0.117}\right\}^2} \quad (3.2)$$

Microsoft Excel Version 12.0; $r^2 = 0.99$

The peak of the subadult curve occurs at 5.90ºC and the peak of the juvenile curve occurs at 10ºC. By comparison, the adult curve peaks at 6.07ºC (Boscarino et al. 2007). For all temperatures < 4ºC, I set the value of the equations to 0.04 and 0.31

for the subadult and juvenile mysids, respectively. These values represent the value of the curves in Eqs. 3.1 and 3.2 at 4ºC, respectively. I also modified the original adult curve, $f_{MOD}(T)$ published in Boscarino et al. (2007) so that the function was defined as 0.05 (value of curve at 4ºC) for all temperatures < 4ºC.

Light experiment

A Gaussian curve based on the logarithm of light in mylux units was fitted to the experimental data for light intensities $>10^{-9}$ and $\leq 10^{-4.6}$ mylux, which minimized the sums of squares of differences between observed and predicted Region E: Region C ratios (Eq. 3.3, Microsoft Excel Version 12.0, $r^2 = 0.85$; Fig. 3.3). The peak of this curve occurs at $10^{-7.06}$ mylux. For all values of $L > 10^{-4.6}$ mylux, the observed probabilities were better described by a second order polynomial (Eq. 3.3, $r^2 = 0.92$, Fig. 3.3). All values on the curve at intensities greater than 0.17 mylux (the x intercept of the second degree polynomial in Eq. 3.3) are defined as zero, as mysids were never observed at these high light levels in the experiments. Cumulatively, this function can be summarized by the following relationships, where L equals light intensity, in mylux:

(3.3)

$$\text{for } L < 10^{-9}: g_j(L) = 0.20$$

$$\text{for } 10^{-9} \leq L \leq 10^{-4.6}: g_j(L) = e^{-.5\left\{\frac{\log_{10}(L)-(-7.06)}{1.06}\right\}^2}$$

$$\text{for } 10^{-4.6} < L < 0.17: g_j(L) = 2.60 \bullet (L)^2 - (1.33 \bullet L) + 0.1411$$

$$\text{for } L \geq 0.17: g_j(L) = 0$$

After Gal et al. (2004), I set the $g_j(L)$ function equal to 0.20 for all values < 10^{-9} mylux (the function value for 10^{-9} mylux), so that the lower light limit of the curve

would remain consistent with other mysid light preference studies. These results suggest that 10^{-9} mylux is also a reasonable lower limit for juvenile mysids as they neither preferred nor avoided these light levels.

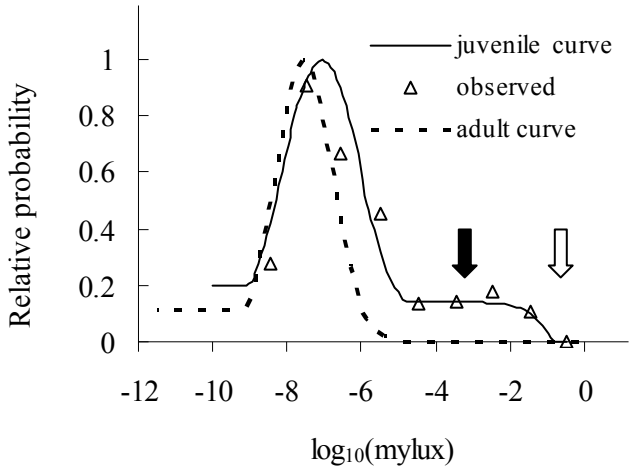

Figure 3.3: Juvenile (this study) and adult (see Chapter 2) mysid light preference curves. Both the juvenile and adult light curves are based on the logarithm of light, in units specific for mysid vision, fit to describe the probability of observing a mysid at a particular light level. The juvenile curve was fit through the observed probabilities represented by the open triangles. Observed probabilities for adults are not shown (see Chapter 2). The dark arrow points to the upper light threshold for adult mysids, while the open arrow points to the upper light threshold for juveniles.

DISCUSSION

The vertical migration and distribution patterns of zooplankton often vary by the size or age of the migrating organism (e.g., De Robertis et al. 2002; Kessler and Lampert 2004). Theoretical studies suggest that younger stages optimize fitness by occupying near-surface, higher light habitats where feeding and growth rates are maximized whereas larger, more mature individuals should select for deeper, safer habitats potentially at the sacrifice of growth rate (e.g., Fiksen and Giske 1995). Given that growth rate and predation risk are partly governed by a migrating organism's abiotic environment (see review in Ringelberg 1999), different size classes in a

migrating population should have evolved distinct preferences for factors such as light and temperature.

In this study, I use behavioral observations of juvenile mysids given different light and temperature gradients in the laboratory to determine whether the temperature and light preferences of *M. relicta* have an ontogenetic component. Juvenile and adult light preferences were approximately equal (both prefer light levels ~10^{-7} to 10^{-8} mylux), but juvenile mysids were attracted to temperatures between10-12 ºC compared to adults which prefer temperatures between 6-8 ºC. We did not observe avoidance behaviors in the smallest size class until 14ºC compared to 10ºC in the subadults and 12ºC adults. In the *Light* experiments, avoidance behaviors were not observed in juveniles until $10^{-0.6}$ mylux compared to adults, which avoid light levels above 10^{-3} mylux. This lower light sensitivity and higher temperature preference in the smallest mysid size class should place them several meters closer to more abundant food resources in near-surface waters than adults and translate into a greater degree of overlap with visual planktivores.

I believe that the temperature preferences and thresholds of mysids presented in this study are good indicators of what mysids choose to inhabit and avoid in the field. Firstly, the temperature ranges implemented in the experiments span the range of temperatures likely to be experienced by mysids in the field (Gal et al. 2004). Although laboratory-raised mysids can tolerate temperatures higher than 16ºC for short periods of time, their survival is greatly reduced at such levels (Rudstam et al. 1999; DeGraeve and Reynolds 1975). Observations of juvenile mysids in the field generally corroborate the upper temperature threshold of 16 ºC derived in this study, as mysids are rarely found at these temperatures, independent of the population's size class distribution, the system being studied or the season of sampling. However, Johannsson et al. (1994) argued that mysids likely inhabit temperatures greater than

16ºC in the field for short periods of time in order to meet their caloric demands in Lake Ontario. It is therefore important to note that the upper thresholds reported in this study represent only those avoided by mysids in the absence of any other biotic cues such as prey or predator abundance, and are unlikely to be "absolute" thresholds for mysids in the field. For example, Boscarino et al. (2007) demonstrated that temperature preference of adult mysids may be modified by predator kairomones and prey abundance and the same likely applies for juveniles.

I also believe that the light conditions introduced in the experiments accurately represent the light levels likely to be experienced by mysids in the field. Firstly, light levels are reported in units relevant to mysid vision, the "mylux", by accounting for the spectral sensitivity of the mysid eye to different wavelengths of light (after Gal et al. 1999). Secondly, twilight conditions at a lake's surface will typically range between 1 and 25 lux (~10^{-2} to 10^{-1} mylux); thus, mysids are unlikely to experience light levels above 10^{-1} mylux during the course of their migration. Mysids were also never observed at a light level treatment of 10^{-1} mylux or greater in the laboratory, further suggesting that these light levels represent a reasonable upper limit for mysids. This upper light threshold has also been corroborated by various field studies which suggest that even the shallowest distributions of mysids (presumably juveniles) are not found at light levels above 10^{-1} mylux during either their day or nighttime distribution phases (Gal et al. 1999; see Chapters 2, 4).

Boscarino et al. (2007) demonstrated that temperature and light preferences alone provide reasonably accurate predictions of mysid distributions in the field. Given the different temperature preferences of adult and juvenile mysids in this study, I would expect bimodal vertical distribution patterns for mysids during periods of the year when the water column is thermally stratified, with a peak of juvenile mysids in near-surface, 10-12ºC waters and another peak of adults in deeper 6-8 ºC waters.

Conversely, I would not expect as strong of a segregation of the size classes during isothermal periods nor as a result of varying moon phases given the similarity in light preferences of adult and juvenile mysids. However, the laboratory experiments do indicate that juvenile mysids are less sensitive to the light levels that are avoided by adults. Thus, while a bimodal distribution may be more pronounced during periods of thermal stratification, I would still expect shallower distributions of juveniles on most dates throughout the year owing to the lower light sensitivities of the juveniles.

If size classes are segregated at certain times of year in most systems inhabited by mysids, it raises an important question as to why a mysid vertical distribution model based exclusively on temperature and light preferences of adult mysids (Boscarino et al. 2007; see Chapter 2), was capable of predicting the entire vertical distribution of mysids across different seasons and light conditions in Lake Ontario. One possible explanation is that I used acoustic backscattering to measure field distributions in that study. Smaller mysids are relatively weak scatterers and will contribute less to the overall backscattering than adult individuals (Rudstam et al. 2008). Hence, acoustic estimates will under-represent the contribution of smaller mysids to the overall abundance and density distribution of mysids throughout the water column. This bias towards larger mysids may explain why the mysid distribution model provided accurate predictions of mysid distribution despite the model only considering adult temperature and light preferences. It should also be noted that the one date on which the vertical distribution model underestimated the upper extent of the mysid distribution (15 August 1995), the lake was strongly thermally stratified. Hence, while I do not consider juvenile mysid preferences in Chapter 4 (the goal of that study is to determine if mysid distribution could be predicted based on the simplest form of the model- i.e., adult temperature and light and preferences alone), future modeling efforts may wish to consider including both

the juvenile temperature and light preference curves derived in this study to provide a complete picture of how light and temperature influence the distribution of the entire population of mysids, including juveniles. However, given the high degree of overlap between the adult and subadult curves in the *Temperature* experiments (72% overlap, Czekanowski index of overlap, Feinsinger et al. 1981; Fig. 3.1b), I do not believe that a modification of the mysid vertical distribution model (Chapter 2, Chapter 4) that accounts for the different responses of subadults to temperature is warranted. Whether subadults display different light preferences than adults is still unknown.

There are several possible explanations as to why juveniles are less sensitive to high temperatures and light levels than adults and subadults. Firstly, higher temperature preferences in juveniles could be an adaptation to maximize feeding rates on zooplankton prey or to maximize their overall growth rate. Both Chipps (1998) and Rudstam et al. (1999) demonstrated maximum feeding rates of mysids that were given *ad libitum* densities of *Daphnia pulex* and *Artemia* nauplii, respectively, in the laboratory between 10-12ºC. Similarly, Gorokhova (2002) and Johannsson et al. (2008) demonstrated increased growth rates of juvenile mysids at temperatures between 10-12 ºC relative to those temperatures most preferred by adults (6-8 ºC). Although smaller mysids rely more on phytoplankton (Branstrator et al. 2000) and do not forage as efficiently or frequently on the types of zooplankton introduced in the feeding experiments of Chipps (1998) and Rudstam et al. (1999) as adults, phytoplankton biomass is often several orders of magnitude greater in the upper metalimnion and lower epilimnion relative to deeper, colder waters primarily inhabited by adult mysids (Benoit et al. 2002). This increased plankton biomass in warmer waters would also act to enhance juvenile mysid feeding and growth rate. A strong correlation between growth rate and final thermal preference is common to

many species of fish and (McCauley and Casselman 1980; Jobling 1981; Larsson 2005) and invertebrates (see review in Moore et al. 1996).

In Chapter 2, I hypothesized that predation pressure from visual planktivores was an important selective driver of the relatively low light preferences of adult mysids in Lake Ontario. The lowest light levels required by most visual planktivores closely coincide to those avoided by adult mysids (Blaxter 1966), indicating that adult mysids select for habitats that would minimize detection by fish predators (see also Chapter 5). Conversely, juvenile mysids display light preferences that overlap to a greater degree with those required for visual predation; however, juveniles should be less visible to fish as their bodies are almost completely transparent and their eyes are much smaller than those of adults (Beeton and Bowers 1982).

Alewives, one of the primary mysid predators in Great Lakes systems, actively select for larger mysids (e.g., Janssen and Brandt 1980) and therefore larger mysids are at a higher risk from fish predation in these systems. Conversely, juveniles are likely at increased risk from other types of predation, such as cannibalism from conspecifics, which may drive selection of the smallest size classes to outgrow this predation pressure as quickly as possible. For example, Quirt and Lasenby (2002) noted high rates of cannibalism of *M. relicta* reared in the laboratory and demonstrated that juvenile mysids display directed movements away from waters previously inhabited by adult conspecifics. A high rate of cannibalism in mysids has been noted in field studies as well (DeGraeve and Reynolds 1975; Nordin et al. 2007) and is thought to be a common driver of habitat selection and in the regulation of population dynamics in a variety of different invertebrate species (e.g., Daan et al. 1988; Buonomo and Lacitignola 2006). Thus, the lower sensitivities to high light and temperature conditions may have evolved as mechanisms to avoid intraspecific

predation particularly in the mid-summer in Great Lakes ecosystems, when adults comprise a large percentage of the population (Johannsson 1995).

I therefore argue that the optimal strategy for mysids is to inhabit near-surface, more productive waters largely uninhabited by adult conspecifics when the risk from fish predation is lower relative to adults, but they are still vulnerable to cannibalism by adult conspecifics. As the mysid grows and matures and the risk of cannibalism decreases, there should be a greater selective pressure to inhabit deeper depths to avoid the increasing predation risk from fish. This hypothesis has support in the theoretical literature of zooplankton depth selection behavior. For example, Titelman and Fiksen (2004) use a model of habitat optimization to demonstrate that the largest members of a population of marine copepods, *Oithona nana*, should select for depths much deeper in the water column than their juvenile counterparts due primarily to differential predation pressures (invertebrate versus vertebrate predation) exerted on the size classes. I argue that the size-dependent light and temperature preferences observed in this study and its predecessors (Boscarino et al. 2007; Chapter 2) are governed by similar selection pressures.

In summary, this study is one of the first to demonstrate that light and temperature preference in a mysid species has an ontogenetic component. The higher light and temperature preferences of juveniles suggest that this size class of mysids inhabit portions of the water column that adults do not, when temperature and light preferences alone are considered. I argue that these different preferences have evolved as responses to different types and levels of predation risks exerted on the respective size classes. Previous studies of mysid vertical distribution and DVM behavior have largely neglected to consider size-dependent depth selection behavior in the field, and may therefore underestimate the potentially important contribution of juvenile mysids in habitats above the thermocline.

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CHAPTER 4:

ASSESSING THE IMPORTANCE OF LIGHT, TEMPERATURE, ZOOPLANKTON, AND FISH ON THE NIGHTTIME VERTICAL DISTRIBUTION OF *MYSIS RELICTA*: A TEST OF THREE MODELS*

* = A slightly modified version of this chapter appears as: Boscarino, B.T., Rudstam, L.G., Eillenberger, J.L. and O'Gorman, R. 2009. Assessing the importance of light, temperature, zooplankton, and fish on the nighttime vertical distribution of *Mysis diluviana* (formerly *M. relicta)*: A test of three models. Aquatic Biology. In press. Accepted April 17, 2009.

ABSTRACT

The opossum shrimp, *Mysis relicta*, perform large amplitude diel vertical migrations in Lake Ontario and their nighttime distribution is likely influenced by temperature, light and the distribution of their predators and prey. At one location in southeastern Lake Ontario, the vertical distribution of mysids, mysid predators (i.e., planktivorous fish) and mysid prey (i.e., zooplankton) were measured, in addition to light and temperature, on eight occasions from May to September, 2004 and 2005. These data were used to test three different predictive models of mysid habitat selection. The first is based on laboratory-derived responses of mysids to different light and temperature gradients in the absence of predator or prey cues. The second is based on the growth rate of mysids as estimated with a mysid bioenergetics model, given known prey densities and temperatures at different depths in the water column. The third model is based on the ratio of growth rates (g) and mortality risk associated with the distribution of fish predators (μ). The model based on light and temperature preferences was a better predictor of mysid vertical distribution than the models based on growth rate and g : μ on all eight occasions. Although mysid temperature and light

preferences likely evolved as mechanisms to reduce predation while increasing foraging intake, the response to temperature and light alone appears to be sufficient to predict mysid vertical distribution across seasons in Lake Ontario.

INTRODUCTION

Diel vertical migration (DVM) of invertebrates is a widespread phenomenon in both freshwater and marine systems, and likely evolved as a mechanism for maximizing food intake in upper, food-rich waters during periods of low risk from visual predators (Gliwicz & Pijanowska 1988, Lampert 1993, Hays 2003). Most vertical movement into warmer, more productive waters to feed therefore occurs between dusk and dawn, when light levels are too low for efficient visual predation from planktivores. The vertical distribution of a migrating population at night is therefore either directly or indirectly influenced by the organisms' abiotic (i.e., light and temperature) and biotic (i.e., predator and prey distribution) environment.

The opossum shrimp, *Mysis relicta* (or *M. diluviana* after Audzijonyte & Väinölä 2005- hereafter referred to as "mysids" unless otherwise noted), undergoes DVM in most of the deep lakes where it occurs, including Lake Ontario – one of the Laurentian Great Lakes of North America (Beeton & Bowers 1982). In Lake Ontario, mysids ascend from their daytime, benthic habitat into the water column at dusk, when they serve as both prey for and competitors with planktivorous fish such as alewife (*Alosa pseudoharengus)* and rainbow smelt (*Osmerus mordax)* (Johannsson et al. 2003).

Although mysid DVM is a well known phenomenon, the factors shaping the nighttime distribution of mysids are still poorly understood. Laboratory-derived temperature (Boscarino et al. 2007) and light preference (Chapter 2) functions have been used to predict mysid vertical distributions when either temperature or light was

the dominant environmental factor. However, little is known about how the relative influence of temperature or light on mysid distribution will vary across different seasons. Moreover, it is unclear as to how fish and zooplankton distributions modify the temperature and light preferences of mysids because the preference functions derived by Boscarino et al. (2007) were developed in the laboratory in the absence of predators and prey.

In Lake Ontario, the zooplankton prey of mysids is concentrated in the upper portion of the water column (Gal et al. 2006) and their distribution may influence the nighttime habitat selection of mysids. Larsson (1997) demonstrated that a population of *Daphnia pulex* were distributed throughout different sections of an experimental chamber in direct proportion to the relative abundance of algal food resources and argued the distribution approximated an ideal free distribution (Fretwell & Lucas 1970). Lampert et al. (2003) expanded this approach by predicting the distribution of a population of *Daphnia hyalina x galeata* in combined food and temperature gradients in large plankton towers based on growth rates at each depth in the column (ideal free distribution with costs model, Lampert et al. 2003). In this study, I use a modified version Lampert et al.'s (2003) model to predict mysid vertical distribution based on estimated growth rates of mysids at each depth as a function of both food availability and temperature.

In addition to growth rate, mortality risk is commonly invoked in models of vertical migration. The distribution of alewives, the most abundant fish in Lake Ontario (Owens et al. 2003), changes seasonally (Mills et al. 1992, Rand et al. 1994) and could also influence mysid nighttime distribution particularly because alewives are known to feed at night (Janssen & Brandt 1980) and are able to feed in total darkness (Janssen 1990, Janssen et al. 1995). Mysids may respond to predation risk

by avoiding waters inhabited by alewives because they sense fish kairomones (Hamrén & Hansson 1999, Gal et al. 2004, Boscarino et al. 2007).

The potential effect of both predator and prey distributions can be combined by calculating the ratio of mortality risk (μ) to gain (typically estimated by either gains in growth (g) or in foraging (f)- e.g., Werner & Gilliam 1984), or vice versa (g : μ). Risk : gain ratios have been used to successfully predict both the timing and amplitude of migration in a variety of fish (Scheurell & Schindler 2003, Jensen et al. 2006) and invertebrate species (Fiksen 1997, Liu et al. 2003). These models assume that an organism should always choose a depth that would minimize μ : g (or similarly, maximize g : μ). In order to predict entire distributions based on g and μ, one would need to either: (1) have prior knowledge of an organism's preference for different combinations of g : μ, or (2) assume that a population is distributed in direct proportion to its g : μ profile and test this assumption empirically. Given the absence of laboratory-derived data on the preference of mysids to different g : μ ratios, I compared predictions based on the magnitude of difference between estimated growth and risk at each depth to observed distributions of mysids in the field.

Thus, I present three different models of the nighttime vertical distribution of mysids: (1) a model based on laboratory-derived light and temperature preferences (e.g., Gal et al. 2004, Boscarino et al. 2007, Chapter 2), (2) a model based on mysid growth rate (e.g., Lampert et al. 2003), and (3) a model based on the ratio between growth rate and mortality risk. I elected not to test a model based on mortality risk alone since alewife densities drop markedly below the thermocline in the offshore of Lake Ontario (Gal et al. 2004), which would virtually assure minimization of predation pressure at the deepest depth evaluated if foraging gains in shallower waters were not considered. We have already shown that this is an unrealistic prediction for mysids in Lake Ontario (Gal et al. 2004, 2006). The objective of this study is to test

whether mysid distribution can be predicted based on adult light and temperature preferences alone, or whether predator and prey distributions must be invoked to predict their distribution. Predictions made by all three models were compared to observed mysid vertical distributions measured on eight nights in southeastern Lake Ontario in 2004-2005.

METHODS

General sampling design

Eight research cruises were conducted on Lake Ontario on May 19, August 16, August 27, and September 30, 2004 and May 5, June 20, July 7 and September 27, 2005 aboard the United States Geological Survey's research vessel, *Kaho*. Hereafter, I will refer to these sampling nights by the date in which the boat left the harbor even though the boat did not return until the following morning at dusk. Sampling dates were selected to measure the nighttime distribution of mysids under "high" and "low" light intensities (full moon or new moon) in each of three seasons (spring, summer, fall). During most cruises, the following procedures were performed: (1) acoustics data with at least one or some combination of three different frequencies (70, 123 and 430 kHz) was collected to determine the vertical distribution of mysids and fish (Table 4.1) (2) plankton, mid-water trawl, and gill nets were used to identify acoustic targets and capture fish for diet analysis, (3) zooplankton data were collected at discrete depths to determine zooplankton vertical distribution, and (4) depth profiles of light and temperature were collected with a combination of a SeaBird instrument and a high-sensitivity light meter. All night sampling was conducted at or near a 170-m deep station located 11.1 km north-northwest of Oswego, New York (see Table 4.1 for exact bottom depths where sampling took place).

