The abiotic environment and predator-prey interactions: direct and indirect effects within aquatic environments with a specific look at temperature

Melissa Pink

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences

University of Manitoba

Winnipeg

Abstract. Species have specific tolerances to a variety of environmental variables including temperature, dissolved oxygen (DO) and turbidity. Changes in either of these variables can therefore be expected to affect predator-prey interactions in shallow water ecosystems. Temperature drives the metabolic rates of poikilotherms, including fish. Hypoxic conditions generally affect larger fishes to a greater degree than smaller fishes, though the presence of physostomous swim bladders in certain species can alter that relationship. Finally there are species of fish that rely on vision for food acquisition while other species rely on other senses such as chemical cues. Changes in turbidity levels could therefore affect foraging efficiency of visual foragers. This thesis examines the role that each of these environmental variables (temperature, DO and turbidity) can have on community composition and therefore predator prey interactions, with a specific focus on the role of temperature in structuring predator-prey interactions.

Laboratory, field and theoretical studies suggest that as temperature increases, encounter rates between predators and prey will increase. Prey are more active, spend more time foraging, and increase their use of risky habitats in warmer environments in laboratory experiments. In the field, prey and predator activity and/or abundance is positively related to temperature. These laboratory and field studies suggest that temperature increases should result in increased predation rtes of prey. Finally, the results of a dynamic state dependent optimization model also suggest that periods of warming will result in a lowering of the probability of survival of the fathead minnow, *Pimephales promelas,* a prey species, over the-ice free season.

A reduction in DO levels in aquatic ecosystems results in a reduction in the number of and/or activity of predators present. This should result in a reduction in predation risk to prey. However, when endothermic predators are factored in to this equation, this reduction in risk may

not occur. The presence of avian predators of small forage fish are directly related to the level of DO in the water, regardless of the abundance of prey fish present. This relationship is likely a result of behavioural decisions of prey that occurs in hypoxic conditions. In periods of low DO, prey fishes may exploit areas of higher DO that are closer to the surface of the waters. While their piscine predators may not be able to tolerate the low DO levels regardless of the position of prey in the water column, avian predators appear to be able to cue in to this increase in availability of potential prey, reducing any benefits that might occur by occupying surface areas where DO levels might be slightly higher than lower in the water column.

As compared to temperature and DO, turbidity does not appear to affect the potential risk of predation to forage fish. The catch per unit effort (CPUE) of foragers who rely on vision and those that rely on chemical cues to forages, were not related to turbidity levels. Turbidity levels were also not related to the abundance of avian predators. This suggests that in this generally turbid, shallow water ecosystem, changes in turbidity do not affect the overall species composition of the system. Predator-prey interactions in the system are also not likely to be affected by turbidity.

In contrast to this, temperature and DO are likely to influence the interactions between predators and their prey in a shallow water ecosystem. Both increases in temperature and decreases in DO may result in increases in predation pressure on prey. While temperature increases will likely result in increased predation on prey by piscine predators, a reduction in DO, which often occurs as temperature increases, will likely result in increased predation on prey by avian predators, even as predation pressure by piscine predators decrease.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Theoretical framework linking temperature and predator-prey interactions:

Temperature and fish distribution. In North America, there are three thermal guilds of fishes:

cold-, cool- and warm-water. General upper lethal limits of these three guilds of fishes are 25°C,

32°C and 40°C respectively, though species-specific exceptions occur (Magnuson and de Stasio

1997). These thermal preferences of fishes are likely the result of recent evolutionary histories

(Johnson and Kelsh 1998). For example, fishes of the family Salmonidae belong to the cold

water guild; percids and esocids, which are closely related phylogenetically, are both cool water

species; Siluriformes and Cypriniformes, which are more closely related to each other than to the

percids and esocids generally belong to the warm water guild (thermal guilds: Magnuson et al.

1979). Given that thermal microhabitats do not generally exist in aquatic ecosystems - the

thermal conductivity of water is 24.5 times greater than that of air (Hammel 1955) - the

temperatures under which fishes persist may play a large role in the structuring of community

composition and the interactions between predators and their prey.

It is this quality of the aquatic environment, the fact that microhabitats of significantly

different temperatures do not typically exist (save for within lakes that thermally stratify), that

make changes in the thermal regime of an aquatic ecosystem potentially challenging for the

organisms that live there. Temperature of both the land and the oceans are on the rise with an

observed increase in air temperature of 0.6 °C in the past three decades and 0.8 °C in the past

100 years (Hansen et al. 2006). Concerns associated with changes in temperature in aquatic

ecosystems are primarily associated with thermal preferences of fishes. Unfortunately the impact

of this climate change on fish populations and interactions between fish species, including

predators and their prey, is unknown. As fishes are poikilotherms, their body temperature will

follow the temperature of their environment. As their body temperature changes, so will their metabolic rates. It is therefore probable that temperate aquatic ecosystems may be among the most affected by a changing thermal environment. To better predict the responses to warming waters, we must first understand the role that the current temperature regime plays on community composition and interactions between predators and their prey.