Table 4.1: Sampling times, dates, acoustics equipment and calibration settings used in analysis. Detection limits for mysids with 430 kHz and *123* kHz represent the depth at which background noise is equal to a density of 5 mysids·m^{-3}. Depth range refers to the bottom depth of the waters that were sampled, in meters. Detection limits for fish at 70 kHz and 123 kHz represent the depth at which background noise is equal to the backscattering produced by a single alewife with an average target strength of –54 dB. Noise levels are presented as volume backscattering strength (S_v) at 1 m depth.

Date (M-D-Y)	Time of day	Bottom Depth Range (m)	Acoustics Frequency Used (kHz)	Noise at 1 m (430 or *123*)	Noise at 1 m (70 kHz)	Detection Limit (Mysids)	Detection Limit (Fish)
05-19-04	3:37-3:55	120-170	430, 70	-116.7	-119.0	58 m	93 m
08-16-04	2:44-4:00	116-170	430, 70	-117.2	-125.0	68 m	133 m
08-27-04	1:29-2:52	110-170	430, 70	-116.4	-124.5	64 m	127 m
09-30-04	00:44-1:39	150-170	430, 70	-117.0	-115.2	67 m	75 m
05-05-05	3:14-3:39	116-170	430, 70	-116.9	-113	67 m	66 m
06-20-05	22:18-23:41	165-170	123	*-134.7*	N/A	Bottom	Bottom
07-07-05	22:00-23:45	165-170	123	*-135.9*	N/A	Bottom	Bottom
09-27-05	12:00-3:12	165-170	123	*-131.0*	N/A	Bottom	165 m

Temperature and light profiles

Temperature data were collected with a SeaBird profiler that was lowered to the bottom of the 170-m station. All temperature readings were taken at night and recorded at 1-m intervals. In 2004, light extinction was obtained with a PAR light meter that integrated the total light available between 400 to 700 nm (PAR range). Light extinction was measured during the day because the SeaBird was not sensitive enough to measure light at night. For each sampling date, I calculated the average k_{PAR} at 20-m intervals and used the relationships in Jerome et al. (1983) to calculate

wavelength-specific extinction coefficients for each 20-m depth interval of the water column (see Gal et al. 1999, 2004). These wavelength-specific extinction coefficients were then combined with the calculated nighttime surface irradiance (see below), to derive wavelength-specific irradiance values at 1-m depth intervals in the water column at night. These calculations assumed a moonlight spectrum at the surface (see Gal et al. 1999). Following Gal et al. (1999, 2004) and Boscarino et al. (2007), I calculate light at depth in "mylux" by applying the normalized mysid visual sensitivity curve (ranging from 0 to 1 after Gal et al. 1999) to the estimated total amount of light available at each depth and wavelength (Gal et al. 1999). The concept of mylux units is similar to the concept behind lux in that it is a scale adjusted to an organism's relative spectral sensitivity. Mysid visual pigments have been shown to retain the same absorbance characteristics regardless of season or developmental stage (Lindström & Nilsson 1988) so I assumed that all mysids, regardless of size or season, had identical spectral sensitivities.

Surface irradiance in lux was predicted with the moonlight illuminance modeling program of Janiczek & DeYoung (1987) for all full moon nights. The Janiczek & DeYoung model is not capable of predicting light levels at new moon and I therefore used values reported by Austin et al. (1976) for new moon nights and times when the moon was below the horizon. These two studies yield illuminance values within a factor of two of each other when moon phase and zenith angles are the same (Boscarino, unpubl.). All predicted surface values, in lux, can be converted to mylux using the conversions of Gal et al. (1999) which are valid for a moonlight spectrum: 1 mylux = 175 lux = 0.51 Watts (W) m^{-2}.

In 2005, light data were collected using a specially designed light meter (the mk9 archival tag from Wildlife Computers), which was equipped with a filter (Rosco® Roscolux® filter # 91, peak transmission between 510 – 520 nm) that closely

resembles the spectral sensitivity of the mysid eye (wavelength of maximum absorbance, $\lambda_{max,}$ = 520 nm; Gal et al. 1999). Differences in λ_{max} between the filter and the mysid eye pigment were reconciled by applying a correction factor to measurements obtained with the mk9 device. This mk9 device was therefore able to measure light in units directly proportional to mylux - see Chapter 2 for details.

The mk9 tag was calibrated to a Gamma Scientific light source, which has an accuracy of ± 2% of the International Light calibration transfer standards (± 2 % for NIST transfer). This tag is capable of storing light levels in millisecond intervals which allowed us to measure light at 1-m depth intervals throughout the water column. Because the mk9 archival tag had not yet been purchased in 2004, I compared light level estimations using both techniques in 2005 to check for any inconsistencies between the two methods. Differences between the two techniques were less than a factor of 5 even as far as 50 m below the surface. These discrepancies would result in a maximum change in the predicted peak mysid distribution of 5 m on June 20, 2005 (differences on all other dates were less than 2 m). Although I consider the mk9-derived light profiles to be a better representation of the light perceived by mysids, I did not adjust the 2004 light profiles because there were no consistent directional differences between the two methods in the 2005 surveys.

Mysid distributions: Acoustic collection and analysis

Mysid vertical distributions were measured with hydroacoustics at night along a transect from the 170-m station to a bottom depth no less than 110 m (2004) or while stationary at the 170-m station (2005) (Table 4.1). Ship lights were minimized during data collection. Two transducers were mounted on a tow body positioned 5 m away from the starboard side of the boat and towed with the transducer face at a depth of 1.5 m. The tow body was balanced as to remain horizontal when the ship was stationary. A 70-kHz unit (11.4^{o} beam width, Simrad EY500 split beam) and a 430-kHz unit (6^{o}

beam width, Biosonics DtX, single beam) were used in 2004. In 2005, the 70-kHz unit was replaced by a 123-kHz Biosonics DtX unit (7.8^{o} beam width, split beam). I initially expected to use the 430-kHz data for mysids following Gal et al. (2004) and the lower frequency (70 or 123 kHz) for fish. Rudstam et al. (2008a) showed that mysid target strength (TS) is about 5 dB higher at 430 kHz than at 123 kHz. However, the higher TS of a mysid at 430 kHz does not make up for the increased sound absorption at the higher frequencies, and frequencies between 120 and 200 kHz are better for detecting mysids in deep water than 430 kHz (Rudstam et al. 2008a). The acoustics units used for analysis on each date are summarized in Table 4.1. All data analysis was done with EchoView 3.4 (SonarData 2004).

Calibration of the 430-kHz single beam unit was done by the manufacturer on April 4, 2004, May 25, 2005 and February 20, 2007; source levels ranged from 218.55 to 218.18 dB and no additional corrections were applied to the 430-kHz data. The 123-kHz unit was calibrated by the manufacturer in May 2005, and found to be within 0.1 dB of the previous calibration in October 2005 using a -40.4 dB standard copper sphere. The 70-kHz unit was calibrated before each survey with a standard –39.2dB copper sphere and adjusted as necessary. Calibration varied less than ± 1 dB on this unit during 2004 and 2005. All acoustics data were collected at a pulse duration of 0.6 msec and a ping rate of 1 ping sec^{-1}. Biosonics data (123 and 430 kHz) were collected with a square threshold of –130 dB, no lower threshold was applied to the 70 kHz data.

Hereafter, I refer to any acoustic scattering layer as the "mysid layer" if the layer was (1) not apparent before sunset, (2) stabilized within a distinct depth range within 1-2 hours after sunset, and (3) was no longer observed at depths < 50 m in the water column at dawn- all observations consistent and unique to mysids in Lake Ontario (Johannsson et al. 2003). Net samples (conical opening and closing net, 1-m

diameter, mesh size = 1 mm) were obtained at the 170-m station on each night to confirm that this scattering layer was primarily composed of mysids. Replicate tows were made "above", "through", and "below" the mysid layer after visual inspection of acoustic echograms. All sampling was done under minimal red light. Mysids were preserved in 95% alcohol in the field and later enumerated and measured (tip of rostrum to the cleft of the telson) in the laboratory. Lengths were converted to biomass using a length to dry weight regression (Ln (W, dry wt, g) = -12.55 + 2.72 Ln (L, mm); originally derived by Johannsson et al. 1995 and modified by Rudstam et al. 2008b) and then converted to wet weight (WW, Morgan 1976), as the bioenergetics applications used in this study are based in grams mysid (WW) (Rudstam 1989, see Methods: Growth model). Total mysid abundance (in no.$\cdot m^{-2}$) was estimated by dividing the total number of individuals caught in a net haul, by the area of the net opening. Mysid net tows were not taken on August 16, 2004 due to time constraints and abundance estimates were instead made through acoustic procedures on this date.

Fish echoes were defined as data pixels with echo returns > -60 dB in the uncompensated TS domain of the 70 or 123 kHz data and the corresponding pixels were replaced by "no data" tags in the 430 or 123 kHz data set. This threshold was used for all surveys based on inspection of echograms. Ambient noise was removed by subtraction of the expected noise level at each depth calculated from the noise levels at 1 m (Korneliussen 2000). The depth limit for detection of a density of 5 mysids m^{-3} was calculated using a TS of a single mysid of -80.1 dB at 430 kHz and -84.9 dB at 123 kHz (12 mm mysid, Rudstam et al. 2008a), sound absorption, and measured noise level (Table 4.1). Acoustic data from the mysid layer was exported in 1-m intervals after removing noise and contributions from fish. Sound scattering from above the mysid layer were excluded, as that depth layer includes backscattering from

other zooplankton and from larval fish that will not be removed by the fish exclusion threshold chosen here. The method is described in detail in Rudstam et al. (2008b).

Fish densities: Acoustic collection and analyses

Fish densities were obtained from the same transect and same time periods as the mysid densities with the 70- or 123-kHz data. I first applied a data threshold in the uncompensated TS data of -60 dB and converted this filtered data set to volume backscattering strength (S_v). This will exclude most mysid backscattering (see above) and include most backscattering from fish with a TS > -54 dB (see Rudstam et al. 2008b). Fish density at depth was calculated by scaling the volume backscattering coefficient with the *in situ* σ_{bs} calculated separately for the epiliminion and meta/hypolimnion (the mysid layer) for targets > -54 dB. Fish density was calculated for each 2-m depth interval from 2 m below the transducer (depth of 3.5 m in most surveys and 2.5 m in June 2005) to 2 m above the bottom of the lake. Total fish abundance in fish·ha^{-1} was calculated for depths from 3 or 4 m to 60 m. I chose to sum all estimates down to 60 m so that direct density comparisons could be made between sampling dates that may have had different detection limits. The depth of maximum mysid density was shallower than 60 m on all sampling dates.

Fish species identification was verified based on either mid-water trawls or gillnetting conducted at each station, with the exception of May 19, 2004 (nets not available) and July 7, 2005 (when more emphasis was made towards mysid TS estimations). Each gillnet set consisted of a series of seven separate 3-m wide by 20-m deep nets, each tied together by a 15-m rope. Each net had a different mesh size (6.25, 8, 10, 12.5, 15, 18.5 and 25-mm bar mesh). This range of mesh sizes catches alewife from 50 to 250-mm long (total length) with similar efficiencies (Warner et al. 2002). Each gillnet set was allowed to drift several hundreds of meters away from the boat for at least five hours. Gillnets were suspended between 15 and 35 m in the water column.

Decisions on the depth of the set were made prior to each sampling night and were based on the likely depth ranges associated with the upper edge and peak of the main mysid scattering layer. The fish caught were identified to species, the depth caught in the net was noted, and total length was measured to the nearest mm. I also evaluated gut contents of all fish caught for presence/absence of mysids. The number of fish caught per hour of gillnet set was also recorded to compare catch per hour across dates in which gillnets were used. Gillnet and trawl catches (see below) were not used to derive overall abundance estimates.

Mid-water trawling was conducted on June 20, 2005 and September 27, 2005. Trawls were conducted through the mysid layer, as determined by visual inspection of echograms. Trawls through the mysid layer were between 23-51 m on June 20, 2005 and between 22-60 m on September 2005. Fish caught in each trawl haul were identified to species, enumerated, measured (nearest mm, total length), and evaluated for presence/absence of mysids in the gut. The number of alewives caught per hour trawled was also recorded to compare abundance between the two dates in which mid-water trawling was used.

Zooplankton distributions

Zooplankton vertical distribution information was obtained at the 170-m station with a submersible pump (Dayton® submersible sump pump) for all dates in 2004 and on the May, June and October, 2005 cruises. Zooplankton pump samples were not taken during the July 2005 sampling trip due to time constraints and instead relied on two replicate stratified net tows for every 10-m depth interval down to a depth of 50 m. Pump samples on all other nights were taken at 2-m intervals from the surface down to 30 m (the length of the hose) and at 4-m intervals on the way back to the

surface. One hundred liters of water were strained through a 64-µm mesh net for each depth interval and samples were immediately preserved in 95% ethanol.

Stratified net tows (0.5-m diameter opening/closing, 64-µm mesh nylon net) through the 30-40 m and 40-50 m depth strata were also collected in 2005 to assess the zooplankton community structure at depths greater than 30 m. These net tows were not taken in 2004 and I assumed the density of zooplankton in the deepest depth sampled (30 m) was representative of depths down to 50 m (see Discussion). Because pump and net sampling may have different sampling efficiencies for size groups and species (Johannsson et al. 1992, Masson et al. 2004), net tows were taken through the top 22 m of the water column on September 27, 2005 to compare the species composition and absolute density estimates obtained by the two gears.

All zooplankton were categorized into nine major groups: daphnids, nauplii, *Cercopagis pengoi*, *Bythotrephes longimanus*, cyclopoid copepods, calanoid copepods, bosminids, *Holopedium gibberum* and *Limnocalanus macrurus*. I counted and measured at random 100 or more organisms from each sample using a compound microscope at 10-40x magnification. *C. pengoi* and *B. longimanus* were sieved out separately from smaller zooplankton and the entire sample was counted given these larger zooplanktons' propensity for clumping together and biasing subsamples. I used length:dry weight regression equations previously used for Lake Ontario zooplankton (see Benoit et al. 2002) to estimate total zooplankton biomass (µg zooplankton DW·L^{-1}) and the biomass of each group for each depth interval. This procedure follows the standard methods used by the Lake Ontario Biomonitoring program (e.g., Warner et al. 2006). Biomass was averaged down to 30 m to arrive at a mean zooplankton biomass estimate for each night.

Temperature-light model (TLM)

I use the model of mysid vertical distribution from Chapter 2, hereafter referred to as the temperature-light model, or TLM- to predict the vertical distribution of mysids on each of the eight different nights. This model uses laboratory-based light and temperature preferences, derived in the absence of predator or prey cues, to yield an index of habitat preference for each 1-m depth interval given ambient temperature (ºC) and light levels (mylux) by depth. The two preference curves are assumed to be independent and have equal weight - assumptions that have some support from experiments presented in Chapter 2. The probability of finding a mysid at depth z ($P_{TLM}(z)$) and consequently the distribution of mysids in the water column can therefore be described by:

$$P_{TLM}(z) = \frac{g(L_z) \times f(T_z)}{\sum_{z=1}^{z_{max}} g(L_z) \times f(T_z)} \quad (4.1)$$

where $f(T_z)$ and $g(L_z)$ represent the value of the temperature and light functions at depth z, respectively, and z_{max} is the maximum depth included in the analysis. The denominator is the sum of this product over all depths considered. The light preference function, $g(L)$, and the temperature preference function, $f(T)$, are defined in Boscarino et al. (2007) and in Chapter 2 and reproduced here:

$$g(L) = 0.10 \text{ for } L \leq 10^{-10} \text{ and } g(L) = e^{-.5\left\{\frac{\log_{10}(L)-(-7.53))}{0.76}\right\}^2} \text{ for } L > 10^{-10} \quad (4.2)$$

$$f(T) = e^{-0.5\left\{\frac{\ln(T)-(\ln(6.07))}{0.23}\right\}^2} \quad (4.3)$$

Direct comparisons were made between differences in predicted versus observed depth of peak mysid density whereas the percent overlap between predicted and observed mysid distributions were compared with the use of the Czekanowski Index of Overlap ($\left| 1-(0.5 \times \sum(\text{observed-predicted}) \right| \times 100$), Feinsinger et al. 1981). A perfect fit of predicted to observed distributions would therefore result in a Czekanowski overlap index of 100%.

Growth (g) model

The second model is based on calculating the estimated growth rate of an individual mysid at each depth of the water column and assumes that mysids are distributed in proportion to their depth-specific growth rates (e.g., Lampert et al. 2003). Growth rate was estimated as the difference between energy intake and physiological costs. Energy intake is based on a functional response model (Cooper & Goldman 1980) modified by temperature (Rudstam et al. 1999). Physiological costs were calculated for a mysid with a length of 12 mm and are temperature dependent following a bioenergetics model for mysid growth and consumption by Rudstam (1989), which was independently validated for *M. relicta* by Chipps & Bennett (2002).

Depth-specific consumption was estimated by applying the Type I functional response curve published in Figure 2 of Cooper & Goldman (1980) for *Mysis relicta* feeding on *Epischura nevadensis* in the laboratory. Applying a Type I functional response curve to the field data is reasonable given the low to medium zooplankton observed in this study and others (e.g., Johannsson et al. 1994). Prey densities reported in Cooper & Goldman (1980) were converted into dry weight (DW) to derive a functional response equation relating prey biomass (in μg of zooplankton $DW \cdot L^{-1}$) to the total zooplankton biomass consumed per day (*C*), in (g DW of zooplankton)·(g WW of mysid)$^{-1}$·day^{-1}). The regression was forced through the origin so that feeding

rate would be zero if no prey were available. This relationship can be expressed as follows:

(4.4) $C = 2 \cdot 10^{-5} \cdot$[Prey biomass], $r^2 = 0.99$, $n = 5$

This consumption relationship was evaluated for all measured prey densities and temperatures from the surface down to 50 m at 1-m intervals on each of the eight nights sampled. Because ingestion and gut evacuation rates vary with temperature, I applied a temperature-specific multiplier (based on the feeding rates of mysids on *Artemia* spp. at different temperatures- Rudstam et al. 1999, Gal et al. 2004) to account for variations in food intake rate with temperature. The peak of this feeding curve occurs at 9ºC representing a temperature-specific multiplier of 1. The multiplier at other temperatures ranged from 0 to 1 following the curve of Gal et al. (2004). Thus, total consumption at any depth was calculated as the functional response (dependent on prey abundance) and this multiplier (dependent on temperature). Although feeding rate may decrease in the presence of conspecifics (Hansson et al. 2001), I did not include this effect in the model. Caloric intake was calculated from zooplankton biomass consumed using a value of 5411 cal·g DW^{-1} (Johannsson et al. 1994).

Each depth-specific growth value was then used to construct a vertical growth profile from the surface down to 50 m on each of the sampling nights. The probability of observing a mysid at any given depth z,($P_g(z)$) can be described by the following equation:

(4.5) $$P_g(z) = \frac{h(z)}{\sum_{z=1}^{z_{max}} h(z)}$$

where $h(z)$ represents the value of the growth function at depth z and z_{max} is the maximum depth included in the analysis. Direct comparisons were made between differences in predicted versus observed depths of peak mysid density and the percent overlap between predicted and observed mysid distributions was assessed by use of the Czekanowski index.

Growth : mortality risk (g : μ) model

I model the vertical change in the ratio of estimated growth rate of mysids to the perceived mortality risk -hereafter referred to as the "g : μ model"- with respect to temperature, predator abundance and prey biomass at 1-m depth increments in the water column for each of the eight sampling nights. Predation risk is modeled as fish abundance multiplied by a light dependent function relating the proportion of fish feeding to ambient light levels.

Because no data currently exists on alewife reaction distance at the low light levels experienced by fish feeding in the mysid layer at night, mortality risk was estimated by deriving a best-fit linear equation through data presented in Figure 2A of Batty et al. (1990), for a related clupeid- the herring, *Clupea harengus*. This figure describes the relationship between light levels (0 to 270 lux) and the proportion of herring feeding on zooplankton in the laboratory. I converted all lux values presented by Batty et al. (1990) to mylux using the conversions of Gal et al. (1999) and log-transformed all light levels to linearize the relationship. A third-order polynomial curve was fitted to the data describing the proportion of fish feeding as a function of log-transformed light values, between $10^{-1.24}$ to $10^{-5.24}$ mylux, such that the sums of squares of differences between observed and predicted proportions of fish feeding were minimized (Third-order polynomial regression; Microsoft Excel Version 12.0; adjusted $r^2 = 0.72$, $n = 31$). For all light levels at least one order of magnitude lower than the visual threshold of 10^{-3} lux, (or $10^{-5.24}$ mylux), the function was set to 0.1,

which represents the proportion of fish feeding in complete darkness. The equation for this light dependent multiplier, *n(L),* evaluated at all light levels $L < 0.058$ mylux ($\log(L) < -1.24$) is:

(4.6) $$n(L) = -.009(\log L)^3 - .0979(\log L)^2 - .1777(\log L) + .6181$$

for $-6.24 < \log L < -1.24$.

$n(L) = 0.10$ for $\log L \leq -6.24$

I assumed mortality risk, *m,* to be proportional to the abundance of fish (a, in fish m^{-3}), multiplied by the proportion of fish feeding at the light level L ($n(L)$), such that:

(4.7) $$m(a,L) = a \cdot n(L)$$

Growth : mortality risk ratios were then constructed by dividing the value of the growth function, *h,* by the value of the risk function, *m,* evaluated for each depth, *z*, in 1-m depth intervals. Therefore, the probability of finding a mysid at any depth z ($P_{g:u}(z)$), given all available depths (1, z_{max}) equals:

(4.8) $$P_{g:u}(z) = \frac{\frac{h(z)}{m(z)}}{\sum_{z=1}^{z_{\max}} \frac{h(z)}{m(z)}}$$

Comparisons with observations were done in the same manner as the other two models.

RESULTS

Light and temperature conditions

Average k_{PAR} in the top 20 m of the water column varied seasonally with the highest k_{PAR} values found in the summer and the lowest values in the fall and spring (Table 4.2). Surface irradiance was about two orders of magnitude higher on full moon compared to new moon nights (Table 4.2).

Thermal conditions ranged from isothermal at 3.5ºC in May 2004 and 2005 to a strongly stratified water column during the summer of 2004 and 2005 (Table 4.2). The depth of the thermocline (defined as the depth at which the rate of temperature change with increasing depth is maximized) ranged from 7 m in June, 2005 to 27 m in September, 2005 (Table 4.2).

Mysid abundance and length

Mean mysid size ranged from a minimum of 8.0 mm on May 5, 2005 to a maximum of 11.4 mm on May 19, 2004 (Table 4.3). Mean mysid abundance, as estimated through net tows, ranged from 71 mysids m^{-2} on September 27, 2005 to 801 mysids$\cdot m^{-2}$ on July 7, 2005 (Table 4.3). Acoustically derived densities were generally lower than net tow estimates and ranged from 44 mysids$\cdot m^{-2}$ to 290 mysids$\cdot m^{-2}$; however, no significant differences were found when acoustic and net tow estimates were compared across all dates in which net tows were taken (Paired t-test, t-stat = 1.85, $p = 0.11$, $n = 7$) and frequent net hauls in July 2005 confirmed acoustic abundance estimates (see details of mysid acoustic and net comparisons in Rudstam et al. 2008b).

Table 4.2. Light, temperature and depth representing the shallowest 10% and 90% of the mysid population as well as the peak of the mysid distribution. The thermocline depth is defined as the depth at which temperature change is fastest. The size of the scattering layer represents the difference, in meters, between the depth of the shallowest 10% and 90% of the distribution.

	Mo-D Yr	05-19 04	08-16 04	08-27 04	09-30 04	05-05 05	06-20 05	07-07 05	09-27 05
Moon		New	New	Full	Full	New	Full	New	New
Light	Surface	$5{\cdot}10^{-6}$	$5{\cdot}10^{-6}$	$1{\cdot}10^{-4}$	$5{\cdot}10^{-4}$	$5{\cdot}10^{-6}$	$2{\cdot}10^{-4}$	$5{\cdot}10^{-6}$	$5{\cdot}10^{-6}$
	10%	$1{\cdot}10^{-7}$	$1{\cdot}10^{-8}$	$4{\cdot}10^{-7}$	$2{\cdot}10^{-7}$	$2{\cdot}10^{-7}$	$2{\cdot}10^{-7}$	$4{\cdot}10^{-8}$	$2{\cdot}10^{-8}$
	Peak	$9{\cdot}10^{-9}$	$6{\cdot}10^{-9}$	$2{\cdot}10^{-7}$	$2{\cdot}10^{-8}$	$3{\cdot}10^{-8}$	$8{\cdot}10^{-8}$	$2{\cdot}10^{-8}$	$9{\cdot}10^{-9}$
	90%	---	$1{\cdot}10^{-9}$	$2{\cdot}10^{-8}$	---	$1{\cdot}10^{-8}$	$3{\cdot}10^{-8}$	$8{\cdot}10^{-9}$	$1{\cdot}10^{-9}$
	k_{PAR} to 20	0.21	0.32	0.24	0.13	0.16	0.21	0.23	0.13
Temp (ºC)	Surface	3.8	21	21.5	17.4	3.6	18.5	21.7	20
	10%	3.5	9.3	5.6	4.1	3.5	6.2	6.9	10.2
	Peak	3.5	6.4	4.5	4.1	3.5	5.0	5.5	5.4
	Thermocl. depth	NA	21 m	19 m	15 m	NA	7 m	19 m	27 m
10% depth		25 m	25 m	30 m	45 m	26 m	24 m	21 m	29 m
Peak depth		45 m	30 m	36 m	58 m	46 m	29 m	24 m	35 m
90% depth		---	46 m	53 m	---	53 m	36 m	30 m	47 m
Size of scattering layer		---	21 m	23 m	---	27 m	12 m	9 m	18 m

Mysid vertical distribution

Mysid vertical distribution varied with moon phase. Mysids were consistently found deeper in the water column on full moon versus new moon nights when temperature conditions were similar (i.e., surface temperature was within 2ºC and thermocline depth was within 5 m, Fig. 4.1, Table 4.2)). Light levels at the peak of the mysid distribution were also consistently higher on full moon versus new moon nights when temperature conditions were similar (Table 4.2). I never found more than 10% of the population above $1{\cdot}10^{-7}$ mylux in any season (Table 4.2).

Table 4.3: Fish and mysid abundances and lengths and zooplankton biomass for each sampling night. Average lengths of mysids (tip of rostrum to cleft of telson) are based on net tows and mean total length of alewife and percent alewife in catch are based on trawl (June and September 2005) and gillnet sampling (all other applicable dates). Mysid abundance was determined by full water column net tows or acoustic sampling (430-kHz or *123-kHz* unit). Fish abundance (summed down to 60 m) is based on acoustic sampling of the water column and zooplankton biomass was estimated via stratified pump sampling down to 30 m. Fish abundance below the thermocline was summed for all depths from the thermocline down to 60 m during stratified conditions and between 10 and 60 m for both May 2005 and 2004 when the water column was isothermal. "Fish caught for gut contents" refers to the total number of fish caught in either the trawls or gillnets that were used in gut content analyses. Fish caught for gut contents was divided by the total hours of the gillnet set or hours trawled to arrive at fish·hr^{-1} (*in italics*). "% presence" refers to the percent of the total fish catch from within the mysid layer that had mysids in their stomachs. Three dashes indicates data were not collected on that night.

Mo-D Yr	05-19 04	08-16 04	08-27 04	09-30 04	05-05 05	06-20 05	07-07 05	09-27 05
Peak of mysid layer (m)	45	30	36	58	46	29	24	35
Mysid length (mm, *SD*)	11.4, *3.1*	---	11.3, *4.3*	11.1, *3.3*	8.0, *3.0*	10.7, *3.1*	9.5, *3.2*	10.9, *3.2*
Mysids (# m^{-2}, net)	167	---	392	185	174	386	801	71
Mysids (# m^{-2}, acoustics)	155	125	290	46	44	*162*	*202*	*182*
Zooplankton biomass (µg L^{-1})	2.5	24.7	60.3	19.0	1.8	70.0	33.0	31.0
Fish length (mm, *SD*)	---	163, *13*	161, *16*	160, *7*	160, *22*	163, *13*	---	166, *10*
Total fish (# ha^{-1})	2520	462	1852	5761	462	208	36	108
Fish below thermocline (# ha^{-1})	130	148	313	1303	183	12	15	60
Fish caught for gut contents (#, # *hr.*$^{-1}$)	---	74, *14*	30, *5*	85, *11*	34, *16*	34, *36*	---	31, *46*
% presence	---	5%	55%	28%	26%	0%	---	64%
% alewife	---	98%	96%	100%	100%	100%	---	30%

Temperatures associated with the peak of the mysid layer during stratified conditions varied from 4.1ºC in September 2004 to 6.4ºC on August 16, 2004 (Table 4.2). Temperatures at the peak of the mysid distribution were significantly higher on new moon versus full moon nights during periods of thermal stratification (Two-tailed t-test, t-stat = 2.95, $\alpha = 0.05$, $p = 0.04$, $n_{new} = 3$, $n_{full} = 3$).

The peak of the mysid layer was significantly deeper during spring when the lake was isothermal (May 2004, 2005) than during early summer (June and July 2005) when a shallow thermocline was present (Two-tailed t-test, t-stat = 7.45, $\alpha = 0.05$, $p = 0.02$). This result was independent of moon phase. Furthermore, mysids were spread over a significantly larger range of depths during spring (mean depth range = 33 m, SE = 5.0) than all other times of year that data were available (mean depth range = 17 m, SE = 3.0) (Two-tailed t-test, t-stat = 3.0, , $\alpha = .05$, $p = 0.03$, $n_{spring} = 2$, $n_{other} = 5$).

Mysid depth distributions obtained with the 430-kHz unit were very similar to the depth distributions obtained with the 123-kHz unit. For example, for the July 07, 2005 data, mysid density estimates obtained with the 123-kHz unit were regressed on those obtained simultaneously with the 430-kHz unit and found a highly significant relationship between the two frequencies ($r^2 = 0.90$, slope = 0.99- evaluated for all depths between 20 and 50 m) (see Rudstam et al. 2008b for detailed discussion).

Fish vertical distribution, length and abundance

Fish vertical distribution tended to be bimodal when the lake was thermally stratified with the general trend of a large peak in the epilimnion and a smaller peak in the metalimnion (Fig. 4.1). The upper peak tended to coincide with high zooplankton biomass in epilimnetic waters and the lower peak with the upper edge of the mysid layer in metalimnetic waters (Fig. 4.1). An exception to this bimodal pattern during

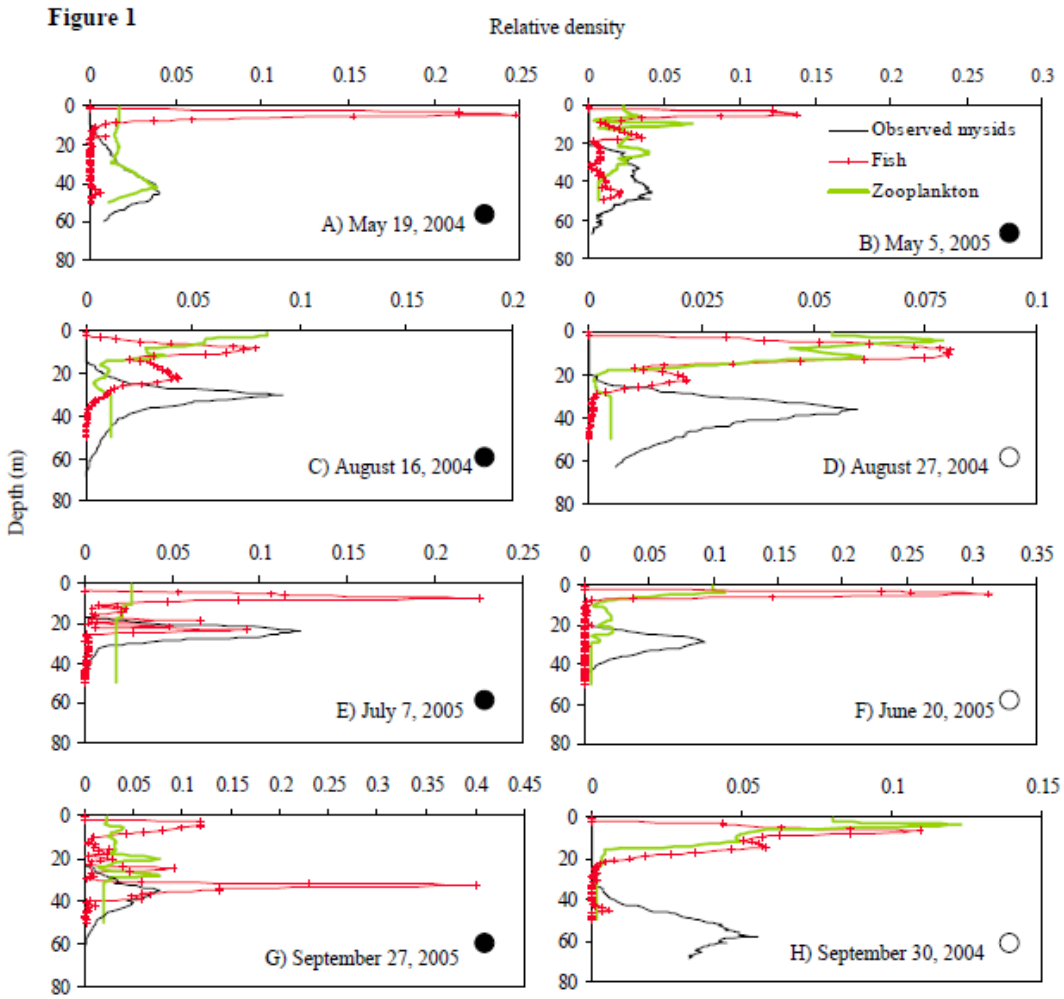

Figure 4.1: Vertical distribution of mysids, zooplankton and fish for eight sampling nights on Lake Ontario. The left hand panels represent the new moon nights (black circles) and the right hand panels represent full moon nights (open circles) with the exception of May 2005 which was a new moon night. Fish and mysid distributions are based on acoustic sampling of the water column. Zooplankton distribution was determined by stratified pump sampling, with the exception of July 2005 which was estimated by vertical net tows. The distributions are given as relative densities and therefore the total density for each profile equals 1. Note the different scales on the relative density axes.

stratified conditions occurred in June 2005 when there was only one epilimnetic peak between 5-10 m, which coincided with the zooplankton peak.

Fish were found deepest in the water column in May 2005. On this sampling date, fish had a bimodal distribution with one peak between 45-50m (which coincided with the peak of the mysid distribution), and a shallower peak between 8-10 m, which coincided with the zooplankton peak (Fig.4.1). A bimodal distribution was not observed in May 2004, when there was only one peak between 8-10 m (Fig. 4.1).

There were no effects of moon phase on the vertical distribution of fish. The depth of the main peak of fish distribution was nearly identical during new and full moons in August 2004 and in June (full) and July (new) 2005. Fish distributions were quite different in the September new moon-full moon comparison, but this was likely due to the higher contribution of rainbow smelt below the thermocline in 2005 (see below).

Fish abundance estimates near the 170-m sampling station in 2004 ranged from 462 fish ha^{-1} on August 16 to 5761 fish ha^{-1} on September 30 (Table 4.3). The majority of these fish were found in the upper epilimnion, as total abundance dropped sharply below the thermocline (Table 4.3). Abundance estimates were significantly lower in 2005 (range = 36 fish·ha^{-1} in July to 462 fish·ha^{-1} in May). A larger proportion of these fish were found below the thermocline (relative to the epilimnion) than in 2004 (Table 4.3). Gillnet and trawl catch through the mysid layer indicated that nearly 100% of the fish sampled through the mysid layer were alewife on five of the six nights in which fish sampling was conducted (mean fish length = 162 mm, range of sizes = 50 to 190 mm, Table 4.3). These results confirm that alewives can frequently be found within the mysid layer during all three seasons. Gut content analyses confirmed that alewives and smelt were feeding on mysids on all nights sampled, with the exception of June 20, 2005 (Table 4.3).

No consistent patterns in alewife length by depth were noted on any of the sampling nights in which gillnets were used and no differences in mean alewife length on June 20, 2005 among fish caught in and above the mysid layer. These results indicate that alewives were not segregated by size within the mysid layer (i.e., between 15-35 m) and were not segregated in epilimnetic waters at night during June 2005. The one exception to alewives dominating the gillnet and mid-water trawl catches occurred in September, 2005 when over half of the trawl catch through the mysid layer (22-60 m) was rainbow smelt. It was during this time period that a larger proportion of the fish backscattering occurred below the thermocline relative to the other sampling nights (Fig. 4.1, Table 4.3). I assume that the fish in this deeper layer in September 2005 were primarily rainbow smelt, while fish caught above the thermocline (< 27 m) were primarily adult and juvenile alewives (see discussion in Gal et al. 2006). Because so few alewives were caught in the trawls in September, 2005, I cannot draw conclusions about segregation of alewife age classes on this date.

Zooplankton vertical distribution and total biomass

Zooplankton vertical distributions varied seasonally and by moon phase. Zooplankton biomass generally peaked in the top 10 m of the water column and dropped off considerably at depths below the thermocline (Fig. 4.1). One notable exception was September 2005 when the thermocline was at 27 m and there was a substantial *Limnocalanus* peak below it. Results from net tows below 30 m in 2005 suggest that zooplankton biomass remains low and relatively constant in hypolimnetic waters (biomass estimates in the 30-40 m depth strata were nearly identical to estimates in the 40 –50 m strata for all nights in 2005) (Fig. 4.1). Zooplankton biomass peaks were slightly deeper in the spring (Fig. 4.1). Mean zooplankton biomass down to 30 m depth was 11 to 32 fold higher during summer than during

spring and varied nearly three fold during June to August (Table 4.3). Mean biomass in September 2005 was about 60% higher than in September 2004.

Comparisons of the net and pump samples failed to show any significant differences between the two techniques. Estimates for mean zooplankton biomass down to 22 m were identical between the two techniques (26 $\mu g \cdot L^{-1}$) and species composition of the integrated samples was also similar (percent biomass, pump: net = 41%: 42% for cyclopoids, 31%: 39% for calanoids, 17%: 9% for *Bythotrephes*, 9%: 5% for *Daphnia* spp., 2%: 5% other).

Model performance

Temperature-light model (TLM)

The temperature-light model (TLM) predicted the peak of the mysid distribution to within 5 m on seven of the eight nights sampled and within 10 m in May 2004 (Fig. 4.2, Table 4.4). Percent overlap between TLM predictions and observed mysid distributions was greater than 74% on all sampling nights and as high as 84% on August 16, 2004, indicating that the model was a good predictor of both the peak and range of the mysid distribution in the field (Fig. 4.2, Table 4.4).

Growth (g) model

The model based on mysid growth at depth predicted the peak of the mysid layer to within 10 m on three of the eight nights, but vastly underestimated the observed peak in May 2005 (Fig. 4.3, Table 4.4). Percent overlap between growth model predictions and observed distributions ranged from 39% in May and July, 2005 to 79% in September, 2005 (Table 4.4). There were no significant differences in percent overlap (two-tailed t-test, t-stat = 0.14, α= 0.05, p = .19) or difference from observed peak (two-tailed t-test, t-stat =0.81, α= 0.05, p = .45) predictions when means were compared on new versus full moon nights (n_{new} = 5, n_{full} = 3), or between

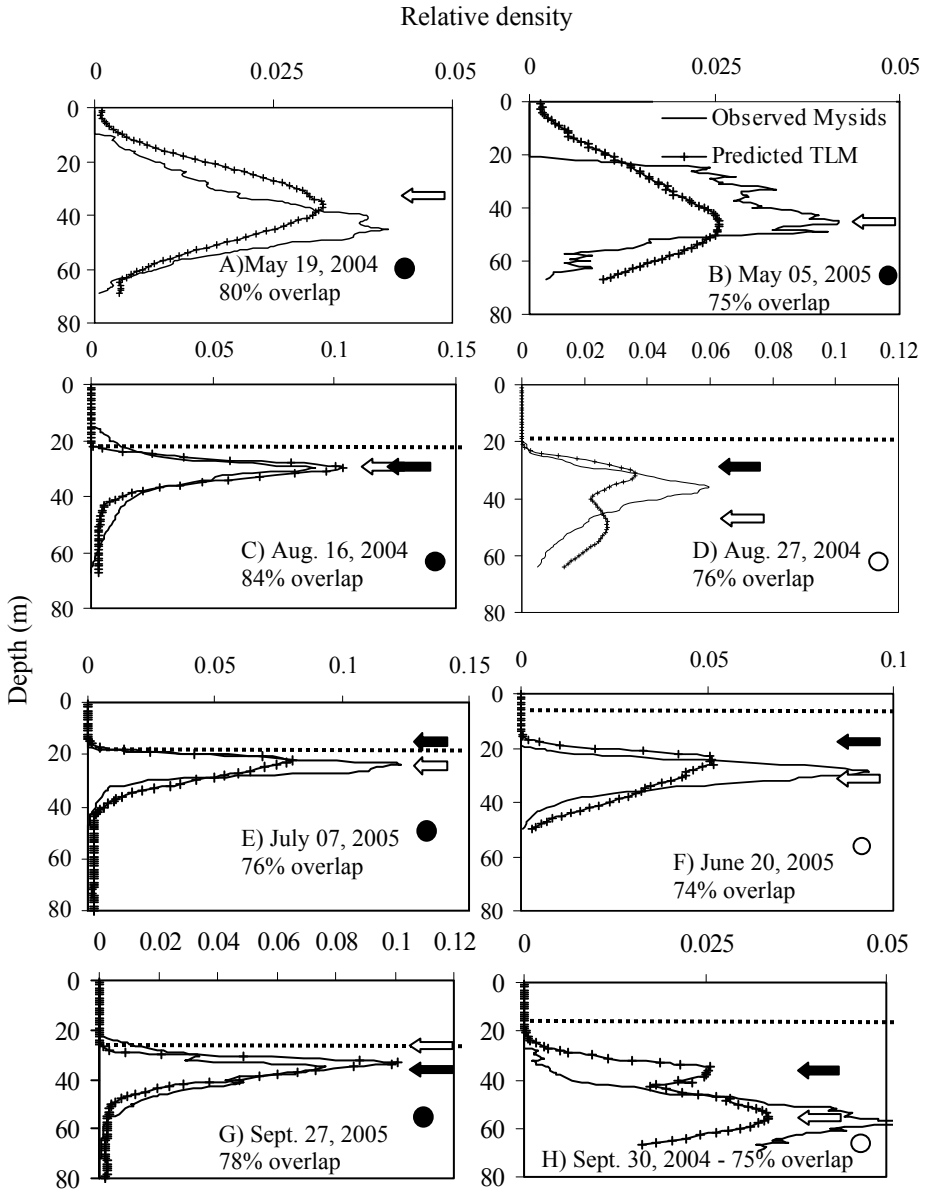

Figure 4.2: Observed mysid distributions versus temperature-light model (TLM) predictions during eight sampling trips on Lake Ontario in 2004 and 2005. All full moon nights (open circles) are on the right hand panes and all new moon nights (dark circles) are on the left hand panes with the exception of the May sampling dates which both took place during new moon conditions. Dashed lines indicate thermocline depths. May profiles were isothermal. Dark arrows point to the depth at which the temperature preference function is maximized and open arrows refer to the depth at which the light preference function is maximized. Percent overlap was calculated using Czekanowski's Index of Overlap (Feinsinger et al. 1981). The distributions are given as relative densities and therefore the total density for each profile equals 1.