Predator-prey interactions: the potential influence of the abiotic environment. Consumption of prey by predators occurs as a result of consecutive interactions between predator and prey in which the predator is successful. Initially there is detection and encounter of the prey by the predator. After the prey has been detected by the predator an attack occurs - this attack must lead to capture if the predator is to consume the prey. After capture of the prey the predator then handles and finally ingests the prey which completes the predation event (*sensu* Holling 1959). The purpose of this thesis is to determine how temperature, dissolved oxygen and turbidity influence piscine predator-prey interactions including instances where the predators are birds.

In a natural ecosystem, the very first step in a predation event requires the spatial overlap of predators and their prey. This means that the current conditions of the aquatic ecosystem have to be able to support both predators and prey. If measures of temperature, dissolved oxygen or turbidity fall outside of the ranges necessary to support populations of given species, predator-prey interactions may be altered. Even if species are able to survive under given conditions, those conditions may not be optimal for foraging therefore changing the interactions between species. For example, temperature and dissolved oxygen can influence encounter rates of piscine predators and their prey as these fishes will generally have different optimal and lethal temperatures and dissolved oxygen levels in which they can inhabit (Chapman et al. 1995).

Encounter and detection rates on a small scale can also be influenced by the abiotic environment, including temperature. There is the potential for temperature to influence foraging and activity rates of prey, as well as risk taking by prey in the presence of predators. This likely occurs through the influence of temperature on hunger levels via the effect of temperature on the energetic cost of metabolism (Sogard and Olla 1996). Metabolic rate increases with increasing temperature, though not necessarily in a linear pattern. Metabolism generally peaks at a given temperature and then decreases (Wootton 1990; Holker 2003), suggesting that Q_{10} values are not applicable throughout a range of temperatures for all fishes. This implies that in response to increased temperatures, fishes may forage more to meet the demands of increased metabolism (Weetman et al. 1998), though this depends on the range of temperatures encompassed by the increase.

As metabolism may not be linear, feeding rates may also be non-linear and interactions between species may be temperature dependent. Bergman (1987) suggests that ectothermic animals, which appear to have temperature-dependent foraging rates for a range of temperatures found naturally, may mediate coexistence of species by altering feeding rates as well as the temperatures selected to inhabit. In fact, Bergman (1987) determined that while both perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) experienced increased capture rate and decreased handling times of prey with an increase in temperature, routine swimming performances increased with temperature for perch only. As in many lakes, perch occupied a much narrower temperature range than ruffe, which suggests that the foraging abilities of ruffe are less temperature dependant than perch. The temperature-dependent foraging and swimming abilities of different species will have differential effects on prey, especially if the species of prey differ between species of ectotherms.

Temperature can also affect predator-prey interactions by affecting growth rates. Anderson et al. (2001) determined that temperature influenced growth rate of tadpoles (*Hyla regilla*); at increased temperatures, growth rates also increased. However, high temperatures during periods of starvation may lead to a redistribution of energy away from growth and towards functions such as maintenance (van Dijk et al. 2002). As well, after the optimal temperature for growth has been reached, escalating metabolism can reduce the rate of growth (Morgan and Metcalfe 2001); in times of starvation it is thought that fish prefer to use cooler water habitats to reduce metabolic demands (behavioural hypothermia). In fact, Sogard and Olla (1996) ascertained that fish avoided cold water when satiated, however as rations decreased, the use of cold water increased. This result is not consistent however, as others have observed the preferred temperature increasing during periods of starvation (Javaid and Anderson 1967; Morgan and Metcalf 2001). With redistribution of energy from growth to maintenance functions with changes in rations present, increased temperature does not necessary result in an increased growth rate.

Influencing the growth rate at given temperatures are the associated feeding rates at various temperatures. As aforementioned, feeding rates can be temperature dependent. Van Dijk et al. (2002) determined that roach (*Rutilus rutilus*) feeding rates increased until a temperature of 18°C was reached. After the maximum feeding rate was reached at that temperature, feeding rates leveled off and then declined. However, van Dijk et al. (2002) did not determine if weight loss occurred with the decrease in feeding rates. Contradicting the study by van Dijk et al. (2002) is the study by Meeuwig et al. (2004). Meeuwig et al. (2004) observed no real pattern in feeding rates with temperature in juvenile cutthroat trout (*Oncorhynchus clarki henshawi*) with feeding rates greatest at 18°C. Feeding rates were less at 12°C than at 18°C, but greater at 12°C than

24°C; growth rates were highest for cutthroat trout at 12°C. In a marine ecosystem, at increased temperatures fishes foraged more (Smith 2008); in a freshwater ecosystem the same result was also observed (Ojanguren et al. 2001). However, in both aforementioned studies the amount of food available was not controlled for, a factor that can influence growth of individuals in a natural setting under various temperature regimes.

The relationship between temperature and growth can influence predator-prey interactions because of the role size plays on capture and consumption rates of prey by predators. Different sized prey, differ in energetic availability to predators and they differ in their visual availability to predators. In order for a predator to consume a prey, the predator must first observe/encounter the prey; the prey has to be large enough for the predator to see, given the particular environment (turbid water or structurally complex environments make prey harder to see). The predator must then capture the prey – larger prey, with longer body lengths are faster than smaller prey (though smaller prey are capable of greater changes in angular velocity) (Wootton 1990). The predator must then manipulate the orientation of the prey so that it can be ingested. While large prey may provide more energetic value to the predator, the prey cannot be too large for the gape size of said predator. In fact, Lundvall et al. (1999) demonstrated that there is an optimal size selection with predators selecting mid-sized prey. This is likely due to the predators being unable to see the small prey, and the large prey being too costly to chase.