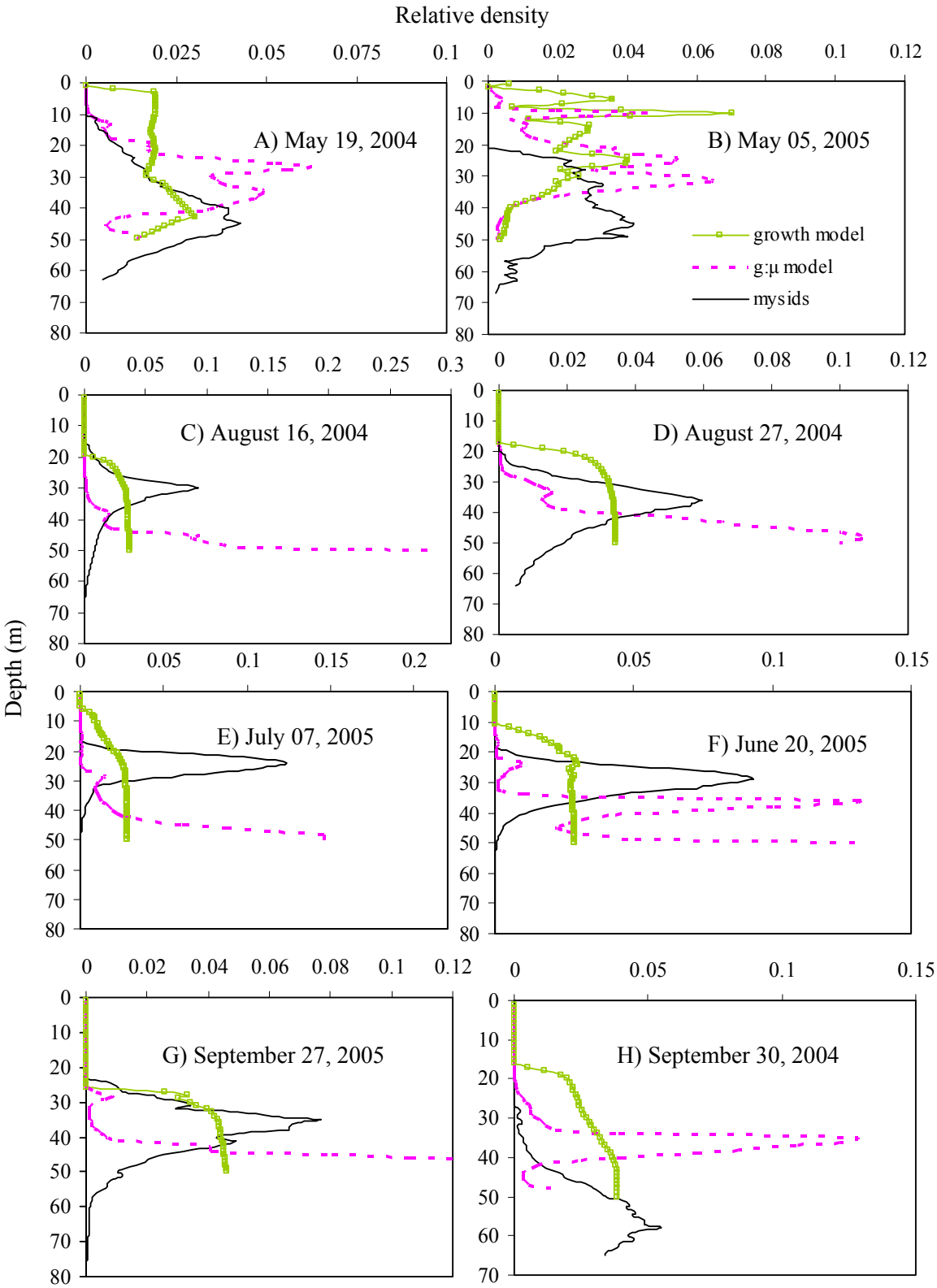

Figure 4.3: Observed and predicted mysid distributions for the growth model and the growth : mortality risk model.

Table 4.4. Comparison of the mysid temperature-light model (TLM), the growth (g) and the growth : mortality risk (g : μ) models to observed mysid distribution. Percentage overlap was calculated using Czekanowski's Index of Overlap (Feinsinger et al. 1981). Difference from peak values were calculated as the difference, in meters, between model predictions and actual observations. Significant differences of "mean differences from peak" and percent overlap are indicated by differences in letter superscripts. All pairwise comparisons were evaluated with Tukey-Kramer HSD post-hoc test at an alpha level of 0.05.

MoD Yr	0519 04	0816 04	0827 04	0930 04	0505 05	0620 05	0707 05	0927 05	Mean ± 1 SE
Observed Peak (m)	45	30	36	58	46	29	24	35	N/A
Difference from peak (TLM) (m)	9	0	5	3	0	1	2	1	2.6 ± 1.1^{a}
Difference from peak (g)	2	19	13	9	36	5	26	15	15.6 ± 4.0^{b}
Difference from peak (g:μ)	18	20	13	8	15	7	25	12	14.8 ± 2.1^{b}
% overlap (TLM)	80%	84%	76%	75%	75%	74%	76%	78%	77.2 ± 1.2^{a}
% overlap (g)	68%	68%	75%	53%	39%	52%	39%	79%	59.0 ± 5.5^{b}
% overlap (g: μ)	65%	22%	49%	48%	45%	22%	12%	28%	36.4 ± 6.4^{c}

stratified (n_{strat} = 6) and isothermal (n_{iso}= 2) conditions (p> 0.50 when both percent overlap and differences from observed peak means were compared). These results indicate that the growth model was not a better predictor of mysid distribution under any particular light or seasonal temperature conditions.

Growth : mortality risk (g : μ) model

The model based on the ratio of growth to mortality risk (i.e., the g : μ model) predicted the peak of the mysid distribution to within 10 m on only two out of the eight nights sampled (Table 4.4). Percent overlap ranged from as low as 12% in July 2005 to 65% in May 2004. Percent overlap values were not significantly higher during the spring, isothermal months than during stratified conditions (two-tailed t-test, t-stat

= 0.43, n_{spring} = 2, $n_{stratified}$ = 6, p = 0.68) or on new moon versus full moon nights (two-tailed t-test, t-stat = 0.17, n_{new} = 5, n_{full} = 3, p = 0.87).

Comparison of all models

The TLM was a significantly better predictor of the depth of peak mysid density (Table 4.4, One-Way ANOVA, $F_{2, 21, \alpha = .05}$, F-stat = 8.2, p =.002) and the range of depths occupied by the mysid layer (as approximated by percent overlap- Table 4.4, One-Way ANOVA, $F_{2, 21, \alpha = .05}$, F-stat = 14.2 $p < .0001$) than either the growth or g : μ models when the respective mean values were compared across all dates. Tukey-Kramer HSD post-hoc tests (JMP Version 5.1) revealed significant differences between all three models in terms of percent overlap (mean percent overlap- TLM > g > g:μ; all $p < 0.02$; Table 4.4) but between the TLM and growth model and the TLM and g : μ model only when comparing difference from peak means (mean difference, g > g:μ > TLM; for g to g:μ, p = 0.84; for TLM to g, p = .0020, for TLM to g : μ, p = 0.0027; Table 4.4).

DISCUSSION

I show that a model based on two readily measured environmental factors, temperature and light, was able to provide reasonable predictions of the entire nighttime distribution of mysids during the spring, summer and fall in Lake Ontario. In contrast, two models based on estimated growth rate and on the ratio of growth rate to predation risk did not accurately predict the depth of maximum mysid density or the range of depths occupied by mysids (lower overlap between predicted and observed distributions). Thus, I conclude that the response to temperature and light alone appears to be sufficient in predicting mysid vertical distribution across seasons in Lake Ontario.

I do not believe that the mysid acoustic returns were biased due to backscattering contributions of other species. Net samples taken above, through, and below the mysid layer confirmed acoustic returns in both 2004 and 2005, with greater than 85% of the catch occurring at depths deemed to be the "mysid scattering layer" (as determined through visual inspection of acoustic echograms) on all dates. Estimates were likely not confounded by smaller zooplankton, as invertebrates < 4 mm are weak scatterers and likely not contributing substantially to backscattering in the mysid layer (see Rudstam et al. 2008b). In addition, very few juvenile fish were found within the mysid layer in the gillnets which should decrease the probability of including fish scattering in the mysid distribution analyses.

Differences in absolute mysid and fish abundance between years were likely due to sampling variance given that only a relatively small region of the lake was surveyed. These estimates should therefore not be extrapolated to lake-wide abundances and I present them only as a means of describing densities near the 170-m sampling station. That being said, the abundance estimates for mysids were reasonable compared to literature estimates at similar times of year (Johannsson et al. 2003). Fish density at the sampling station, however, was lower than the mean alewife density in Lake Ontario on all but one date. In 2004-2005, numbers of alewives in U.S. waters of the lake averaged 4329 $\cdot ha^{-1}$ as estimated from area swept by bottom trawls in early spring, when alewives are close to bottom (R. O'Gorman, unpublished data). The lower fish densities at the station is not surprising given that there are large differences in alewife density along the U.S. shoreline in early spring and the geographic region with peak density varies from year to year suggesting that alewives are highly mobile. Moreover, alewives move seasonally between off shore and near shore, moving near shore in spring and spawning near shore in summer.

I never found more than 10 % of the mysid population above 10^{-7} mylux, regardless of moon phase, the depth of the thermocline, or relative predator and prey abundances. These results indicate that mysids do not move into light levels higher than 10^{-7} mylux (i.e, 10^{-5} lux) even if abundant food is available in brighter light conditions. This is similar to earlier observations in Lake Ontario (Gal et al. 1999, 2004) and elsewhere (Janssen & Brandt 1980, Moen & Langeland 1989, Rudstam et al. 1989). However, mysids were found deeper (and thus at lower temperatures) on full moon nights and at slightly higher light levels than the light preference function alone would predict on nights with shallow thermoclines. Despite these substantial differences in temperature and light preference predictions on some nights, the TLM was able to predict the depth of peak mysid density to within 10 m on all sampling occasions and to within 3 m on six of the eight sampling nights. These results support the shape of the light and temperature preference functions and indicate that the model, which assumptions that light and temperature functions are independent and have equal weight, yields reasonably accurate predictions of distribution even when light and temperature functions predict peak depth distributions several meters apart.

Although I did not test the models in the winter, the ability of the TLM to predict both the range and peak depths occupied by the mysid layer across such a wide variety of environmental conditions from spring to late fall suggests that mysid distribution can be predicted based on temperature and light alone during most of the year. This result is somewhat surprising given that the light and temperature preference functions were derived based on adult mysid behavior only. Juvenile mysids are typically found higher in the water column than adults (Grossnickle & Morgan 1979, Bowers 1988, Rudstam et al. 1989), indicating that smaller mysids may have higher light and temperature tolerances than larger mysids. An alternative explanation is that the acoustic sampling procedure did not accurately detect smaller

mysids. Mysids < 7 mm made up a large proportion of the overall mysid catch in May through July 2005, suggesting a large brood release in spring 2005. Given that small mysids are relatively weak scatterers, they will contribute less to the overall mysid backscattering than adult individuals (Rudstam et al. 2008b). However, the model was able to accurately predict both the range and peak of mysid vertical distribution in Lake Ontario for most of the sampling nights analyzed, suggesting that mysid size differences may not be playing a large role in structuring the overall distribution.

There are several potential explanations as to why both growth models were not as strong predictors of mysid distribution as the TLM. First, there were no zooplankton biomass data through the peak of the mysid layer on several occasions in 2004 (August 16, August 27 and September 30, 2004) and on those sampling dates, I assumed that zooplankton biomass in the mysid layer was the same as at the deepest sampled depth of 30 m. This assumption was supported by the data collected in May, June, July and September 2005, when zooplankton was sampled down to 50 m depth (through at least 90% of the mysid layer on these nights). Even if I exclude the three profiles in 2004 for which there were no zooplankton data down to 50 m, the TLM was a better predictor of peak mysid density than either the growth or g : μ models. However, it should be noted that the observed mysid distribution in September 2004 was several meters deeper than the 50 m depth limit of the growth and g : μ model, which made it impossible to accurately predict the actual depth of peak mysid density on this date. If I assume similar low zooplankton densities past 50 m on this date (as I assumed between 30- 50 m), the model would still predict the peak of the mysid distribution to be much shallower than what was observed (Boscarino, unpubl.).

It is unlikely that zooplankton peaks in depth strata below 30 m would be significant enough to alter the predictions of the depth of maximum growth. Zooplankton densities are typically very low below the thermocline in Lake Ontario

(Johannsson et al. 1994, Gal et al. 2006) and remain at constant, low-density levels below 30 m (see Benoit et al. 2002 for discussion). Given (1) that the thermocline was shallower than 30 m in all eight profiles, and (2) the similarity in zooplankton density estimates in the 40-50-m and 30-40-m stratified net tows in 2005, I do not believe that there would have been a substantial peak in zooplankton density below 30 m that is correlated with the mysid peak; however, I cannot exclude this possibility and future investigations may provide further insight into the prevalence and importance of deep zooplankton layers on mysid behavior.

One possible explanation for why the g : μ model did not provide better predictions of mysid distribution is that predation risk may be better approximated with a reaction distance or feeding rate-based model rather than a model based on the product of predator abundance and proportion of fish feeding. Batty et al. (1990) based their estimates of the proportion of fish feeding entirely on the number of fish displaying feeding-oriented swimming behavior, and did not measure capture success or feeding rate. However, it is possible that the proportion of fish engaged in feeding-oriented swimming behavior does not translate proportionally into foraging success. For example, alewife may switch between different types of searching behaviors depending on the light level present, particularly given that alewives are capable of feeding in complete darkness using lateral line sensitivity (Janssen et al. 1995).

Another possible explanation for why the growth and g : μ models were not better predictors of mysid distribution relates to the main assumption of both models-that mysid distribution is directly proportional to growth or growth : mortality risk. Lampert et al. (2003) reported that *Daphnia pulex x galeata* were distributed vertically in experimental plankton towers in direct proportion to their growth profiles. They described the resulting distribution as approximating an ideal free distribution, given known concentrations of (and predicted gains and losses associated with) food and

temperature at 1-m depth intervals in the water column. A true ideal free distribution, however, assumes that organisms select habitats in proportion to the supply rate of resources so that each animal receives identical food resources regardless of their location. Lampert et al. (2003) argued that in filter-feeding daphnids, feeding rate is directly related to food concentration and therefore that a relatively constant food gradient (owing to daily replenishment) should mimic a constant supply rate. However, these assumptions may not hold for mysids in the same way as they do for filter-feeding daphnids.

It is important to note that I am not implying that mysid distributions are unaffected by predators and prey. These results suggest that mysid distribution is best approximated by absolute light and temperature preferences, but these preferences likely evolved as mechanisms to increase food intake during periods of low predation risk. Constantly searching for the exact optimum depth that would maximize $g : \mu$ (i.e., displaying direct responses to relative prey and predator abundances over a short time period) may be too risky for *Mysis relicta*. Mysids have slow growth rates, long generation times and low life-time fecundity which would lead to a strong selection for avoiding predators by staying in colder and darker waters. R-selected species with high clearance rates, such as daphnids, can more effectively exploit higher prey concentrations over short time periods in shallow waters and this could explain why daphnids are more plastic in their depth selection than mysids.

The ability to model entire distributions of a migrating population based on relatively simple parameters, such as light and temperature, has important ecological and management implications. The success of the TLM in predicting mysid distribution across three different seasons and two different moon phases is encouraging, and suggests that the model should be able to forecast distributional shifts resulting from long-term environmental changes such as global warming or

increased light penetration, as have been observed in Lake Ontario and other North American lakes (Anderson et al. 1996, Magnuson et al. 2000, Mills et al. 2003). Similar models have been used to forecast impacts of climate change on vertical and horizontal distributions of migrating organisms (DeStasio et al. 1996, McDonald et al. 1996, Schindler et al. 2005). Given the direct link between mysids, alewife and salmonids, the ability to predict entire distributions also has important implications for both the current and future management of salmonid fisheries in the Great Lakes and other systems that mysids and salmonids both inhabit.

This study also provides one of the first accounts of a bimodal distribution of alewives in the pelagic waters of Lake Ontario - with an upper peak that appears to coincide with the main zooplankton layer and another deeper peak which overlaps with the upper edge of the mysid layer. By extension, this study demonstrates that much of the interaction between mysids and their fish predators and zooplankton prey is occurring at the upper edge of the mysid distribution. If an assessment of the contribution of mysids to the pelagic food web were based on the "average" mysid alone, it would underestimate the significance of mysid feeding and their availability as a food resource to alewives over the deeper waters of the lake during thermal stratification.

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CHAPTER 5:

PREDATOR-PREY INTERACTIONS IN THE PELAGIA: INFLUENCE OF LIGHT ON THE FEEDING RELATIONSHIPS AND SPATIAL DISTRIBUTIONS OF ALEWIFE AND MYSIDS IN LAKE ONTARIO

ABSTRACT

Light plays a central role in determining the degree of spatial overlap between predators and prey and in influencing the foraging behaviors of predators in pelagic food webs, including relationships between the mysid shrimp, *Mysis relicta,* and alewife, *Alosa pseudoharengus* in Great Lakes ecosystems. In this study, visual pigment analyses of dark-adapted alewife were used to derive an alewife-specific unit of brightness- the "alelux" (wavelength of maximum absorbance= 505 nm)- which formed the basic unit of light intensity in feeding experiments performed with alewife at different light levels and mysid densities in the laboratory. Behavioral observations of alewives at different light intensities demonstrated that alewife can orient and strike at mysids in complete darkness, but do so along the horizontal axis only; conversely, alewives engaged in visual search and strike behaviors down to 10^{-7} alelux (~$10^{-4.1}$ lux) and attack mysids from below at an average angle of 37º to the vertical. Clearance rates of alewives were at least twice as high as those in complete darkness at light levels down to 10^{-7} alelux at densities of 100 mysids·m^{-3} or greater. Field observations from Lake Ontario showed that light levels at the upper edge of the mysid layer were within the range of those required for visual feeding in the laboratory on a full moon night, but not on a new moon night. These increased light levels translated into alewife feeding rates on mysids that were over thirty times higher on the full moon night, despite a lower degree of overlap between the two species. Predicting the effect

of increased light penetration on alewife-mysid feeding interactions requires attention to both the effect of light on alewife feeding rates and on the distributions of both species.

INTRODUCTION

The amount of light available to an organism can influence habitat selection, prey detection and the ability of prey to escape predation- all processes that influence the strength of trophic interactions in an aquatic food web. Surface light intensity changes with time of day, moon phase, and cloud cover; light intensity at depth in the water column also decreases with depth and with the degree of attenuation in the water. Many aquatic organisms have evolved unique adaptations to survive in such dynamic light environments. Diel vertical migration or alteration of swimming behavior to maximize feeding at times of day when the risk from visual predation is low is common for a variety of animals in both lakes and seas (Clark and Levy 1988; Ryer and Olla 1999). Other organisms have evolved physiological mechanisms for maximizing overall quantal catch, such as light-reflecting tapeta behind the retina or visual pigments matched to the spectral radiance of downwelling light, to enhance feeding rates and survival in low light environments (Lythgoe 1979). These adaptations to light have important implications for both the spatial and temporal dynamics of predators and prey in aquatic food webs.

Light is likely playing a central role in structuring the trophic interactions of the alewife, *Alosa pseudoharengus,* and the mysid shrimp, *Mysis relicta,* in the lower Laurentian Great Lakes of North America (Please note: the North American species has recently been renamed as *Mysis diluviana* by Audzijonyte and Väinölä (2005) and I hereafter refer to this North American species as "mysids" unless otherwise noted*)*. Mysids are a high-energy food resource thought to be important to over-winter

survival and gonad development of alewife (Arts 1999); however, mysids likely do not become available as a pelagic prey item until after dusk when mysids ascend from their daytime, benthic habitat into open waters to feed. Studies comparing diet contents of alewife caught at night with those caught during the day suggest that alewife are capable of exploiting mysids only between the dusk to dawn hours when mysids become pelagic (Beeton 1960; Janssen and Brandt 1980) and that the depth of the main alewife-mysid interface will vary with the amount of light entering the water column at any given time. For example, Janssen and Brandt (1980) reported that alewife-mysid feeding interactions were occurring deeper in the water column on full moon relative to new moon nights, but did not explore how the different moon phases impacted the degree of spatial overlap of the two trophic levels.

In addition to influencing the spatial dynamics of alewife-mysid trophic interactions, light may also affect the feeding rates and behaviors of alewife at night. Alewife cannot filter-feed on mysids, but instead employ an active "darting" technique described in detail by Janssen (1978). This type of feeding behavior was originally deemed to be a vision-oriented method of capture (Janssen 1976, 1978) and whether alewife engage in darting behavior to capture mysids at night (when light levels at the mysid-alewife interface are much lower than those tested by Janssen 1978) is still unknown. Janssen et al. (1995) demonstrated that alewives are capable of feeding on *Artemia* spp. in complete darkness via. lateral line sensitivity in the laboratory, although *Artemia* has a weaker escape response than *Mysis* spp. (Drenner et al. 1978; Viitasalo and Rautio 1998). It is still unknown if alewife can capture mysids in total darkness and to what degree the limited light levels present at the mysid layer are sufficient to increase alewife capture efficiency on mysids.

Experiments with other clupeids suggest that the light intensity necessary for visual feeding is at least ten times greater than the light level likely to be experienced

by alewife feeding within the mysid layer. For example, Batty et al. (1990) found that the Atlantic herring, *Clupea harengus,* ceased particulate feeding at a light level of 0.001 lux when fed a natural assemblage of zooplankton; however, when fed *Artemia* nauplii*,* the visual threshold was even greater (~0.01 lux)- a value which is over two orders of magnitude brighter than the 10^{-4} lux that limits mysid ascent (Gal et al. 2004; Chapter 2, 4). Given that mysids are over ten times larger than most other pelagic zooplankton prey of alewife in northern lakes the light level required for visual feeding may be lower for alewife feeding on mysids than on zooplankton such as copepods and cladocerans.

Furthermore, the light level thresholds reported by Batty et al. (1990) were recorded with a microphotometer designed to measure light in photopic lux. Lux is a unit of measure based on the absorption characteristics of visual pigments in the human eye; however, the spectral sensitivities of humans and alewife are likely to be different, as they have evolved in very different environments and were shaped by unique selection pressures. Thus, measuring light in lux is not the most appropriate method of quantifying the amount of light perceived by an alewife eye. Secondly, clupeids likely do not use photopic vision to feed at night, but instead use scotopic vision (via. absorption of light through rod visual pigments) to capture the small amount of light available at night. Therefore, an alewife-specific photometer that accounts for the scotopic spectral sensitivity of the alewife eye to different wavelengths of light is required in order to accurately convey the amount of light available to alewife for feeding. Similar species-specific photometers have been constructed for a number of aquatic organisms (e.g., Widder and Frank 2001; Cohen and Forward 2005) by placing a set of filters that closely matches the spectral sensitivity curve of the organism of interest in front of a light-recording device.

This study is designed to investigate the effect of light on alewife-mysid trophic interactions and to determine whether alewife use vision to enhance feeding rates on mysids at night. Since alewife foraging success depends on the encounter rate with potential prey, the prey density, and the amount of light available for feeding at any given depth, information is necessary on all of the following to determine the degree to which alewife use vision to enhance feeding rates on mysids: (1) the absorbance characteristics of alewife rod visual pigments, (2) fish feeding behavior and capture success at different light levels and mysid densities, and (3) light's effect on the vertical distribution of both mysids and alewife. Spectral sensitivity analyses of alewife visual pigments are combined with behavioral experiments of fish feeding at different alewife-specific light levels and mysid densities and with vertical distribution and gut content analyses of alewife caught on both a new moon and full moon night (representing both extremes of light conditions) in August, 2004 in Lake Ontario. I hypothesize that alewife use vision to enhance their feeding rates on mysids and, therefore, feeding rates on mysids will increase with increasing light intensity. The alternative is that alewife primarily use other senses, such as the lateral line or olfaction, to feed on mysids and that feeding rates are not affected by changes in light intensity. I also hypothesize that the distribution of both alewife and mysids are influenced by ambient light conditions, and that the degree of spatial overlap between the two trophic levels will vary with light intensity. I propose that a combination of changes in feeding rates and distributions associated with different light conditions will lead to changes in the availability of mysids to alewife as a function of moon phase. The combined physiological, experimental and field data presented in this study may be used to predict the seasonal dynamics of alewife-mysid interactions under past, current or future light regimes in deepwater systems that are inhabited by both alewife and mysids.

MATERIALS AND METHODS

Collection and maintenance of experimental alewives and mysids

Alewives collected for use in the feeding experiments were caught with a beach seine (38 m by 3 m, 0.25 inch stretch mesh) off the shore of Meyers Point on Cayuga Lake, New York on June 13, 2006- a time when adult alewives are abundant in the nearshore of the lake (Klumb et al. 2003). Cayuga Lake is a deep, mesotrophic lake in the Finger Lakes region of New York State. Fish were transferred into an aerated 800-L round, fiberglass tank filled with 20°C lake water. These tanks were held at a conductivity level of 1500 $\mu S\ cm^{-1}$ and were treated with Proline™ defoamer. Such conditions have been shown to decrease the stress levels of alewife immediately following capture and during transportation back to the laboratory (Lepak et al. 2008).

Upon arrival to the Cornell Biological Field Station's laboratory facilities, alewife were transferred to another 800-L stock tank, which was maintained between 1500 and 1800 $\mu S \cdot cm^{-1}$ until the end of the feeding experiments. Conductivity levels were maintained through use of a peristaltic pump (MityFlex® 14-rpm Peristaltic Pump, Anko Products, Inc.) that delivered the appropriate concentration of saltwater at regular intervals to the stock tank. A steady flow of freshwater was also added to help control any buildup of urea and other nitrogenous wastes in the stock tank. Ammonia levels were monitored on a daily basis in addition to salinity levels and temperatures. Stock tanks were cleaned with a siphon on a daily basis to remove any feces that had accumulated on the bottom of the tank.

A total of 234 alewife were held in these tanks on a 13h : 11h light : dark photoperiod through to the end of the feeding experiments on December 15, 2005. Fish were inspected daily for signs of disease or abnormal behaviors; mortality levels were very low during this time period (<3%). Fish were fed Hikari® fish fry plankton

(0.37-.61 mm) at hourly intervals through the use of an automatic fish feeder (AF6 Fish Feeder, Sweeney Enterprises, Inc.©)

Mysids used as prey in the fish feeding experiments were collected with vertical net hauls (1-m diameter, 1-mm mesh) at a 70-m site on Cayuga Lake, NY. Mysids were immediately placed into light-proofed coolers and transported back to the Cornell Biological Field Station where they were held at 12°C prior to experimentation. Mysids were fed *ad libitum* densities of Cyclop-eez® and all feeding and handling of mysids were done in infrared or far-red light (mysids are not sensitive to these wavelengths- Gal et al. 1999) to ensure that mysids were not blinded when placed into the alewife feeding experiments.

Spectral Sensitivity Analyses

Three adult alewife were selected, at random, from the 800-L stock tanks for microspectrophotometric (MSP) examination. These fish were placed into opaque bags and were transported to the Department of Biomedical Sciences at Cornell University where they were held in the dark for a minimum of 4 hours to complete dark adaptation.

The dark-adapted fish were euthanized with MS-222 and rapidly enucleated under dim red light. All further isolation and preparation was done using a dissecting scope equipped with infrared illuminators and image converters. The eyes were hemisected and the retinas isolated from the posterior segment under PBS (pH 7.4) supplemented with 6% sucrose. Small pieces of isolated retina were transferred in buffer to cover slips, cut and teased with #11 scalpel blades, and sandwiched with another cover slip edged with silicone vacuum grease.

The computer-controlled, single-beam MSP has been previously described (Loew 1994). Absorbance was measured at 1 nm intervals from 750 nm to 350 nm with a return scan done to confirm that there had not been significant bleaching during

measurement. Since only scotopic spectral sensitivity was of interest, only rod photoreceptors were measured.

Using the results from the MSP analyses, a photometer was constructed that measured the brightness of the environment as perceived by the alewife eye. Following the approach of Widder and Frank (2001), a filter was inserted in front of a radiometer (International Light® light meter, Model IL1400A) that mimicked the absorbance properties of the visual pigment of an alewife. Hereafter, I refer to all light levels as perceived by the alewife eye in units of "alelux" (see below).

Derivation of "alelux" units

Researchers interested in using alelux units in field applications can use the following conversions, specific to the relative spectral output of moonlight at the surface of the water (Gal et al. 1999): 1 $W \cdot m^{-2}$ = 0.424 alelux = 343 lux = 1.96 mylux (the mysid-specific unit of brightness derived by Gal et al. 1999) over a wavelength range of 400-700 nm. Note that these conversions will change with depth since the spectral distribution of light changes with depth due to differences in wavelength-specific attenuation. Therefore, using these conversions below the surface will only be approximate for comparison with other studies in which the spectral distribution of light is unavailable. If the spectral distribution of light is known or can be estimated, these units can be calculated absolutely at any depth with the following equations:

(5.1) $$W \cdot m^{-2} = \int_{400}^{700} W(\lambda) \cdot d\lambda$$

(5.2) $$\text{Alelux} = \int_{400}^{700} Y_a(\lambda) \cdot W(\lambda) \cdot d\lambda$$

(5.3) $$\text{Lux} = 683 \int_{400}^{700} Y_l(\lambda) \cdot W(\lambda) \cdot d\lambda$$

where $W(\lambda)$ is irradiance, in $W \cdot m^{-2}$, as a function of wavelength of light, λ (nm, from Gal et al. 1999). If a source other than moonlight is of more interest to the researcher (such as that of a slide projector, sunlight or starlight), these units can still be derived by substituting this source's spectral irradiance for $W(\lambda)$. $Y_a(\lambda)$ represents the value of the normalized alewife visual spectrum (range 0 to 1), as a function of wavelength, evaluated at 10 nm intervals (see *Results: Microspectrophotometry* and Fig. 5.1 for these values). $Y_l(\lambda)$ is the value of the luminosity coefficient of the standard CIE photopic curve with $Y_l(555\text{ nm}) = 1$ (wavelength of maximum absorption, $\lambda_{max} = 555$ nm in Eq. 5.3, see Williamson and Cummins 1983). The constant in front of the photopic lux curve represents the absolute value of luminous efficacy (683 $lumens \cdot watt^{-1}$) at $\lambda_{max} = 555$ nm (Williamson and Cummins 1983). Since the absolute value of luminous efficacy at λ_{max} is not known for alewife, I set the value of this constant to equal one in Eq. 5.2.

This method of deriving the alelux represents a modification of the Gal et al. (1999) conversions used to derive the similar "mylux" units for *M. relicta,* which was based on the absorbance properties of the mysid visual pigment. Gal et al. (1999) defined one mylux as the total irradiance perceived by a mysid after 1 $W \cdot m^{-2}$ of moonlight irradiance, integrated over wavelength range of 400-650 nm, had passed through a mysid eye pigment (which translated into1 mylux = 0.51 $W \cdot m^{-2}$). I modified this definition so that alelux could be directly reported as the amount of total radiant light available to alewife after having passed through an alewife visual pigment. If this definition was applied to mysids, then 1 $W \cdot m^{-2}$ of available light would be equivalent to 0.51 "mylux". Thus, unlike the definition of Gal et al. (1999) the mylux value would always have a smaller absolute value than the corresponding $W \cdot m^{-2}$ value.

I made this modification to the former procedure used to derive the mylux unit for ease of use in future field applications. As defined in this study, researchers can now calculate alelux in one of two ways: (1) by applying Eq. 5.2 given the spectral irradiance of the light source and absorbance properties of the alewife visual pigment, or (2) by measuring alelux directly by placing a Rosco® Roscolux® filter, #91 in front of the light meter. In the latter case, the light values that are obtained after having passed through the "alelux filter" can be reported directly in alelux units, after applying slight correction factors for the transparency and absorbance properties of the filter paper (see the *Results: Visual pigment analysis* section below).

Alewife feeding experiments

Alewife selected for use in the feeding experiments were removed from the stock tanks and placed into round, 100-L polypropylene tanks in a 14°C, temperature controlled room. Round tanks were used for experimentation to ensure that there were no "corner" effects on clearance rates. Tanks were chosen such that they were taller (1 m) than they were wide (0.5 m) to increase the probability of mysids being found in the upper region of the tanks, as mysids respond to kairomones by choosing depths farthest from alewife (Boscarino et al. 2007). Exploratory trials confirmed that alewife consistently swam in the bottom of these tanks, and mysids were frequently found in the upper half of the tanks.

Three alewives were placed into each tank and six tanks were used in each trial. A trial was defined as a light level treatment administered concurrently to a set of six experimental tanks. No significant tank effects with regard to fish behavior were noted throughout the experiments and therefore each tank was assumed to be a replicate. Light level treatments were selected based on preliminary field sampling and extrapolation of light levels at the depth of the mysid layer based on surface light readings and wavelength-specific attenuation coefficients (see Table 4.2 in Chapter 4).

Eight different light level treatments were administered to the tanks, including one completely dark condition, which served as a control against which the proportion of mysids eaten at other light levels was tested.

Light was delivered to each of the experimental tanks from a diffuse light source (120 V, 1 Watt LED bulb, EliteLED.com) which transmitted light primarily within the green portion of the visual spectrum (range = 480 -570 nm, λ_{max} = 525). The alewife-specific photometer (see above) was placed near the bottom of each of the tanks to record light intensity in alelux both before and after each trial. Since the variance in light levels between each of the six tanks was low (<5%), I assumed that each was exposed to the same light level for each trial. Light level treatments were controlled through the addition of different combinations of fabric that served as neutral density filters. The overall attenuation of each of the fabrics was quantified prior to experimentation and later tested at the end of the clearance rate experiments to ensure that the attenuation properties of the fabric remained the same over the course of the experiment.

Feeding experiments were run at a high (300 mysids·m^{-3}), medium (100 mysids·m^{-3}) and low (40 mysids·m^{-3}) mysid density treatment which equated to 30, 10 and 4 mysids·$100L^{-1}$ tank, respectively. The size of mysids used in the feeding experiments ranged from 5-15 mm and were selected at random from the stock mysid aquarium.

Feeding experiments were run for a total of three hours. At the end of this time period, alewives were taken out of the tank and the water strained through a 1-mm mesh net to collect any remaining mysids. Tanks were selected at random in all three mysid density treatments for gut content analysis to confirm that the above procedure was correctly accounting for the proportion of mysids eaten in a given trial. In all

cases (n = 12), the number of mysids missing from the tanks were accounted for in the stomachs of alewife.

The proportion of mysids eaten per tank and clearance rate (m^3 cleared·$fish^{-1}$·hr^{-1}) in each tank were calculated for each 3-hr trial period. I assumed that all three alewife were feeding at equal rates and cleared a constant proportion of the mysids available in the tank over a three hour time interval. Clearance rate (CR) was calculated based on the following relationship:

(5.4) $CR = (\ln(N_o) - \ln(N_t))\cdot t^{-1} \cdot fish^{-1} \cdot v$ (Wetzel & Likens 2000)

where v represents the volume of water of the experimental tanks (0.1 m^3), and N_o and N_t represent the number of mysids introduced at time t = 0 and the number of mysids remaining at time, t = 3 hrs (feeding trial length), respectively.

Calculation of alewife clearance rates

Results from the feeding experiments were used to derive an equation relating the effect of mysid density and light level on the clearance rate (*CR,* in $m^3 \cdot fish^{-1} \cdot hr^{-1}$) of alewife in the field. This function will also vary with depth, *z*, and time, *t,* because light levels vary with depth and time. Input variables for the clearance rate function were light level (*L*, in alelux) and mysid density (*D,* in individuals·m^{-3}). I also evaluated the effect of a light-density interaction term. Therefore, the clearance rate given known light levels and densities of mysids equals:

(5.5) $CR(L, D) = c + \alpha \cdot L + \beta \cdot D + \gamma \cdot L \cdot D$

where c is the intercept coefficient, α, β and γ are regression coefficients for light level, mysid density and light level-mysid density interaction, respectively.

Significance of all regression coefficients and relationships were performed using multiple regression analysis in Microsoft Excel Version 12.0.

Behavioral observations

In addition to the above alewife feeding experiments, I video taped an additional set of feeding trials at five different light levels (10^{-2}, 10^{-6}, 10^{-7}, 10^{-8} alelux and complete darkness- i.e., infrared light) to provide insight into the feeding behavior of alewife. Each light level treatment was taped both with and without mysids present to better elucidate differences in predator behavior with and without prey. All taped trials were run with three alewife in a 0.5 m^3, rectangular aquarium. The aquarium was fitted with white sheets of PVC on three of the four sides to maximize the contrast between the alewife and the background of the aquarium. All taped trials were conducted at a mysid density of 100 mysids$\cdot m^{-3}$ and filmed horizontally with an infrared-sensitive camera (Sony Digital Handycam®, Model TRV18) mounted approximately 5 m from the aquarium. Each trial was conducted over a 45-min. time period.

I was not present in the room at the time of videotaping to minimize disturbance and quantified feeding behaviors on a television with a videocassette recorder after the trials had finished. Janssen et al. (1976, 1978) provides a comprehensive description of the range of feeding behaviors employed by alewives and I used his description as a basis for the analyses of alewife feeding on mysids. Since alewife are constantly moving in the water column, it is difficult to determine when the fish has actually "located" the prey, rendering estimates of reaction distance subject to judgment error (Janssen pers. observation). Therefore, as an alternative to measuring reaction distance, I measured the total number of attacks and number of successful prey captures to quantify how well alewife are sensing and capturing their prey at different light levels. Hence, analysis of video observations and gut contents

yielded the following statistics for all treatments: (1) total number of strikes, (2) total number of captures (determined by gut content analyses), (3) percent of attacks that led to successful capture and (4) angle of strike. Percent of attacks leading to capture was determined by dividing the total number of mysids found in the stomachs of the fish at the end of the 45-min trial by the total number of strikes observed from the tape at each light level. Strike angles were determined by pausing the videotape during the strike and measuring the body angle with a protractor in relation to the vertical (after Janssen 1981). Preliminary analyses of videotape indicate that body angle acted as a direct measure of swimming angle, or angle of attack. I also made note of more general observations of swimming/search behavior to determine how other aspects of predator behavior may have varied between trials. All tape analysis was performed blind (I recorded all strike and capture data without prior knowledge of the light treatment) so as not to bias the data analysis. Only one video trial was recorded for each of the different five light treatments.

Field sampling and analyses

Two sampling cruises on Lake Ontario on August 16, 2004 (new moon) and August 27, 2004 (full moon) were conducted to investigate the effect of moon phase on the degree of spatial overlap between mysids and alewife and the prevalence of mysids in the stomachs of alewife. The data for these two field profiles were collected at a 170-m deep site several kilometers offshore of Oswego, New York (43ºN 33.220', 76 ^{o}W 34.849') and represent a subset of a larger spatial modeling project of alewife and mysids for the offshore of Lake Ontario conducted between 2004-2005, the methods of which are described in detail in Chapter 4.

Depth-specific light and temperature data were collected on both nights with a SeaBird profiler lowered to a few meters above the lake bottom. The normalized alewife visual spectrum (Fig. 5.1) was applied to the spectra available between 400

and 700 nm (in $W \cdot m^{-2}$) for each depth and wavelength to calculate alelux at depth (see *Derivation of alelux units* above). Wavelength-specific attenuation was accounted for by applying the equations of Jerome et al. (1983) (see Chapters 2,4).

Mysid and fish vertical distributions for both August nights were measured with a 70-kHz (Simrad EY500, 11.4º beam width, split beam) and a 430-kHz (Biosonics DtX, 7.8º beam width, single beam) hydroacoustics units, both operating at 0.6 ms pulse length, and 1 ping s^{-1}. Data was collected while in transit from a 100-m to 170-m bottom depth station. The Simrad unit was calibrated before the survey with a standard -39.2dB copper sphere. The Biosonics unit was calibrated by the manufacturer in the spring of 2004 and 2005 with only small differences in calibration constants (+/- 0.1 dB). Here I used the calibration constants from 2004. Mysids and fish were separated using a threshold of -60 dB at 70kHz; all fish targets were removed from the 430 kHz data using the methods in Rudstam et al. (2008a). Mysid distributions were based on the 430 kHz data after removal of backscattering from fish and noise. Noise was measured *in situ* and removed by subtraction (Korneliussen 2000). The depth limit for detection of a density of 5 mysids m^{-3} was calculated from an assumed TS of a single mysid of -80.1 dB (Rudstam et al. 2008b), ambient sound absorption and noise level. Fish distributions were obtained from the 70 kHz data following the standard operating procedure for Great Lakes (Rudstam et al. 2009). In this region of Lake Ontario, a -60dB threshold in the uncompensated TS domain excludes most backscattering from mysids and zooplankton (Rudstam et al. 2008a). Fish density at depth was obtained by scaling the volume backscattering coefficient with the *in situ* target strength calculated separately for the epilimnion and meta-/hypolimnion. Depth-specific density estimates were made from 2 m from the transducer face down to the acoustic detection limit. Total mysid and fish abundances were also based on acoustic analyses and represent the total abundance summed from

the surface down to the acoustics detection limit. More details on acoustic analyses can be found in Chapter 4.

The degree of spatial overlap between fish and mysids on the two sampling nights were compared using the Czekanowski index of overlap ($\left| 1-(0.5 \cdot \Sigma(M_i - F_i) \right| \cdot 100$, Feinsinger et al. 1981), where M_i and F_i represent the relative mysid and fish density value at depth i, respectively, evaluated at 1-m depth intervals from the surface to the maximum depth of detection (z_{max}). I define the upper edge of the mysid layer as the depth associated with the upper 10% of the peak of the mysid distribution.

Fish were collected for species identification and gut content analyses by setting mid-water gillnets between 15-35 m on both nights. Decisions on the depth of set were made prior to each sampling night and were based on the depth of the water column expected to be inhabited by mysids. Each gillnet set consisted of seven different 3-m wide by 20-m deep nets, each with a different mesh size (6.25, 8, 10, 12.5, 15, 18.5 and 25 mm bar measure). This set should capture alewife between 50 and 250 mm (Warner et al. 2002). Gillnets were set before dusk and retrieved at 0200 the next morning on both sampling dates. Total catch was recorded in terms of number of fish caught per hour sampled. Fish were immediately flash frozen on dry ice after gillnets were pulled in to preserve gut contents. All fish caught in gillnets were analyzed for presence/absence of mysids as well as the number of mysids per stomach at the Cornell Biological Field Station. Proportion of alewife with mysids in their stomachs and number of mysids per stomach per hour were both used as the basis for comparing capture success of fish on the new moon versus the full moon night and for comparing with model predictions of feeding rate (see below).

Model predictions

The alewife clearance rate function was used to make predictions of alewife feeding rate on each of the sampling nights and to compare to gut contents of alewives

caught in the gillnets. The predicted number of mysids eaten by one alewife at each depth was calculated as clearance rate (Eq. 5.5) multiplied by mysid density (ind.·m^{-3}) at depth, as determined by acoustic sampling of the water column (see above). These predicted feeding rates on each night were averaged across the depth interval of the gillnet sets (15-35 m) to arrive at an overall feeding rate that would be directly comparable to those derived from the gillnet catch (observed feeding rates are reported as the average number of mysids·$fish^{-1}$·hr^{-1} on each of the nights).

A second, modified feeding rate model was also run to evaluate the influence of predator distribution on the clearance rates of mysids. This "predator-modified" feeding rate model was calculated by multiplying each depth-specific predicted feeding rate (Eq. 5.5) by the value of the relative density distribution of alewife between 15-35 m at the time of acoustic sampling. Hereafter, I refer to this form of the model as the predator-adjusted feeding rate model and the former model (Eq. 5.5) as the alewife feeding rate model.

Model assumptions

Feeding hours were counted from the end of civil twilight to the time in which the nets were retrieved (which equated to 5.3 hrs. on the new moon night and 5.6 hrs. on the full moon night). The model therefore assumes that mysids do not become available to alewife until the end of civil twilight and that the mysid distribution remained the same as at the time of acoustic sampling. Both of these assumptions are consistent with acoustic observations at other times of day on both of these sampling occasions (Boscarino, unpubl.).

The model also assumes that the light level impinging upon the water column (which is reported as the light level at the time of acoustic sampling) remained the same throughout the course of the night; however, light levels will change slightly due to differences in cloud cover or moon altitude during different periods of the night.

That being said, these differences in surface light due to moon altitude varied less than a factor of five throughout the hours of the gillnet set on the full moon night and even less on the new moon night (Janiczek and DeYoung 1987). Given the log-scale of the model applications presented in this study, these slight differences in surface intensity will not equate to large changes in predicted feeding rates at the depth of the mysid layer.