Given that foraging and activity (Krause and Godin 1995) of fishes increase with temperature and influence growth rates, and encounter rates are influenced by the activity of predators and prey, predation risk is also likely to change with changes in temperature. Changes in behaviour of the prey fishes in response to changes in temperature and predation risk can also affect the predators themselves. If predators are more interested in more active prey (Krause and

Godin 1995), and activity and foraging of prey increase with temperature, the relationship

between temperature and risk of predation may be further exacerbated.

Dissolved oxygen has also been implicated as an environmental factor that can influence

fish distribution, thus affecting predator-prey interactions. Large and small fishes (as well as

different species) also have different requirements for dissolved oxygen and different rates of gas

exchange with the environment (Abrahams 2006). Therefore dissolved oxygen can influence the

spatial overlap of prey and their predators, thereby affecting the encounter rates of said predators

and prey. In summary, larger fish are generally observed in areas of highest oxygen

concentration, while smaller bodied fishes are generally observed in more oxygen deprived

areas, both in the lab (Burleson et al. 2001) and in natural environments (Suthers and Gee 1986,

Chapman and Chapman 1998; Chapman et al. 2002). Areas of low dissolved oxygen may

therefore provide small fishes refuge from predation by piscine piscivores in these instances.

However, Almeida-Val et al. (2000) determined that for the *Astronotus ocellatu,* an Amazonian

hypoxia tolerant fish, tolerance to hypoxia increased with fish size. Lactate dehydrogenase and

malate dehydrogenase were used as indicators of oxidative flux capacity and experiments were

run on survivorship at differing levels of hypoxia. Both enzyme activity and survivorship

increased with increasing body mass (Almeida-Val et al. 2000) suggesting that hypoxic areas of

the Amazon floodplain inhabited by *Astronotus ocellatu* would not necessarily provide a refuge

for smaller fishes when larger fishes with adaptations to low dissolved oxygen are present. There

are species-specific tolerances to hypoxia, as well as a relationship between size of the fish and

hypoxia tolerance.

Finally, dissolved oxygen can also affect the relationship between piscine prey and their

avian predators. As dissolved oxygen decreases, there is the potential for prey fishes to exploit

areas closest to the air water interface where dissolved oxygen is highest (Kramer 1987, Chapman and Chapman 1998). This use of waters with higher levels of dissolved oxygen may be physiologically advantageous for small fish, but it may also make them more easily detected, encountered and captured by their plunge diving avian predators.

In shallow water ecosystems, turbidity may also play a role in the interaction between predators and prey. Turbidity can reduce a prey's chances of being eaten by a predator, but turbidity can also reduce the prey's ability to observe the predator, as well as the prey's own prey/food items. Nilsson et al. (2009) describe how an increase in turbidity levels reduces the per capita prey consumption by northern pike when the pike are foraging in a group. While foraging alone, increases in turbidity results in an increase in the consumption rates of prey by the pike. De Robertis et al. (2003) found the reduction in visibility to result in a decrease in the absolute mortality rate on prey by piscivores, while Abrahams and Kattenfeld (1997) found no difference in the absolute mortality rates from clear to turbid water; Abrahams and Kattenfeld (1997) instead observed predators consuming small size fishes in clear water, while in turbid water, there was no preference of any size range of fishes. The feeding rates of planktivorous fishes are not necessarily negatively affected by turbidity (Bonner and Wilde 2002; De Robertis et al. 2003). The effect of increasing turbidity on foraging ability of both predators and prey is therefore not consistent between systems.

The response to turbidity, as measured by foraging success, is species-specific and dependent on the sensory mechanisms of the species, including the presence of a tapetum lucidum. The tapetum lucidum is a reflecting layer found in some species of fishes. It acts to reflect light back towards the retina, providing photoreceptors with another opportunity for stimulation, enhancing the sensitivity of eye; acuity may be reduced (Braekeveklt 1980). For

example, pikeperch (*Sander lucioperca*), which have tapetum lucidum, are not affected by increases in turbidity, while European perch (*Perca fluviatilis*) foraging efficiency declines with increasing turbidity (Ljunggren and Sandström 2007). Morphologies of fishes can therefore influence their ability to forage under different turbidity levels.

Overview of research conducted:

My research addresses four questions pertaining to the role of the abiotic environment in predator-prey interactions:

1) Temperature: Given what is known regarding the increase in energetic demands in poikilothermic individuals with increasing temperature, as temperatures increase what are the behavioural responses of prey? Do these responses change in the presence of a predator? Do the prey, in order to meet increased metabolic demands, increase their activity and foraging rate as temperature increases? Are those prey then willing to increase their risk taking, foraging in the presence of a predator in order to meet metabolic demands (Chapters 2 and 3)?