RESULTS

Visual pigment analysis

Only a single vitamin A_1–based pigment was found in all alewife eyes examined with a peak absorbance, λ_{max}, at 505 nm (Fig. 5.1). The smoothed, normalized visual pigment data were used to select a filter (Rosco® Roscolux® filter # 91, peak transmission, λ_{max}, = 510 nm) that closely resembled the absorbance characteristics of the alewife visual pigment. There were some differences between the absorbance characteristics of this filter and the alewife visual pigment (Fig. 5.1), and thus a correction factor of 8.75 (factor of 5 to adjust for transmission properties of the filter multiplied by 1.75 to adjust for differences in breadth and λ_{max}) was applied to all measurements obtained with the light meter in the laboratory to arrive at the filtered alelux units discussed in the methods. This correction factor is specific for the green LED light source described in the methods. No correction factor was necessary for all light levels estimated in the field as these were done theoretically according to Equations 5.1-5.3 and not measured *in situ* with the photometer. The respective visual spectrum curves for alewife, mysids and humans are compared in Fig. 5.1.

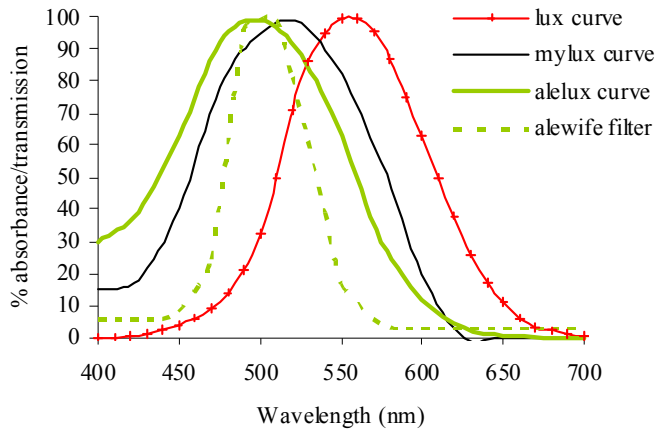

Figure 5.1. Absorbance characteristics of the visual pigment of *Alosa pseudoharengus* (alelux curve) and the transmission properties of the filter used in the alewife-specific photometer in comparison to the human photopic visual spectrum (lux curve) and the mysid visual spectrum (mylux curve- e.g., Gal et al. 1999). Percent absorbance represents the relative probability (in percentage) of photon absorption at a given wavelength (spectrum normalized to range between 0 and 100). Percent transmission represents the probability of a photon of light at that wavelength passing through the filter. Please note that percent transmission values were multiplied by 5 for the alewife filter curve, as the filter allows only 20% transmission at its peak transmission.

Alewife feeding experiments

The clearance rate of alewives feeding and the proportion of mysids eaten in a trial generally declined as light levels decreased; however, feeding did not cease entirely under completely dark conditions (Fig. 5.2), indicating that alewives can use other senses besides vision to feed on mysids. While there was no significant effect of mysid density on clearance rate in the dark, I found that at least one mysid was consumed in the dark at the highest mysid density treatment (300 mysids·m^{-3}) whereas this happened in only 33% and 25% of the dark trials at the medium (100 mysids·m^{-3}) and low (40 mysids·m^{-3}) density treatments, respectively.

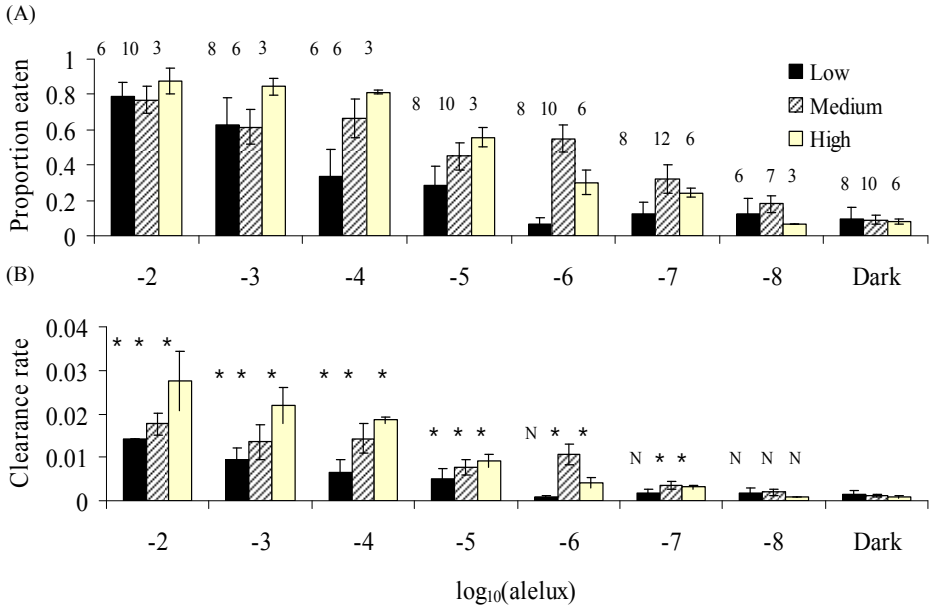

Figure 5.2. Mean proportion of mysids consumed (A) and clearance rates (m^{-3}·$fish^{-1}$·$hr.^{-1}$) (B) of alewife at different light intensities and mysid densities. All trials are 3 hrs in length without replacement of prey items. A star indicates that the clearance rate was at least two times higher than in complete darkness for that particular mysid density treatment; "N" indicates the difference was less than a factor of two. The number of replicates is shown above each mean proportion. Low, medium and high density treatments are at a 40, 100 and 300 mysid·m^{-3} density.

Under simulated dusk to full moon light conditions at the surface of the lake (10^{-2} to 10^{-4} alelux), mean clearance rates remained above 0.02 m^3·$fish^{-1}$·$hr.^{-1}$ at the highest mysid density treatment (Fig. 5.2B), which equated to over 80% of the mysids originally introduced into the tanks (Fig. 5.2A). The mean clearance rate was lower at densities of 100 mysids·m^{-3} and 40 mysids·m^{-3} (0.015 and 0.010 m^3·$fish^{-1}$·$hr.^{-1}$, respectively) over this same light treatment interval (Fig. 5.2B). Clearance rates increased with mysid density between light levels of 10^{-2} to 10^{-5} alelux but showed no consistent pattern in light levels lower than 10^{-5} alelux (see Discussion).

I defined the threshold for visual feeding for each density treatment as the light level at which mean clearance rates were doubled relative to completely dark

conditions. This threshold for the high and medium mysid density treatments occurred at 10^{-7} alelux - a light intensity close to that experienced by alewife at the upper edge of the mysid scattering layer on a full moon night in Lake Ontario (Chapter 2). Clearance rates at 10^{-8} alelux were less than a factor of two greater than in complete darkness for all three density treatments. The visual feeding threshold was 10^{-3} alelux as mysid density decreased to 40 mysids·m^{-3}.

Results from the feeding experiments were used to derive a predictive model of alewife feeding rates in the field given input parameters of mysid density (*D,* in mysids·m^{-3}*)* light level, (*L* in alelux) and light level-density interaction at any given time, *t,* and depth in the water column, *z* (see Eq. 5.5). Both the response variable, clearance rate (*CR,* in m^{-3}·$fish^{-1}$·$hr.^{-1}$*),* and the predictor variable, *L*, were $\log_{10}$-transformed to equalize variance and ensure normality of the residuals. When the full model was run, all predictors were significant at the $\alpha = 0.05$ level (Table 5.1) and can be summarized by the following equation:

(5.6) $\log CR\ (L, D) = -1.83 + 0.11 \cdot \log L + 0.0030 \cdot D + 0.00043 \cdot \log L \cdot D$

$r^2 = 0.70$; Microsoft Excel, Version 12.0

Behavioral observations

Strike frequency and capture success varied significantly across light level treatments (Table 5.2). I observed 3, 1, 28, 24 and 20 strikes per trial for the dark, 10^{-8} alelux, 10^{-7} alelux, 10^{-6} alelux and 10^{-2} alelux trials, respectively. Out of these strikes, the highest capture success occurred in the 10^{-2} alelux trial (90% of observed strikes led to successful captures), followed by 83% and 61% for the 10^{-6} alelux and 10^{-7} alelux trials, respectively. No successful captures were recorded in the 10^{-8} alelux and dark trials.

Table 5.1. Multiple regression analysis of the response variable, $\log_{10}$ (clearance rate), in $m^3 \cdot fish^{-1} \cdot hour^{-1}$ against predictor variables mysid density ($mysids \cdot m^{-3}$) and $\log_{10}$ (light level), in units of alelux. Clearance rates were log-transformed to equalize variance across treatments.

ANOVA					
	Df	*SS*	*MS*	*F-stat*	*F significance*
Regression	3	14.96	4.99	42.97	1.60E-19
Residual	134	15.56	0.12		
Total	137	30.52			
	Coefficients	*SE*	*t-stat*	*P-value*	
Intercept	-1.83	0.13	-14.17	<0.0001	
log (light)	0.11	0.024	4.68	<0.0001	
density	0.003	0.0009	3.39	0.00093	
interaction	0.00043	0.00016	2.64	0.0093	

Alewife swimming and search behaviors in the feeding trials also varied significantly depending on the amount of light available in the tank (Table 5.2). Alewife in both the dark and the 10^{-8} alelux trials tended to stay near the bottom of the tank, while alewife in the higher light level trials ventured more into "open" waters to search for food. I stopped the video tape at regular 2 minute intervals to observe alewife position in the water column and noted that >90% of observations of alewife were in the lower half of the tank in both the 10^{-8} alelux and completely dark trials relative to an average of 82%, 76% and 63% in the 10^{-7} alelux, 10^{-6} alelux, 10^{-2} alelux trials, respectively. In addition, alewives in darker trials were almost always found swimming in a horizontal position and displayed lower activity levels than those fish swimming in higher light conditions (Boscarino, pers. obs.). Fish tended to slowly flick their tails to maintain approximately the same depth every 2-3 seconds in the two darkest treatments. In the 10^{-2} alelux trials, fish were swimming more rapidly,

regularly moving between the lower and upper half of the tank with stronger, more frequent tail movements.

Table 5.2: Behavioral observations of alewife feeding on mysids. Trials were run in 0.5 m^3 tanks at a prey density of 100 mysids·m^{-3} of water. Number of strikes and captures are based on one taped 45-min. trial for each light treatment. Each trial had three alewife in a tank. Point of attack refers to the position of the fish in the tanks relative to the prey prior to a strike. Mean attack angles are reported in degrees from the vertical. Percent presence in bottom half refers to the percent of total recorded observations of fish in which the fish was located in the bottom half of the tank.

	Light treatment (alelux)				
	10^{-2}	10^{-6}	10^{-7}	10^{-8}	Dark
No. strikes	20	24	28	1	3
No. captures	18	20	17	0	0
Capture success	90%	83%	61%	0%	0%
Coasting?	Yes	Yes	Yes	No	No
Point of attack	From below	From below	From below	From below (straight up)	Horizontal
Attack angle from vertical	36º	37º	38º	0 º	90 º
Percent presence in bottom half	63%	76%	82%	95%	93%

Alewives in the highest light level treatment of 10^{-2} alelux were commonly found coasting at a tilt of approximately 70º to the vertical. When tilted at the 70º orientation, the fish ceased flicking its tail and seemed actively engaged in prey searching above them, as evidenced by movement of their eyes towards the top of the tank- presumably to locate prey swimming above them. I hereafter refer to this type of prey search behavior as "coasting"- a behavior which was not evident in any trials in which mysids were absent, indicating that the behavior was prey-induced. Coasting

was also apparent in the 10^{-6} alelux and 10^{-7} alelux trials but ceased altogether in the 10^{-8} alelux and dark trials, suggesting that these light levels are too low to elicit the same type of prey searching behavior seen in the higher light trials.

Strike behavior also varied with light level (Table 5.2). For all light level trials of 10^{-7} alelux and greater, I observed a strike sequence similar to that described by Janssen (1978): (1) coasting (i.e., cessation of tail flick and "faster" horizontal movement, followed by adoption of the 70º tilt to the vertical), (2) quick "dart" toward prey located above the fish in the water. All strikes at these light levels occurred from below- a fish never attacked a prey item that was below it in the water column. In greater than 90% of all strikes, the "dart" was made between an angle of 30-40º to the vertical (median angle = 37º). This angle of strike was consistent across all light level treatments greater than or equal to 10^{-7} alelux. This strike behavior sequence was never noted in any trials in which mysids were absent.

Strike behavior changed markedly in the dark trial (Table 5.2). Out of the three strikes recorded in the dark, all were made entirely along the horizontal plane - never from below. In the 10^{-8} alelux trial, I only recorded one strike- which was made at an angle almost completely perpendicular to the horizontal (straight up). In general, fish preferred to swim along the longitudinal axis and in the center of the tank, avoiding most corners, and I therefore believe that the angle approximations are not biased by fish striking at angles away or towards the camera (see Janssen 1981 for discussion).

Field applications: Mysid and fish vertical distributions

Temperature conditions on the two nights were nearly identical- surface temperature was ~21ºC on both nights and the thermocline (defined as the depth at which the temperature change per meter was maximized) was only 2 m deeper on the full moon night (21 m) than the new moon night (19 m) (Fig. 5.3).

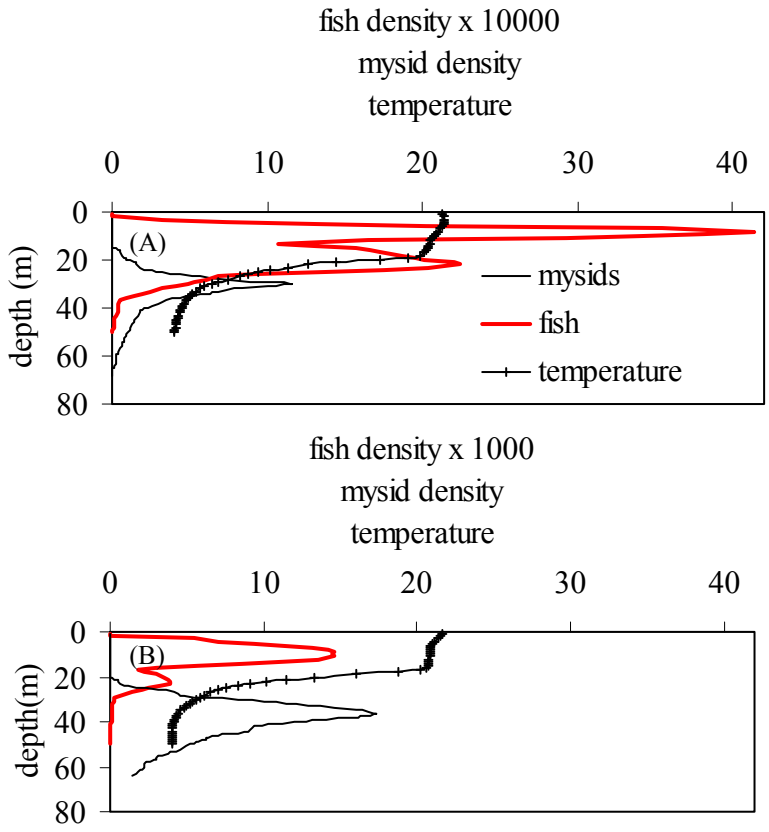

Figure 5.3. Mysid and fish vertical distribution on a new moon night on August 16, 2004 (A) and a full moon night on August 27, 2004 (B). Mysids were found deeper in the water column on the full moon night, but a larger proportion of the total fish abundance was found deeper on the new moon night. Mysid and fish densities are reported in no.·m^{-3}. Please note the different scales on the x-axis for each panel. Gillnets were set between 15 – 35 m (dotted rectangle) and sampling revealed that the majority of fish present were alewife. Temperature (ºC) conditions were similar on both nights.

Average k_{PAR} down to 20 m (see Chapter 4) was 0.32 on the new moon night (August 16) versus 0.24 on the full moon night (August 27). Light levels at the surface of the water were almost two orders of magnitude greater on the full moon night than the new moon night (Table 5.3). Differences in k_{PAR} and surface light conditions contributed to higher light levels penetrating deeper into the water column on the full moon night.

Table 5.3: Environmental conditions and observed versus predicted feeding rates (mysids·fish^{-1}·hr^{-1}) of alewife for both sampling nights on Lake Ontario. Light levels are reported in alelux. Light at peak and upper edge refer to the light conditions at the depth of maximum mysid density and at the depth of the upper 10% of the peak of the mysid distribution. Mysid and fish density represent the mean density (no.·m^{-3}) across the depth range of 15-35 m, or the depth of the gillnet sets. Predictions of feeding rate (unadjusted) were made based on the model presented in Eq. 5.6 and the feeding rates (predator adjusted) account for the relative distribution of alewife in the water column at the time of acoustic sampling. Observed feeding rates are based on gut contents of alewife caught with the gillnets. % overlap was calculated using Czekanowski's index.

	August 16, 2004	August 27, 2004
Moon phase	New	Full
Light at surface	$9 \cdot 10^{-7}$	$4 \cdot 10^{-5}$
Light at upper edge (depth)	$5 \cdot 10^{-9}$ (21 m)	$1 \cdot 10^{-7}$ (27 m)
Light at peak (depth)	$9 \cdot 10^{-10}$ (30 m)	$3 \cdot 10^{-8}$ (36 m)
mysid density	4.2	4.6
alewife density	0.0012	0.0017
% overlap	23%	10%
% presence	5%	55%
predicted feeding rate (unadjusted)	0.0055	0.01
predicted feeding rate (predator adjusted)	0.0033	0.0024
observed feeding rate	0.02	0.64

Mysids were significantly deeper in the water column on the full moon versus the new moon night (Fig. 5.3). Total mysid abundance was higher on the full moon versus the new moon night (290 mysids·m^{-2} compared to 125 mysids·m^{-2}, respectively). Mysid density peaked at 17 mysids ·m^{-3} at 36 m on the full moon night compared to a peak of 12 mysids ·m^{-3} at 30 m on the new moon night. The average mysid density across the depth ranges of the gillnet sets (15-35 m) was nearly identical on both nights (Table 5.3).

Fish displayed a bimodal distribution on both nights with a shallower and larger peak found between 5-15 m and a deeper, smaller peak between 20 -30 m (Fig. 5.3). The peak of the mysid distribution was 30 m or deeper on both nights. Total fish abundance was significantly lower on August 16 compared to August 27 (462 fish·ha^{-1} and 1852 fish·ha^{-1}, respectively), although densities averaged across the depth of the gillnet sets were nearly identical (0.0012 fish·m^{-3} compared to 0.0017 fish·m^{-3}, respectively; Table 5.3). Light levels were at least two orders of magnitude higher at the depths of peak fish density than at depths of maximum mysid density, as fish were generally shallower in the water column than mysids.

The deeper peak represented a larger proportion of the total fish abundance on the new moon night than on the full moon night (Fig. 5.3). This translated into a higher degree of overlap between mysid and fish distributions on the new moon (23%) versus the full moon night (10%) (Table 5.3).

Gillnets set between 15 and 35 m on both nights confirmed that greater than 90% of the catch were alewife. Seventy-three and 29 alewife were caught and analyzed on the new moon and full moon night, respectively. These numbers equated to 14 alewife hr^{-1} on the new moon night and 5 alewife hr^{-1} on the full moon night.

The percent presence of mysids in the gut contents was higher on the full moon night (55%, or 16 out of 29 fish) compared to the new moon night (5%, or 4 out of 73 fish) (Table 5.3). The observed feeding rates of alewife were thirty-two times higher on the full moon versus the new moon night compared to the clearance rate model which predicted this difference to be a factor of two greater. On the full moon night, the alewife clearance rate model (Eq. 5.6) predicted feeding rates that were an order of magnitude lower (0.010 mysids·fish^{-1}·hr^{-1}) than what was observed (0.64 mysids·fish^{-1}·hr^{-1}) but predicted the feeding rates to approximately a factor of six of those observed on the new moon night (predicted = 0.0055 mysids·fish^{-1}·hr^{-1}, observed =

0.020) (Table 5.3). When the probability distribution of alewife was considered as part of the clearance rate model (predator-adjusted model), the model predicted slightly higher feeding rates on the new moon night (0.0033 mysids·fish^{-1}·hr^{-1}) than the full moon night (0.0024 mysids·fish^{-1}·hr^{-1}). These predator-adjusted feeding rates were higher on the new moon night despite light levels at the mysid layer being well below the alewife visual threshold due to the increased presence of fish in depths with the highest mysid densities.

DISCUSSION

The importance of habitat edges as areas of high predator-prey interaction has been well-documented in both aquatic (e.g., Selgrath et al. 2007**;** Smith et al. 2008,) and terrestrial (see review in Fagan et al. 1999) systems. In aquatic systems, the strength of these predator-prey interactions is not only influenced by the structural elements of the edge habitat such as substrate or percent vegetative cover (Heck and Thoman 1981), but by abiotic factors such as temperature and light, particularly in pelagic habitats where cover is not available. In this study, I use a combination of visual pigment analyses, laboratory feeding experiments and field observations to demonstrate that alewife are capable of visual feeding at the upper edge, but not at the peak, of the mysid layer under full moon conditions and are not capable of visual feeding at any depth under new moon conditions. These higher light levels at the upper edge of the mysid distribution on the full moon night led to significantly higher overall feeding rates on mysids (0.64 mysids·fish^{-1}·hr.$^{-1}$ compared to 0.020 mysids·fish^{-1}·hr.$^{-1}$), despite a lower degree of spatial overlap between the alewife and mysid distributions relative to the new moon night (23% compared to 10% on the new moon and full moon nights, respectively). Cumulatively, these results suggest that although increased light penetration leads to a larger degree of spatial separation

between alewife and mysids, those fish present within the layer will feed more effectively on mysids, leading to higher overall feeding rates on mysids.

Although the photopic spectral sensitivity of an anadromous population of alewives has been previously investigated (Wald 1939), this study is the first to report the absorbance characteristics of the rod visual pigments of a land-locked population of alewife. A single Vitamin A_1-based rod visual pigment was found with a wavelength of maximum absorbance, $\lambda_{max,}$ at 505 nm. These results are similar to those obtained through microspectrophotometric analyses of retinal pigments of dark-adapted herring, *Clupea harengus* (λ_{max} = 500 nm). This observed short wavelength λ_{max} is a common characteristic of most rhodopsin-based pigments in mesopelagic marine fish (Brett 1957; Nicol 1963) and may represent an adaptation to maximize contrast between the spectral distribution of background light and the spectral reflectance of a target prey item, such as *M. relicta.* For example, Lythgoe (1979) hypothesized that a visual pigment with a λ_{max} offset from the wavelength of maximum water transparency may confer an advantage in the detection of a brighter object against a dark background. The peak irradiance at night at the depth of maximum mysid density on both the new moon and full moon nights occurred at significantly longer wavelengths (550 nm) than the wavelength of maximum absorbance derived for alewife in this study (Boscarino, unpubl.). Further support for this hypothesis is offered by observations of Atlantic herring (*Clupea harengus harengus),* which silhouettes its prey against downwelling light (Blaxter 1966), suggesting that clupeids primarily use contrast to capture prey in low light environments.

I believe that the light levels and temperatures used in the laboratory feeding experiments are representative of those likely to be experienced by alewife in the field.

The experimental light level treatments were based on extrapolations from field measurements of light at the depth of the mysid layer. These field estimates of light intensity were made in units relevant to alewife vision (alelux) by correcting the overall radiant flux in the environment to radiation as perceived by an alewife eye. Alelux was measured directly in the laboratory by placing an alewife-specific filter in front of the light meter which scaled the amount of light reaching the light sensor to the spectral sensitivity of the alewife eye. In addition, the field light measurements used as the basis for the experimental intensities in the laboratory were made on both a new moon and full moon night to ensure that the range of light levels likely to be experienced by alewife feeding in the mysid layer was covered. Feeding experiments were also run at a temperature typically experienced at the upper edge of the mysid layer (mysid upward ascent is limited at temperatures > 14ºC, Boscarino et al. 2007). This temperature also falls within the preferred range of alewife in the laboratory (Wells 1968; Coutant 1977) and in the field during thermally stratified conditions (Gibson 1981).

These results indicate that alewives are capable of visual feeding on mysids at light levels similar to those reported for other clupeids, although strike efficiency and capture success declines with decreasing light conditions. Experiments with the herring, *Clupea harengus,* suggest that the threshold for visual feeding in clupeids lies somewhere between 0.01 - 0.001 lux, or 10^{-5} to 10^{-6} alelux, depending on the type of prey source used and direction of the light source (Blaxter 1964; Batty et al. 1990). Unlike these previous attempts to determine a lower light threshold in clupeids, this study also highlights the importance of density-dependent effects on visual feeding. For example, clearance rates were more than double those under completely dark conditions down to light levels of 10^{-3} alelux at the lowest mysid density treatment of

40 mysids·m^{-3}, but clearance rates were still more than double those in complete darkness at light levels as low as 10^{-7} alelux if densities exceeded 100 mysids·m^{-3}.

The increase in clearance rates with mysid density at light levels between 10^{-2} and 10^{-5} alelux is likely due to the depletion of the majority of the mysids at these highest light level treatments- if alewives are seeing well enough to deplete the prey provided in the tanks over a three hour period, the highest mysid density treatment will yield the highest clearance rates. Prey depletion becomes less of an issue at light levels below 10^{-5} alelux when mysids are more difficult to locate and capture and these are the light levels that alewife are feeding on mysids in the field. This experimental artifact of increasing clearance rates with increasing mysid densities at high light levels therefore did not impact the field predictions.

Observations of fish feeding behavior yielded interesting insight into the mechanisms through which alewife are locating and striking at prey at the low light levels present at the mysid layer at night. Greater than 90% of the attacks made on mysids at light levels of 10^{-7} alelux or greater were made at an angle of 30-40º to the vertical, suggesting that alewife are locating prey that are above them in the water column. These results are similar to those found for the blueback herring, *Alosa aestivalis,* which also attacks its prey from beneath but at angles greater than those found in this study (> 48.6º, or just outside the boundary of the cone of downwelling light, often referred to as "Snell's window"; Janssen 1981). Because Snell's window was not replicated in the experiments, I cannot definitively conclude whether alewives use the contrast of Snell's window to locate and capture prey or whether feeding rates would be further enhanced if a natural light field was set up in the experiments However, this study does corroborate these previous findings which suggest that

clupeids tend to attack highly mobile prey like mysids from below and engage in active searching in waters above them at light levels of 10^{-7} alelux and higher.

In addition to its effects on capture success and feeding behavior in the laboratory, light also influenced the degree of overlap between mysids and alewife in the field (23% overlap on the new moon compared to 10% on the full moon night). A higher degree of spatial overlap on the new moon night did not translate into higher feeding rates on mysids; however, alewives did not cease feeding entirely on the new moon night despite light levels being below the alewife's visual threshold. The feeding experiments in the laboratory also confirmed that alewives are capable of feeding on mysids in the absence of visual cues. Janssen et al. (1995) demonstrated that alewife are capable of lateral line-mediated particulate feeding under completely dark conditions and it is likely that alewife in the experiments were doing the same; however, clupeids have highly sensitive auditory (Wilson and Dill 2002) and olfactory systems (Dempsey 1978) that they use to locate prey and predators. It may be that these other senses uniquely interact with light to enhance feeding rates beyond those expected based on light alone. For example, New (2002) demonstrate that the visual and lateral line systems play complementary roles in the feeding behavior of the muskellunge, *Esox masquinongy,* with vision being used primarily in the initial detection of the prey and the lateral line system used in initiating the strike. Because the experiments were not designed to tease apart the relative contributions of each of these other senses to alewife feeding ecology, I cannot definitively state that alewife are using primarily vision to feed at the low light levels available at night, only that their feeding is enhanced by vision at light levels of 10^{-7} alelux and greater.

Alewife strike behavior changed in complete darkness, with alewife instead striking at prey head-on, in parallel to the horizon. Fish swimming behavior was

greatly reduced in the dark as well suggesting that fish may be minimizing turbulence so that prey could be located easier through lateral line sensitivity along the horizontal plane. I caution that I was only able to witness three attacks in the complete darkness (none of which lead to a successful capture); thus, a more thorough analysis of fish feeding behavior in complete darkness would have to be performed before concluding that alewife only attack prey horizontally in the absence of light.

The alewife clearance rate model provided reasonable predictions of observed feeding rates on the new moon night (0.0055 predicted compared to 0.02 observed mysids·fish^{-1}·hr^{-1}) but underestimated the mean feeding rate by well over an order of magnitude on the full moon night (0.010 predicted compared to 0.64 observed mysids·fish^{-1}·hr^{-1}). Predicted feeding rates were even lower when the relative distribution of the predators was accounted for (0.0033 and 0.0024 mysids·fish^{-1}·hr^{-1} on the new moon and full moon night, respectively). There are several possible explanations as to why the clearance rate model underestimated alewife feeding rates in the field. I originally planned to run all feeding experiments with one alewife per tank but preliminary trials with only one alewife revealed that fish did not attack the prey items and were noticeably more stressed during the feeding period if not surrounded by conspecifics. This is a common problem associated with laboratory feeding experiments involving schooling species, like clupeids (Parker 1973; Ross et al. 1992). I therefore calculated feeding rates based on three fish feeding, with the assumption that all three fish had equal access to mysid prey. However, the gut content analysis revealed that in ten out of the twelve trial experiments in which fish were euthanized directly after the feeding experiment, only one out of the three fish was responsible for capturing the mysids. If the feeding rate estimates were adjusted to reflect only one fish feeding, the predictions would have been within a factor of two

of those observed in the field on the new moon night but still close to an order of magnitude lower than those observed on the full moon night.

Lastly, the gillnets were suspended between 15-35 m on both sampling nights, but alewives were potentially feeding outside of this depth range prior to their capture. Although mysid densities were approximately equal over the depth interval of the gillnets, the overall mysid abundance averaged across all other depths was over two times higher on the full moon night. Thus, alewives that had been feeding outside of this depth interval would have proportionally higher clearance rates due to the density-dependent effects on clearance rate, even if light levels at these depths were below the visual threshold. Since these density-dependent effects were not a factor over the depth interval of the gillnet sets, this may explain the underestimation of the clearance rate increase on the full moon night if much of alewives' capture success occurred at depths outside the 15-35 m depth interval. Similarly, alewives may be foraging only within pockets of the densest aggregations of mysids which would lead to significantly higher feeding rates than those predicted based on average feeding rates across a wider depth range.

Despite these limitations in the determination of absolute clearance rates, gut content analyses of alewives caught within the mysid layer revealed an over 30-fold increase in mysid consumption on the full moon night relative to a new moon night despite a lower degree of overlap between the two trophic levels, indicating that increased light penetration led to higher feeding rates of alewives on mysids. Light levels at the upper 10% of the mysid distribution were nearly two orders of magnitude greater on the full moon night than on the new moon night, and fell within the range of light levels for alewife visual feeding in the laboratory. In contrast, light levels at the peak of the mysid distribution on the full moon night and at any depth in the water column on the new moon night were below the laboratory-derived visual threshold for

alewife. Given the relative similarity in mysid abundances in the region of overlap with the alewife distribution on the two nights, these results suggest that alewives can use light at the upper edge of the mysid distribution to enhance their feeding rates on mysids on full moon nights, but are likely not capable of visual feeding at depths associated with the peak of the mysid layer, even when the moon is full.

This study is one step towards a better understanding of one of the most central feeding relationships in the Great Lakes and provides insight into how pelagic food web dynamics may be affected by ongoing ecological change. For example, alewife may be switching from a diet consisting primarily of zooplankton to one that also includes considerable amounts of mysids, indicating a shift towards mysivory commensurate with increased water clarity and light penetration in the lake since the early 1990's (Stewart et al. In press; Mills et al. 2003). This study provides evidence to indicate this diet shift may have resulted through the enhancement of the visual feeding environment for alewife – increased light penetration led to significantly higher feeding rates on mysids despite increased spatial separation between the two trophic levels. This study is also significant because it provides a template for how to study light effects over a range of scales from the physiological characteristics of the visual system, to behavioral experiments in the laboratory, to implications at larger spatial and temporal scales relevant to the populations in the lake.

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APPENDIX

Appendix 1: Field data for May 19, 2004 ("ND" refers to No Data available)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	2.74	3.80	4.34E-06
2	0.00	ND	2.74	3.68	3.67E-06
3	0.00	ND	2.74	3.51	3.11E-06
4	0.00	4.832E-02	2.74	3.50	2.64E-06
5	0.00	5.559E-02	2.74	3.50	2.24E-06
6	0.00	3.453E-02	2.74	3.50	1.91E-06
7	0.00	1.347E-02	2.74	3.50	1.62E-06
8	0.00	8.430E-03	2.69	3.50	1.38E-06
9	0.00	3.388E-03	2.64	3.50	1.18E-06
10	0.00	2.062E-03	2.59	3.50	1.01E-06
11	0.45	7.357E-04	2.54	3.50	8.63E-07
12	0.41	5.120E-04	2.49	3.50	7.39E-07
13	0.46	2.884E-04	2.44	3.50	6.33E-07
14	0.52	3.195E-04	2.39	3.50	5.43E-07
15	0.62	3.506E-04	2.34	3.50	4.65E-07
16	0.94	1.941E-03	2.34	3.50	3.99E-07
17	0.91	1.384E-04	2.43	3.50	3.43E-07
18	1.01	1.011E-04	2.51	3.50	2.95E-07
19	1.22	6.394E-05	2.55	3.50	2.53E-07
20	1.40	2.035E-04	2.60	3.50	2.18E-07
21	1.60	3.430E-04	2.64	3.50	1.91E-07
22	1.58	2.207E-04	2.68	3.50	1.68E-07
23	1.77	9.844E-05	2.61	3.50	1.47E-07
24	2.08	8.140E-05	2.53	3.50	1.29E-07
25	1.99	6.436E-05	2.46	3.50	1.13E-07
26	2.12	5.839E-05	2.39	3.50	9.96E-08
27	2.38	5.242E-05	2.31	3.50	8.75E-08
28	2.59	3.996E-05	2.24	3.51	7.69E-08
29	2.57	2.750E-05	2.09	3.51	6.76E-08
30	2.67	8.815E-05	2.09	3.51	5.94E-08
31	2.75	1.488E-04	2.73	3.51	5.22E-08
32	3.30	1.103E-04	3.38	3.51	4.59E-08
33	3.26	7.178E-05	3.66	3.51	4.04E-08
34	3.70	6.846E-05	3.94	3.51	3.55E-08
35	4.20	6.514E-05	4.23	3.52	3.13E-08
36	4.49	8.934E-05	4.51	3.52	2.75E-08
37	4.91	1.136E-04	4.72	3.52	2.42E-08
38	5.01	1.011E-04	4.97	3.52	2.13E-08
39	5.39	8.873E-05	5.21	3.52	1.88E-08
40	6.21	1.291E-04	5.46	3.52	1.65E-08
41	6.23	1.695E-04	5.70	3.52	1.46E-08
42	6.19	1.779E-04	5.95	3.52	1.28E-08

Appendix 1 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
43	6.03	1.864E-04	6.19	3.52	1.13E-08
44	6.16	7.887E-04	4.88	3.52	9.97E-09
45	6.71	1.391E-03	4.34	3.52	8.79E-09
46	6.40	8.014E-04	3.81	3.52	7.74E-09
47	5.93	2.117E-04	3.28	3.52	6.83E-09
48	5.91	1.895E-04	2.74	3.52	6.02E-09
49	5.65	1.673E-04	2.21	3.52	5.31E-09
50	4.67	1.669E-04	1.67	3.52	4.68E-09
51	4.19			3.52	4.13E-09
52	3.85			3.52	3.64E-09
53	3.39			3.52	3.21E-09
54	3.08			3.52	2.83E-09
55	2.57			3.52	2.50E-09
56	2.20			3.52	2.21E-09
57	1.82			3.52	1.95E-09
58	1.80			3.51	1.72E-09

Appendix 2: Field data for August 16, 2004

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	81.98	21.23	3.90E-06
2	0.00	ND	81.98	21.36	2.97E-06
3	0.00	ND	68.26	21.40	2.27E-06
4	0.00	1.760E-04	54.54	21.39	1.73E-06
5	0.00	1.100E-03	54.16	21.35	1.33E-06
6	0.00	2.024E-03	53.79	21.27	1.02E-06
7	0.00	2.948E-03	40.49	21.15	7.84E-07
8	0.00	3.872E-03	27.18	21.06	6.04E-07
9	0.00	7.744E-03	27.35	20.93	4.66E-07
10	0.00	4.090E-03	27.52	20.78	3.60E-07
11	0.00	4.365E-04	31.86	20.63	2.79E-07
12	0.00	9.387E-04	36.20	20.52	2.16E-07
13	0.00	1.441E-03	23.13	20.44	1.67E-07
14	0.00	1.316E-03	10.06	20.39	1.30E-07
15	0.00	1.191E-03	8.33	20.34	1.01E-07
16	0.46	1.696E-03	6.61	20.28	7.86E-08
17	0.52	2.202E-03	8.56	20.13	6.12E-08
18	0.62	1.922E-03	10.52	19.86	4.77E-08
19	0.94	1.641E-03	10.21	19.10	3.72E-08
20	0.91	1.887E-03	9.90	17.20	2.90E-08
21	1.36	2.132E-03	8.67	14.37	2.47E-08
22	1.49	2.493E-03	7.44	12.67	2.11E-08
23	1.86	2.855E-03	5.67	11.28	1.80E-08
24	2.34	1.860E-03	3.89	10.12	1.53E-08
25	2.79	8.649E-04	4.15	9.35	1.31E-08
26	3.73	6.976E-04	4.41	8.79	1.12E-08
27	5.20	5.303E-04	5.90	8.18	9.54E-09
28	7.62	6.136E-04	7.39	7.47	8.14E-09
29	10.11	6.970E-04	9.36	6.84	6.96E-09
30	11.56	5.070E-04	11.33	6.38	5.94E-09
31	10.06	3.171E-04	11.33	5.97	5.08E-09
32	8.31	2.932E-04	11.33	5.62	4.34E-09
33	6.39	2.694E-04	11.33	5.37	3.71E-09
34	6.20	2.002E-04	11.33	5.18	3.17E-09
35	5.21	1.309E-04	11.33	5.04	2.71E-09
36	4.33	7.309E-05	11.33	4.89	2.32E-09
37	3.52	1.524E-05	11.33	4.75	1.99E-09
38	2.92	1.562E-05	11.33	4.64	1.70E-09
39	2.56	1.601E-05	11.33	4.53	1.46E-09
40	2.27	5.250E-05	11.33	4.45	1.25E-09
41	1.96	8.900E-05	11.33	4.38	1.07E-09
42	1.81	4.680E-05	11.33	4.32	9.13E-10
43	1.73	4.602E-06	11.33	4.26	7.82E-10
44	1.55	4.574E-06	11.33	4.20	6.70E-10

Appendix 2 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	1.46	4.546E-06	11.33	4.16	5.74E-10
46	1.41	9.733E-06	11.33	4.13	4.92E-10
47	1.25	1.492E-05	11.33	4.09	4.21E-10
48	1.20	7.503E-06	11.33	4.06	3.61E-10
49	1.11	8.770E-08	11.33	4.03	3.09E-10
50	1.04	8.770E-08	11.33	4.01	2.65E-10
51	0.95			3.99	2.27E-10
52	0.86			3.97	1.95E-10
53	0.79			3.96	1.67E-10
54	0.71			3.95	1.43E-10
55	0.65			3.95	1.23E-10
56	0.60			3.95	1.05E-10
57	0.52			3.94	9.04E-11
58	0.44			3.94	7.75E-11
59	0.39			3.93	6.65E-11
60	0.32			3.93	5.71E-11
61	0.28			3.92	4.90E-11
62	0.21			3.91	4.20E-11
63	0.19			3.91	3.61E-11
64	0.14			3.91	3.10E-11
65	0.13			3.89	2.66E-11
66	0.04			3.88	2.28E-11
67	0.01			3.89	1.96E-11
68	0.00			3.88	1.68E-11

Appendix 3: Field data for August 27, 2004

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	108.90	21.59	7.05E-05
2	0.00	ND	108.90	21.51	5.73E-05
3	0.00	ND	133.77	21.42	4.67E-05
4	0.00	4.687E-03	158.65	21.19	3.81E-05
5	0.00	8.893E-03	142.30	21.04	3.11E-05
6	0.00	1.242E-02	125.94	20.92	2.55E-05
7	0.00	1.595E-02	107.89	20.85	2.09E-05
8	0.00	1.480E-02	89.83	20.83	1.71E-05
9	0.00	1.365E-02	97.92	20.81	1.41E-05
10	0.00	1.414E-02	106.00	20.81	1.16E-05
11	0.00	1.463E-02	114.09	20.80	9.53E-06
12	0.00	1.501E-02	122.17	20.80	7.86E-06
13	0.00	1.540E-02	100.62	20.78	6.48E-06
14	0.00	8.717E-03	79.07	20.74	5.35E-06
15	0.00	2.032E-03	65.72	20.68	4.42E-06
16	0.00	1.574E-03	52.37	20.57	3.66E-06
17	0.00	1.117E-03	31.47	20.20	3.03E-06
18	0.00	1.810E-03	10.57	18.82	2.51E-06
19	0.00	2.502E-03	7.53	16.01	2.08E-06
20	0.00	3.997E-03	4.49	13.32	1.72E-06
21	0.49	5.491E-03	3.42	11.53	1.50E-06
22	0.46	4.133E-03	2.35	10.13	1.30E-06
23	0.63	2.776E-03	2.48	9.14	1.13E-06
24	0.89	3.301E-03	2.60	8.28	9.87E-07
25	1.66	3.826E-03	3.06	7.57	8.59E-07
26	3.19	2.155E-03	3.52	7.00	7.48E-07
27	4.12	4.846E-04	3.62	6.53	6.52E-07
28	4.81	3.757E-04	3.73	6.14	5.68E-07
29	6.20	2.667E-04	6.78	5.87	4.95E-07
30	8.33	2.667E-04	9.83	5.65	4.31E-07
31	10.06	1.345E-04	9.83	5.41	3.76E-07
32	11.54	1.506E-04	9.83	5.18	3.28E-07
33	12.89	1.666E-04	9.83	4.98	2.86E-07
34	14.67	1.408E-04	9.83	4.76	2.50E-07
35	16.02	1.151E-04	9.83	4.61	2.18E-07
36	17.34	1.900E-04	9.83	4.47	1.90E-07
37	16.39	2.649E-04	9.83	4.37	1.66E-07
38	16.21	1.748E-04	9.83	4.26	1.45E-07
39	13.52	8.461E-05	9.83	4.18	1.27E-07
40	12.83	5.954E-05	9.83	4.12	1.11E-07
41	11.22	3.446E-05	9.83	4.10	9.66E-08
42	9.65	3.900E-05	9.83	4.10	8.44E-08
43	9.21	4.355E-05	9.83	4.09	7.38E-08
44	9.02	3.459E-05	9.83	4.09	6.45E-08

Appendix 3 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	7.55	2.563E-05	9.83	4.08	5.64E-08
46	7.00	2.147E-05	9.83	4.08	4.93E-08
47	6.27	1.731E-05	9.83	4.08	4.31E-08
48	6.22	2.054E-05	9.83	4.08	3.77E-08
49	5.74	2.377E-05	9.83	4.08	3.29E-08
50	5.49	2.377E-05	9.83	4.08	2.88E-08
51	4.94			4.07	2.52E-08
52	4.51			4.07	2.20E-08
53	4.05			4.06	1.93E-08
54	3.78			4.06	1.69E-08
55	3.40			4.06	1.48E-08
56	3.02			4.05	1.29E-08
57	2.94			4.04	1.13E-08
58	2.59			4.04	9.89E-09
59	2.22			4.03	8.66E-09
60	2.22			4.02	7.58E-09
61	1.92			4.02	6.64E-09
62	1.80			4.01	5.81E-09
63	1.76			4.01	5.09E-09
64	1.43			4.01	4.45E-09