2) Temperature, dissolved oxygen and turbidity: In a natural, shallow water ecosystem, what is the role of temperature, dissolved oxygen and turbidity in structuring the fish community composition? Does the community composition of predators change with the changing environment, altering the predation risk to prey (Chapter 4)?

3) Temperature: Given what is known regarding the role of temperature in determining the energetic requirements of prey and predators, the role temperature plays in determining population doubling times of zooplankton and algae - photosynthesis can be temperature dependent - (minnow forage), and the influence temperature has on activity rates of fishes, does

the probability of survival of prey fishes over the ice-free season change with changing temperatures (Chapter 5)?

4) Temperature, dissolved oxygen and turbidity: Behavioural responses to a changing aquatic environment can affect not only fish predator – fish prey interactions but also avian predator-fish prey interactions. In response to physiological demands under differing abiotic conditions, do fishes alter their behaviours in such a way as to change their interactions with avian predators? Specifically, I am interested in whether or not a numerical response in the number of Forster's terns (*Sterna forsteri*) occurs as a result of changes in the aquatic environment (Chapter 6).

Addressing the role of the environment in predator-prey interactions. The research conducted to address the above mentioned questions ranged from large scale monitoring of aquatic ecosystems, to small scale laboratory experiments to computer modeling. The influence of temperature on the activity and foraging rates of fathead minnows (*Pimephales promelas*) was determined by a series of laboratory experiments. As temperature increased, both the activity and foraging rates of the fathead minnows increased. Laboratory experiments using yellow perch (*Perca flavescens*) as predators and fathead minnows as prey fish were also conducted to examine the influence of temperature on a) risk-taking in prey fish and b) the response of predators to changes in prey behaviour. Fathead minnows in this experiment were given food at two locations, a safe and a risky location. In control trials, the risky feeder was next to an empty aquarium while in the predator treatment trials the aquarium contained a perch predator. Increases in temperature increased the number of fishes foraging, but the number of foragers at each temperature did not change with the addition of a predator. However, in the presence of a

predator only fishes held at the warmest temperature did not change their use of the feeder in the risky location. In response to increased numbers of fish foraging and an increase in the use of the risky feeder with temperature, at the warmest temperature the predators spent more time oriented towards the prey.

Field work examining the potential for temperature, dissolved oxygen and turbidity to control the spatial overlap of predatory fish and their prey (thereby influencing encounter and detection rates of these predators and prey) was conducted in Blind Channel, Delta Marsh, Manitoba, Canada. Blind Channel is a shallow water ecosystem found just south of Lake Manitoba and is connected to the lake via one passage. Fish community composition was monitored by gillnetting and minnow trapping from May through August in 2006, 2007 and 2008 and environmental variables (temperature, dissolved oxygen and turbidity) were monitored every 30 minutes via YSI data sondes throughout the entire sampling period. As temperatures increased, the catch per unit effort (CPUE) of both cool- and warm- water fishes increased. Dissolved oxygen (DO) levels were significantly related to two groups of fish with different physiologies. As DO increased, there was an increase in the CPUE of fishes with physostomous swim bladders (those fish that have the potential to perform aerial surface respiration); CPUE of fishes without that capability were negatively related to DO levels. Turbidity levels were not related to the CPUE of either fish species.

Building on the results from my field and laboratory studies to further understand how temperature changes may affect the overall survival of a population of fathead minnows, a computer model was developed that integrated results from field studies with those from the literature. Specifically, the model was developed to incorporate temperature into the costs and

benefits of selecting a specific patch. Temperature increases consistently resulted in a reduction in the probability that an individual survives the ice-free season.

To examine the role of temperature, dissolved oxygen and turbidity on prey fish – avian predator interactions in the field, monitoring of Blind Channel was conducted not only to measure environmental variables and prey fishes as mentioned above, but also to determine Forster's terns, *Sterna forsteri* presence. Only DO was a significant predictor of tern presence; there was no relationship between tern abundance and the abundance of their prey suggesting that it is the availability of the prey and not their abundance that drives the presence of terns.

There are obviously complex interactions that occur between organisms and the temperature as well as the dissolved oxygen and turbidity levels of the habitats they occupy. Future research should attempt to disentangle the role that each of the measured environmental variables plays in predator-prey interactions in a natural ecosystem. This would also allow for more accurate measures of parameters that were used in the model, and the development of more specific predations to be tested. Overall, research conducted for this dissertation predicts that as temperature increases, prey will experience an increase in the risk of mortality.

All experiments and field research described in this thesis were conducted under approved protocols F08-013 and F03-041 by the protocol management review committee at the University of Manitoba as per the guidelines of the Canadian Council for Animal Care. All sampling conducted in Blind Channel was approved by Manitoba Conservation.

References

Abrahams, M.V. 2006. The physiology of antipredator behaviour: what you do with what you've got. In: *Behaviour and Physiology of Fish; Volume 24, Fish Physiology*. K.A. Sloman, S. Balshine, and R.W. Wilson, (editors), pp 79-108. London, UK: Academic Press.

Abrahams, M., Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioural Ecology and Sociobiology **40**: 169-174.

Almedia-Val, V.M.F., Val, A.L., Duncan, W.P., Souza, F.C.A., Paula-Silva, M.N., Land, S. 2000. Scaling effects on hypoxia tolerance in the Amazon fish *Astronotus ocellatu* (Perciformes: Cichlidae): contribution of tissue enzyme levels. Comparative Biochemistry and Physiology Part B **125**: 219-226.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on a predator–prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Bergman, E. 1987. Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus.* Environmental Biology of Fishes **19**: 45-53.

Bonner, T.H., Wilde, G.R. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society **131**: 1203-1208.

Braekevelt, C.R. 1980. Fine structure of the retinal epithelium and tapetum lucidum in the giant danio (*Danio malabaricus*) (Teleost). Anatomy and Embryology **158**: 317-328.

Burleson, M. L., Wilheml, D.R., Smatresk, N.J. 2001. The influence of fish size on the avoidance of hypoxia and oxygen selection by largemouth bass. Journal of fish Biology **59**: 1336-1349.

Chapman, L.J., Chapman, C.A. 1998. Hypoxia tolerance of the mormyrid *Petrocephalus catostoma*: Implications for persistence in swamp refugia. Copeia **1998**:762-768.

Chapman, L.J., Chapman, C.A., Nordlie, F.G., Rosenberger, A.E. 2002. Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. Comparative Biochemistry and Physiology Part A **133**: 421-437.

Chapman, L.J., Kaufman, L.S., Chapman, C.A., McKenzie, F.E. 1995. Hypoxia tolerance in twelve species of East African cichlids: Potential for low oxygen refugia in Lake Victoria. Conservation Biology **9**: 1274-1288.

De Robertis, A., Ryer, C.H., Veloza, A., Brodeur, R.D. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences **60**: 1517-1526.

Hammel, H.T. 1955. Thermal properties of fur. American Journal of Physiology **182**: 369-376.

Hansen, J., Salo, M., Ruedy, R., Lo, K., Lea, D.W., Medina-Elizade, M. 2006. Global temperature change. Proceedings of the National Academy of Sciences, USA **103**: 14288-14293.

Holker, F. 2003. The metabolic rate of roach in relation to body size and temperature. Journal of Fish Biology **62**: 565-579.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist **91**: 385-898.

Javaid, M.Y., Anderson, J.M. 1967. Influence of starvation on selected temperature of some salmonids. Journal of the Fisheries Research Board of Canada **24**: 1515-1519.

Johnson, J.A., Kelsch, S.W. 1998. Effects of evolutionary thermal environment on temperature-preference relationships in fishes. Environmental Biology of Fishes **53**: 447-458.

Kramer, D.L. 1987. Dissolved oxygen and fish behavior. Environmental Biology of Fishes **18**: 81-92.

Krause, J., Godin, J.-G. J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour **50**: 465-473.

Ljunggren, L., Sandström, A. 2007. Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. Journal of Fish Biology **70**: 1319–1334.

Lundvall, D., Svanback, R., Persson, L., Bystrom, P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Canadian Journal of Fisheries and Aquatic Science **56**: 1285-1292.

Magnuson, J.T., Crowder, L.B., Medvick, P.A. 1979. Temperature as an ecological resource. American Zoologist **19**: 331-343.

Magnuson, J.J., de Stasio, B.T. 1997. Thermal niche of fishes and global warming. In: *Global Warming -- Implications of Freshwater and Marine Fish*. C.M. Wood and D.G. McDonald (editors), pp. 377- 408, Cambridge, U.K: Cambridge University Press.

Meeuwig, M.H., Dunham, J.B., Vinyard, G.L. 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. Ecology of Freshwater Fish **13**: 208-216.

Morgan, I.J., Metcalfe, N.B. 2001. The preferred temperature of overwintering juvenile salmon is influenced by future energetic requirements. Canadian Journal of Fisheries and Aquatic Sciences **58**: 762-768.

Nilsson, P.A., Jacobsen, L., Berg, S., Skov, C. 2009. Environmental conditions and intraspecific interference: Unexpected effects of turbidity on pike (*Esox lucius*) foraging. Ethology **115**: 33-38.

Ojanguren, A.F., Reyes-Gavilán, F.G., Braña, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. Journal of Thermal Biology **26**: 165-170.

Sogard, S.M., Olla, B.L. 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy-conserving mechanisms. Marine Ecology Progress Series **133**: 43-55.

Smith, T.B. 2008. Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral-algal competition. Coral Reefs **27**:397-405.

Suthers, I.M., Gee, J.H. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Canadian Journal of Fisheries and Aquatic Sciences **43**: 1562-1570.

van Dijk, P.L.M., Staaks, G., Hardewig, I. 2002. The effect of fasting and refeeding on temperature preference, activity and growth of roach, *rutilus rutilus*. Oecologia **130**: 496-504.

Weetman, D., Atkinson, D., Chubb, J.C. 1998. Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulta.* Animal Behaviour **55**: 1361-1372.

Wootton, R.J. 1990. Ecology of Teleost Fishes: Fish and Fisheries Series 1. Chapman and Hall, London. 404 pages.