Appendix 4: Field data for September 30, 2004

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	47.05	17.40	3.36E-04
2	0.00	ND	47.05	17.40	2.92E-04
3	0.00	ND	59.65	17.40	2.53E-04
4	0.00	2.437E-02	72.25	17.40	1.91E-04
5	0.00	3.508E-02	54.31	17.40	1.54E-04
6	0.00	4.804E-02	36.37	17.40	1.44E-04
7	0.00	6.100E-02	32.77	17.40	9.40E-05
8	0.00	4.790E-02	29.16	17.40	8.16E-05
9	0.00	3.481E-02	28.68	17.40	9.40E-05
10	0.00	3.156E-02	28.20	17.40	6.15E-05
11	0.00	2.831E-02	28.59	17.40	4.63E-05
12	0.00	2.965E-02	28.97	17.20	4.02E-05
13	0.00	3.099E-02	23.50	16.30	3.49E-05
14	0.00	3.166E-02	18.02	15.40	2.63E-05
15	0.00	3.234E-02	10.18	13.95	2.28E-05
16	0.00	2.579E-02	2.34	13.05	1.98E-05
17	0.00	1.923E-02	2.44	12.20	1.60E-05
18	0.00	1.461E-02	2.54	10.95	1.29E-05
19	0.00	9.989E-03	2.21	9.65	9.75E-06
20	0.00	7.045E-03	1.88	9.10	7.88E-06
21	0.00	4.102E-03	2.11	8.90	6.37E-06
22	0.00	2.743E-03	2.33	8.70	5.53E-06
23	0.00	1.384E-03	2.00	8.60	5.53E-06
24	0.00	9.400E-04	1.67	8.40	4.80E-06
25	0.00	4.962E-04	1.35	8.25	3.37E-06
26	0.00	6.234E-04	1.02	8.10	2.72E-06
27	0.00	7.507E-04	0.82	8.05	2.36E-06
28	0.10	4.212E-04	0.61	7.75	2.05E-06
29	0.07	9.159E-05	0.75	7.60	1.91E-06
30	0.07	4.108E-04	0.88	7.30	1.54E-06
31	0.12	7.300E-04	0.88	7.00	1.44E-06
32	0.06	3.857E-04	0.88	6.80	1.25E-06
33	0.08	4.144E-05	0.88	6.60	1.08E-06
34	0.08	2.819E-05	0.88	6.25	1.01E-06
35	0.16	1.494E-05	0.88	5.95	8.74E-07
36	0.17	3.020E-05	0.88	5.75	6.58E-07
37	0.21	4.547E-05	0.88	5.50	6.12E-07
38	0.21	5.475E-05	0.88	5.05	5.30E-07
39	0.26	6.403E-05	0.88	4.70	4.94E-07
40	0.32	8.077E-05	0.88	4.45	4.26E-07
41	0.38	9.752E-05	0.88	4.40	3.57E-07
42	0.48	2.941E-04	0.88	4.15	2.99E-07
43	0.64	4.907E-04	0.88	4.05	2.50E-07
44	0.79	1.883E-03	0.88	4.05	2.10E-07

Appendix 4 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	0.90	3.275E-03	0.88	4.05	1.75E-07
46	1.03	1.665E-03	0.88	4.05	1.47E-07
47	1.31	5.593E-05	0.88	4.05	1.23E-07
48	1.40	4.290E-05	0.88	4.05	1.03E-07
49	1.52	2.987E-05	0.88	4.00	8.63E-08
50	1.64	2.987E-05	0.88	4.00	7.23E-08
51	1.91			4.00	6.05E-08
52	2.05			4.00	5.07E-08
53	2.00			4.00	4.24E-08
54	2.15			4.00	3.55E-08
55	2.10			4.00	2.98E-08
56	2.32			4.00	2.49E-08
57	2.33			4.00	2.09E-08
58	2.62			4.00	1.75E-08
59	2.11			4.00	1.46E-08
60	2.01			4.00	1.23E-08
61	2.12			4.00	1.03E-08
62	1.89			4.00	8.60E-09
63	1.82			4.00	7.20E-09
64	1.65			4.00	6.03E-09
65	1.62			4.00	5.05E-09
66	1.73			4.00	4.23E-09
67	1.52			4.00	3.54E-09

Appendix 5: Field data for May 5, 2005

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	1.62	3.61	2.20E-06
2	0.00	ND	1.62	3.63	1.91E-06
3	0.00	ND	1.68	3.58	1.91E-06
4	0.00	4.770E-03	1.73	3.55	1.66E-06
5	0.00	5.395E-03	2.04	3.54	1.44E-06
6	0.00	3.393E-03	2.36	3.54	1.25E-06
7	0.00	1.390E-03	1.29	3.53	1.08E-06
8	0.00	8.431E-04	0.23	3.53	9.40E-07
9	0.00	2.962E-04	2.49	3.53	8.16E-07
10	0.00	4.113E-04	4.76	3.53	7.08E-07
11	0.00	5.264E-04	2.63	3.53	6.14E-07
12	0.00	6.415E-04	0.51	3.53	6.14E-07
13	0.00	7.566E-04	1.14	3.53	6.14E-07
14	0.00	9.230E-04	1.77	3.53	5.33E-07
15	0.00	1.089E-03	1.83	3.53	4.63E-07
16	0.00	1.235E-03	1.88	3.54	4.02E-07
17	0.00	1.380E-03	1.77	3.54	4.02E-07
18	0.00	7.459E-04	1.65	3.54	3.49E-07
19	0.00	1.115E-04	1.55	3.54	3.03E-07
20	0.00	1.640E-04	1.46	3.54	3.03E-07
21	0.00	2.166E-04	1.41	3.54	2.63E-07
22	0.36	2.421E-04	1.36	3.54	2.63E-07
23	0.46	2.677E-04	2.05	3.54	2.28E-07
24	0.77	2.691E-04	2.74	3.54	1.98E-07
25	1.07	2.705E-04	2.73	3.54	1.98E-07
26	0.97	2.727E-04	2.72	3.54	1.72E-07
27	1.01	2.748E-04	2.06	3.54	1.72E-07
28	1.22	2.770E-04	1.41	3.54	1.49E-07
29	1.08	2.791E-04	1.57	3.54	1.49E-07
30	1.16	1.640E-04	1.74	3.54	1.29E-07
31	1.13	4.880E-05	1.53	3.54	1.29E-07
32	1.30	6.730E-05	1.33	3.54	1.12E-07
33	1.47	8.580E-05	1.31	3.54	1.12E-07
34	1.27	1.882E-04	1.19	3.53	9.75E-08
35	1.27	2.906E-04	1.08	3.54	9.75E-08
36	1.30	2.753E-04	0.94	3.54	8.46E-08
37	1.22	2.600E-04	0.80	3.54	7.34E-08
38	1.30	3.473E-04	0.68	3.54	7.34E-08
39	1.39	4.345E-04	0.55	3.54	6.37E-08
40	1.33	4.479E-04	0.41	3.54	5.53E-08
41	1.56	4.612E-04	0.41	3.54	4.94E-08
42	1.63	3.862E-04	0.41	3.54	4.41E-08
43	1.73	3.112E-04	0.41	3.54	3.94E-08
44	1.67	5.545E-04	0.41	3.55	3.52E-08

Appendix 5 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	1.84	7.979E-04	0.41	3.55	3.14E-08
46	1.84	7.914E-04	0.41	3.55	2.80E-08
47	1.54	7.849E-04	0.41	3.55	2.50E-08
48	1.46	5.753E-04	0.41	3.55	2.24E-08
49	1.76	3.657E-04	0.41	3.55	2.00E-08
50	1.12	3.657E-04	0.41	3.55	1.78E-08
51	1.07			3.55	1.59E-08
52	0.72			3.55	1.42E-08
53	0.72			3.55	1.27E-08
54	0.68			3.55	1.13E-08
55	0.61			3.56	1.01E-08
56	0.52			3.56	9.03E-09
57	0.21			3.56	8.06E-09
58	0.37			3.56	7.20E-09
59	0.24			3.56	6.43E-09
60	0.37			3.56	5.74E-09
61	0.21			3.55	5.13E-09
62	0.33			3.55	4.58E-09
63	0.37			3.55	4.09E-09
64	0.15			3.55	3.65E-09
65	0.14			3.55	3.26E-09
66	0.12			3.55	2.91E-09
67	0.10			3.56	2.60E-09

Appendix 6: Field data for June 20, 2005

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	230.74	18.54	1.74E-04
2	0.00	ND	230.74	18.51	7.07E-06
3	0.00	ND	241.86	18.38	5.05E-06
4	0.00	ND	252.98	18.09	4.38E-06
5	0.00	6.297E-03	174.92	17.32	3.80E-06
6	0.00	2.923E-03	96.87	16.90	3.30E-06
7	0.00	7.646E-04	73.84	15.77	2.87E-06
8	0.00	1.100E-04	50.82	15.18	2.49E-06
9	0.00	3.432E-05	32.65	14.85	2.16E-06
10	0.00	3.526E-05	14.48	14.59	1.87E-06
11	0.00	6.496E-06	25.61	14.23	1.63E-06
12	0.00	6.788E-06	36.75	13.81	1.41E-06
13	0.00	2.826E-05	39.95	13.51	1.23E-06
14	0.00	2.460E-05	43.14	13.18	1.06E-06
15	0.00	4.586E-06	45.02	12.78	8.01E-07
16	0.00	1.373E-05	46.90	12.19	8.01E-07
17	0.00	8.286E-06	47.26	11.64	6.95E-07
18	0.00	2.847E-06	47.61	10.98	6.04E-07
19	0.00	1.038E-06	36.31	10.20	5.24E-07
20	0.90	9.884E-05	25.01	9.36	3.95E-07
21	1.27	6.642E-07	37.19	8.56	3.43E-07
22	2.33	1.411E-06	49.36	7.74	2.97E-07
23	4.06	1.627E-06	49.29	6.94	2.58E-07
24	6.80	8.696E-07	49.22	6.23	2.24E-07
25	9.08	1.119E-07	30.77	5.89	1.69E-07
26	11.21	5.679E-07	12.32	5.56	1.46E-07
27	13.21	3.048E-06	20.17	5.34	1.27E-07
28	14.70	4.117E-06	28.01	5.14	9.58E-08
29	15.09	4.406E-06	19.91	4.98	8.31E-08
30	13.71	3.282E-06	11.81	4.86	7.21E-08
31	12.33	2.569E-05	10.44	4.77	6.26E-08
32	11.41	3.045E-06	10.44	4.73	5.43E-08
33	9.48	8.687E-07	10.44	4.68	4.72E-08
34	7.51	1.177E-07	10.44	4.59	4.09E-08
35	6.17	5.610E-08	10.44	4.53	3.08E-08
36	5.19	3.984E-08	10.44	4.47	3.08E-08
37	4.03	2.358E-08	10.44	4.43	2.68E-08
38	3.06	8.064E-08	10.44	4.41	2.68E-08
39	2.30	1.377E-07	10.44	4.38	2.02E-08
40	1.81	1.377E-07	10.44	4.35	1.75E-08
41	1.44	1.948E-07	10.44	4.31	1.52E-08
42	1.11	2.518E-07	10.44	4.28	1.20E-08
43	0.83	3.089E-07	10.44	4.25	9.52E-09
44	0.61	3.660E-07	10.44	4.23	7.54E-09

Appendix 6 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	0.47	3.660E-07	10.44	4.21	5.97E-09
46	0.36	4.230E-07	10.44	4.18	4.72E-09
47	0.28	4.801E-07	10.44	4.15	3.74E-09
48	0.21	1.927E-08	10.44	4.11	2.96E-09
49	0.16	6.567E-08	10.44	4.09	2.34E-09
50	0.12	1.121E-07	10.44	4.06	1.86E-09
51	0.08			4.03	1.47E-09
52	0.06			4.01	1.16E-09
53	0.04			3.99	9.20E-10
54	0.02			3.98	7.29E-10
55	0.02			3.96	5.77E-10
56	0.01			3.95	4.57E-10
57	0.01			3.95	3.61E-10
58	0.02			3.94	2.86E-10
59	0.00			3.94	2.27E-10
60	0.00			3.94	1.79E-10
61	0.00			3.93	1.42E-10
62	0.00			3.93	1.12E-10
63	0.00			3.93	8.90E-11
64	0.00			3.93	7.04E-11
65	0.00			3.92	5.58E-11
66	0.00			3.92	4.41E-11
67	0.00			3.91	3.49E-11
68	0.00			3.91	2.77E-11
69	0.00			3.91	2.19E-11
70	0.00			3.90	1.73E-11
71	0.00			3.90	1.37E-11
72	0.00			3.89	1.09E-11
73	0.00			3.89	8.60E-12
74	0.00			3.89	6.81E-12
75	0.00			3.89	5.39E-12
76	0.00			3.88	4.27E-12
77	0.02			3.88	3.38E-12
78	0.02			3.89	2.67E-12
79	0.00			3.88	2.12E-12
80	0.00			3.88	1.68E-12

Appendix 7: Field data for July 7, 2005

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
1	0.00	ND	51.00	21.72	3.62E-06
2	0.00	ND	51.00	21.75	2.92E-06
3	0.00	ND	51.00	21.48	2.53E-06
4	0.00	ND	51.00	21.10	2.20E-06
5	0.00	1.918E-04	51.00	20.97	1.91E-06
6	0.00	3.837E-04	51.00	20.94	1.66E-06
7	0.00	4.130E-04	51.00	20.93	1.44E-06
8	0.00	8.150E-04	51.00	20.77	1.25E-06
9	0.00	3.155E-04	51.00	19.60	1.01E-06
10	0.00	1.717E-04	51.00	17.80	8.16E-07
11	0.00	2.779E-05	51.00	16.42	7.08E-07
12	0.00	6.810E-05	40.81	15.20	6.15E-07
13	0.00	1.732E-05	40.81	14.24	4.63E-07
14	0.00	8.341E-05	40.81	13.23	3.49E-07
15	0.00	7.542E-05	40.81	11.74	2.63E-07
16	0.00	1.576E-05	40.81	11.25	2.13E-07
17	0.00	2.257E-05	40.81	10.17	1.25E-07
18	1.78	1.323E-05	33.64	9.14	8.47E-08
19	3.74	2.394E-04	33.64	8.56	6.38E-08
20	7.49	2.710E-05	33.64	7.86	4.81E-08
21	12.17	6.602E-06	33.64	6.88	4.17E-08
22	18.30	1.739E-04	33.64	6.10	3.62E-08
23	23.60	2.207E-05	33.64	5.70	2.73E-08
24	24.92	3.354E-04	33.64	5.53	2.26E-08
25	23.04	9.919E-05	33.64	5.42	1.92E-08
26	22.11	3.929E-06	33.64	5.31	1.55E-08
27	19.08	2.375E-06	33.64	5.22	1.34E-08
28	13.54	5.087E-06	33.64	5.15	1.09E-08
29	10.14	8.212E-07	33.64	5.06	1.01E-08
30	5.49	7.799E-06	33.64	4.95	8.20E-09
31	3.55	7.337E-06	33.64	4.89	6.62E-09
32	2.25	6.875E-06	33.64	4.82	5.74E-09
33	1.61	6.413E-06	33.64	4.70	4.98E-09
34	1.53	5.951E-06	33.64	4.57	4.33E-09
35	1.35	5.490E-06	33.64	4.48	3.76E-09
36	1.18	5.028E-06	33.64	4.36	3.26E-09
37	0.92	4.566E-06	33.64	4.32	2.83E-09
38	0.74	4.104E-06	33.64	4.30	2.64E-09
39	0.68	3.642E-06	33.64	4.25	2.13E-09
40	0.67	3.180E-06	33.64	4.20	1.85E-09
41	0.53	2.718E-06	33.64	4.14	1.52E-09
42	0.36	2.257E-06	33.64	4.11	1.24E-09
43	0.29	1.795E-06	33.64	4.10	1.02E-09
44	0.21	1.333E-06	33.64	4.09	8.37E-10

Appendix 7 (continued)

Depth	Observed mysids (no.·m^{-3})	Fish (no.·m^{-3})	Zoopl. (µg·l^{-1})	Temp. (ºC)	Light (mylux)
45	0.16	8.709E-07	33.64	4.05	6.86E-10
46	0.14	4.091E-07	33.64	4.03	5.63E-10
47	0.10	4.091E-07	33.64	4.01	4.62E-10
48	0.07	4.091E-07	33.64	4.00	3.79E-10
49	0.07	4.091E-07	33.64	3.99	3.11E-10
50	0.06	4.091E-07	33.64	3.99	2.55E-10
51	0.05			3.98	2.09E-10
52	0.04			3.98	1.71E-10
53	0.05			3.97	1.40E-10
54	0.04			3.96	1.15E-10
55	0.03			3.96	9.45E-11
56	0.02			3.96	7.75E-11
57	0.02			3.95	6.36E-11
58	0.01			3.95	5.21E-11
59	0.02			3.94	4.28E-11
60	0.01			3.93	3.51E-11
61	0.01			3.93	2.88E-11
62	0.01			3.93	2.36E-11
63	0.02			3.92	1.93E-11
64	0.02			3.92	1.59E-11
65	0.02			3.92	1.30E-11
66	0.01			3.92	1.07E-11
67	0.01			3.92	8.75E-12
68	0.02			3.92	7.18E-12
69	0.01			3.92	5.89E-12
70	0.00			3.91	4.83E-12
71	0.01			3.91	3.96E-12
72	0.01			3.91	3.25E-12
73	0.02			3.91	2.66E-12
74	0.01			3.91	2.19E-12
75	0.01			3.91	1.79E-12
76	0.02			3.92	1.47E-12
77	0.01			3.92	1.21E-12
78	0.01			3.92	9.89E-13
79	0.01			3.92	8.11E-13
80	0.01			3.91	6.65E-13

Appendix 8 : Field data for September 27, 2005

Depth	Observed mysids ($no.\cdot m^{-3}$)	Fish ($no.\cdot m^{-3}$)	Zoopl. ($\mu g\cdot l^{-1}$)	Temp. (ºC)	Light (mylux)
1	0.00	ND	20.74	19.68	3.36E-06
2	0.00	ND	20.74	19.98	2.92E-06
3	0.00	ND	20.17	19.93	2.53E-06
4	0.00	ND	19.60	19.94	1.91E-06
5	0.00	5.716E-04	28.11	19.94	1.54E-06
6	0.00	4.802E-04	36.61	19.94	1.44E-06
7	0.00	3.887E-04	31.89	19.94	9.40E-07
8	0.00	2.973E-04	27.17	19.95	8.16E-07
9	0.00	2.058E-04	24.63	19.95	9.40E-07
10	0.00	4.707E-05	22.09	19.95	6.14E-07
11	0.00	3.301E-05	26.25	19.95	4.63E-07
12	0.00	1.895E-05	30.40	19.95	4.02E-07
13	0.00	1.781E-05	29.12	19.95	3.49E-07
14	0.00	5.414E-05	27.83	19.94	2.63E-07
15	0.00	4.716E-05	28.81	19.94	2.28E-07
16	0.00	1.249E-04	29.79	19.94	1.98E-07
17	0.00	6.943E-05	27.85	19.93	1.60E-07
18	0.00	1.059E-04	25.91	19.93	1.29E-07
19	0.00	1.242E-05	48.52	19.93	9.74E-08
20	0.00	1.398E-04	71.14	19.91	7.88E-08
21	0.00	8.015E-05	50.48	19.91	6.37E-08
22	0.00	2.960E-05	29.82	19.88	5.53E-08
23	0.00	2.014E-05	23.45	19.88	5.53E-08
24	1.18	1.830E-04	17.09	19.87	4.80E-08
25	1.66	4.400E-04	13.88	19.86	3.37E-08
26	1.86	2.276E-04	26.37	16.82	2.72E-08
27	2.20	3.367E-05	48.65	12.21	2.36E-08
28	3.97	4.664E-05	70.87	11.18	2.05E-08
29	4.38	2.549E-05	24.29	10.29	1.91E-08
30	5.94	4.336E-06	27.38	9.27	1.54E-08
31	6.21	2.791E-04	17.59	8.17	1.44E-08
32	5.46	1.121E-03	17.59	7.02	1.25E-08
33	9.02	1.951E-03	17.59	6.31	1.08E-08
34	11.14	6.681E-04	17.59	5.87	1.01E-08
35	14.03	6.684E-04	17.59	5.48	8.74E-09
36	12.69	2.855E-04	17.59	5.38	6.57E-09
37	12.09	3.257E-04	17.59	5.27	6.12E-09
38	12.14	2.328E-04	17.59	5.22	5.30E-09
39	9.13	2.802E-04	17.59	5.10	4.94E-09
40	7.80	2.561E-05	17.59	5.03	4.26E-09
41	8.95	7.480E-06	17.59	4.88	3.57E-09
42	8.45	5.132E-05	17.59	4.72	2.99E-09
43	7.68	1.272E-05	17.59	4.67	2.50E-09
44	5.77	2.009E-05	17.59	4.64	2.09E-09

Appendix 8 (continued)

Depth	Observed mysids ($no.\cdot m^{-3}$)	Fish ($no.\cdot m^{-3}$)	Zoopl. ($\mu g\cdot l^{-1}$)	Temp. (ºC)	Light (mylux)
45	4.58	7.719E-06	17.59	4.58	1.75E-09
46	4.00	6.286E-06	17.59	4.52	1.47E-09
47	3.55	3.534E-06	17.59	4.43	1.23E-09
48	2.99	6.646E-07	17.59	4.38	1.03E-09
49	2.37	5.484E-06	17.59	4.31	8.62E-10
50	1.92	1.030E-05	17.59	4.27	7.22E-10
51	2.16			4.25	6.05E-10
52	1.59			4.17	5.07E-10
53	1.37			4.12	4.24E-10
54	1.23			4.09	3.55E-10
55	0.95			4.06	2.97E-10
56	0.64			4.04	2.49E-10
57	0.49			4.03	2.09E-10
58	0.35			4.03	1.75E-10
59	0.30			4.01	1.46E-10
60	0.25			4.00	1.23E-10
61	0.22			3.99	1.03E-10
62	0.21			3.97	8.59E-11
63	0.21			3.97	7.20E-11
64	0.19			3.96	6.03E-11
65	0.16			3.94	5.05E-11
66	0.16			3.94	4.23E-11
67	0.15			3.92	3.54E-11
68	0.15			3.93	2.96E-11
69	0.11			3.92	2.48E-11
70	0.10			3.93	2.08E-11
71	0.08			3.94	1.74E-11
72	0.07			3.95	1.46E-11
73	0.05			3.96	1.22E-11
74	0.05			3.97	1.02E-11
75	0.05			3.97	8.56E-12
76	0.04			3.97	7.17E-12
77	0.03			3.96	6.00E-12
78	0.03			3.95	5.03E-12
79	0.03			3.94	4.21E-12
80	0.02			3.92	3.53E-12