Chapter 2: Activity rates and foraging attempts of fathead minnows (*Pimephales promelas*) at three temperatures: implications for predator-prey interactions

Abstract. There is general consensus that the earth is in a warming phase. Fishes in temperate ecosystems are ectothermic and there is potential that this could significantly modify the nature of predator-prey interactions. In particular, I expect that in a warmer environment increasing energetic demands upon both predator and prey will result in a reduction in the indirect effects of predation (e.g., changes in the behaviour to avoid being killed by a predator). To determine whether this is likely to occur I directly measured the how the behaviour of a common prey species, the fathead minnow, changed with temperature. Fish were held at one of three temperature regimes: 4, 15, and 24°C and their activity and foraging rates were determined from 30 minute trials during which food was administered remotely at the 15 minute mark. Fish were significantly more active at 15°C than at 4°C and significantly more active at 24°C than at 15°C. There was also a significant effect of temperature on the foraging rates of the fathead minnow. Significantly more foraging attempts were undertaken at 24°C than at both 15°C and 4°C. No differences in foraging attempts were observed between 15°C and 4°C treatments. The results of this study demonstrate that temperature does influence the foraging behaviour of small fish in a manner that suggests that the influence of predation risk will be reduced at higher temperatures.

Introduction

Studies of predator-prey interactions stress the importance of predation in structuring aquatic environments (Brodeur and Pearcy 1992, Caley 1995, Jackson et al. 2001, Baum and Worm 2009, Palkovacs and Post 2009) through both direct (consumption) and indirect (habitat use patterns, group vigilance, competition, etc) effects (Sih 1987, Mittelbach and Chesson 1987). Short-term responses to predation risk are common and include hiding and "waiting out" a predator (Johansson and Englund 1995) and a reduction in prey activity (Rahel and Stein 1988, Eklöv and Werner 2000). However, individuals cannot hide indefinitely. They must acquire enough energy to meet their metabolic demands, as well as growth, reproduction, and predator avoidance. The presence of predators in the environment imposes the constraint that food be obtained without becoming food for others. In aquatic ecosystems where fishes are ectothermic (Wootton 1990), energy requirements for both predator and prey should be strongly affected by temperature.

There is an obvious role of physiology in predator-prey interactions as the mechanism that links the physical environment to changes in behaviour (Abrahams 2006). For ectothermic individuals, as temperature increases energetic demands the requirement for food should also increase, which in turn should increase foraging rates. At high temperatures, prey should be increasingly affected by these energetic considerations: the hungrier an individual, the more energy it will devote to finding food (Dill and Fraser 1984, Godin and Crossman 1994). A field study (Smith 2008) conducted over a temperature difference of 8 C° (21.1 – 29.4°C) suggested that the feeding rate of a herbivorous fish increases with increasing temperature, though this result was not consistent across sites and the amount of food available was not measured. A

mean temperature increase of 2°C was also enough to increase the feeding rate of another subtropical fish (Mendes et al. 2009).

However, an increase in foraging with increasing temperature does not appear to be a strictly linear relationship, and in some studies, there does not appear to be any relationship at all between temperature and feeding. Van Dijk et al. (2002) determined that roach (*Rutilus rutilus*) feeding rates increased until a temperature of 18°C was reached. Beyond that temperature, feeding rates leveled off and then declined. Similarly, Meeuwig et al. (2004) found that feeding rates in juvenile cutthroat trout (*Oncorhynchus clarki henshawi*) peaked at 18°C relative to those observed 12 and 18°C.

Vital rates in ectotherms are strongly dependent on temperature. Temperature, therefore, has the potential to constrain functions such as energy acquisition, physiological adaptation and behaviour (Schultz and Connor 1999, Biro et al. 2005, Larsson et al. 2005). Both Krause and Godin (1995) and Hurst and Duffy (2005) observed an increase in the activity levels of fishes with increasing temperature, in the absence of food. Under increasing temperatures, it is therefore expected that in the presence of food, activity of fishes might increase further. Understanding how temperature, through its effect on energetic demands of fishes, influences the foraging and activity of these fishes is important to our understanding of how predator-prey interactions will change in response to a changing thermal regime.

Materials and Methods

Study animals. Fathead minnows (*Pimephales promelas*) were used for these experiments. They are common across central North America and are distributed in Canada from New Brunswick in

the east west into Alberta. They average 51 mm total length (Scott and Crossman 1998). Within their range, the minnows may experience a wide range of temperatures both seasonally and daily. Approximately 60 fathead minnows (mean ± SE length: 48 ± 0.8 mm) for this experiment were obtained from small ponds in southern Manitoba, Canada, in the spring of 2007 (at a water temperature of 10°C) and held in 200-l aquaria. The water temperature of all three aquaria was increased to 26°C for a period of two weeks. After that period, the temperature of the aquaria was decreased at a rate of approximately 1°C per day, until one aquaria was at each of three temperatures (4, 15 and 24˚C). Fish were held at these temperatures under a 12 hour light:12 hour dark regime at the Animal Holding Facility at the University of Manitoba for at least two weeks prior to commencement of the experiment. They were fed *ad libitum* Nutrafin flakes and frozen bloodworms.

Experimental protocol. Approximately 24 hours before the start of the experiment, a randomly (haphazardly) selected group of three fish was removed from each of the three tanks and placed in a 76-l aquarium containing water of the same temperature (4, 15 or 24°C). Fish were not fed after being placed in the aquaria until the feeding component of the experiment. Aquaria were covered on three sides preventing visual contact between individuals occupying separate aquaria. A ruler was placed along the bottom edge of each aquarium to allow for measurements of distances travelled (see below for methods). All trials were conducted in an environmental chamber, which minimized disturbance to the fish. Experiments were conducted between 1400 and 1500 hours and lasted for 30 minutes.

The effect of temperature on the activity rate (distance covered/frame) and foraging attempts (number of bites made at the surface/frame) of fathead minnows was observed during

thirty-minute trials. The first 15 minutes recorded baseline information in the absence of food. The second 15 minutes provided foraging information in the presence of 0.5 g of Nutrafin flakes. This food was dispersed remotely; a burst of air was delivered from outside the environmental chamber through tubing that entered the chamber. This tubing was connected to a small piece of polyvinyl chloride with two holes – a large hole was used as a means of placing food into the device, which was covered during the trial, and a small hole through which the food exited upon administration of the burst of air (Figure 2.1). Six trials, each consisting of three fish, were conducted at each temperature. A single Panasonic CCTV WV-CP484 SDIII camera with Pentax 3.5-8mm F/1.4 CS auto iris lenses was used to record each trial. Video data were recorded to Digital Video Disc (DVD) via a Toshiba 1080P UP Conversion D-R7. All tanks were emptied and rinsed between trials to eliminate any remaining food. All video data were converted to stacked frames using VirtualDubMod (Version 1.4.10, Lee 2006) and saved as bitmap files. These files were then imported as a sequence to ImageJ (version 1.38, 2007) for further analysis.

Foraging attempts. I recorded the number of foraging attempts conducted by the most active fathead minnow (hereafter, focal individual) during the 15 minutes post food addition. Foraging attempts were classified as movement by the minnow to the surface of the water followed by mouth opening and closing after food was administered (no observation of this behaviour occurred before addition of the food). Nutrafin flakes remained floating at the

Air hoses – connected to external air source. Circle represents opening from outside to inside of the environmental chamber.

aquarium   aquarium   aquarium
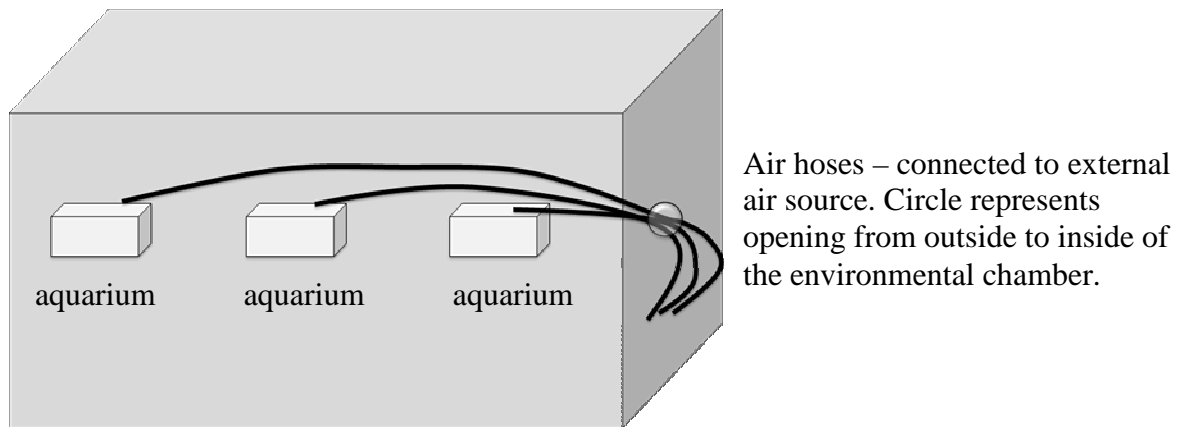
Figure 2.1: Diagram of the experimental set-up. The large box represents the environmental chamber as a whole. Food is located at the end of the air hoses and is delivered to fish in the aquaria when the external air source is turned on.

surface of the aquaria for the remainder of the trial. A single factor ANOVA using $\log_{10}$(number of attempts +1) as the dependent variable and temperature as the independent variable was used to statistically analyze data.

Distance travelled. The distance travelled (a proxy measure of activity) by the focal individual in each aquarium was measured using the position of the minnow in the aquaria at 5 sec intervals (every 150th frame). Analysis of each trial began with a calibration of the ruler tool in ImageJ using the ruler on the bottom edge of the aquarium. Next, the position of the focal individual was marked in ImageJ, again using the ruler tool at time one. After advancing to the next frame (5 seconds later), I marked the new position of the focal individual using the software tool. This continued until the end of the trial. At the end of the trial, the total distance travelled per total time of the trial was determined.

As the presence of food may influence the activity of individuals, an initial analysis was conducted using Student's t-test to determine if there were differences in distances travelled/frame before and after a feeding bout. If there were no differences in activity of fish before and after feeding at any of the temperatures, the average total distance travelled at each temperature for the entire 30 min of the trial would be used in subsequent analysis. A single factor ANOVA with distance travelled as the dependent variable and temperature as the independent variable was used to test for differences in distance travelled/frame among the three temperatures.

Each trial represented a single, independent observation as fish were only used once in the experiment. All data were tested for normality and homogeneity of variance, and any non-normal data were transformed to meet normality standards. Alpha values were set at 0.05 for all

analysis and all analyses were conducted using STATISTICA software (StatsSoft Software, STATISTICA version 8, 2007).

Results

Foraging attempts. There was a significant effect of temperature on foraging attempts made by fathead minnows ($F_{2, 15} = 21.69$, P = 0.00001, Figure 2.2). Post hoc analysis determined that significant differences were observed between mean foraging attempts at both 4˚C and 15˚C temperatures when compared to mean foraging attempts at 24˚C (Table 2.1). No difference was observed between mean foraging attempts of minnows held at 4˚C and those held at 15˚C (Table 2.1). The magnitude of change in foraging attempts was greatest between 4˚C and 24˚C water treatments (a five-fold increase in foraging attempts at 24˚C when compared to 4˚C). There was an approximate two-fold increase in foraging attempts between the 15 and 24˚C treatments.

Distance travelled. The initial two-way ANOVA indicated that there were no significant differences in activity of fish before and after feeding at any of the temperatures (paired t-test: 4˚C: t = 0.276, P = 0.785; 15˚C: t = -1.03, P = 0.315; 24˚C: t = -0.717, P = 0.481; df = 10 for all analysis; Figure 2.3). With no differences in distance travelled (cm) per frame
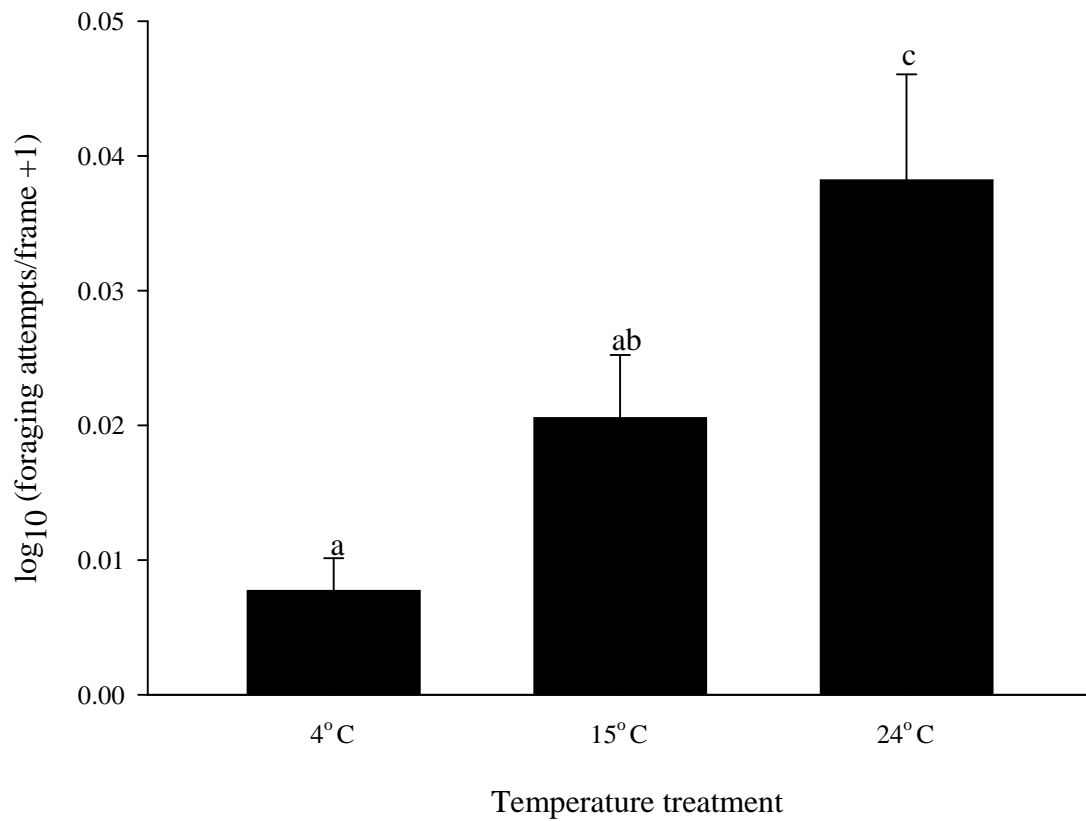
Figure 2.2: Mean number of foraging attempts per frame of fathead minnows at three temperature regimes. Bars represent standard error around the mean. Letters above the bars represent significant differences at α = 0.05 using Tukey post hoc tests.

Table 2.1: Summary of Tukey's HSD post hoc test of the influence of temperature on foraging attempts of minnows. Significant differences were observed between foraging attempts made at both cold and cool temperatures when compared to mean foraging attempts/ frame made at warm temperatures. Significant differences are indicated with bold values. No difference was observed between mean foraging attempts/ frame made under cold and cool water treatments.

Treatment	4°C	15°C	24°C
4°C	-	0.252	**0.00359**
15°C		-	**0.0890**
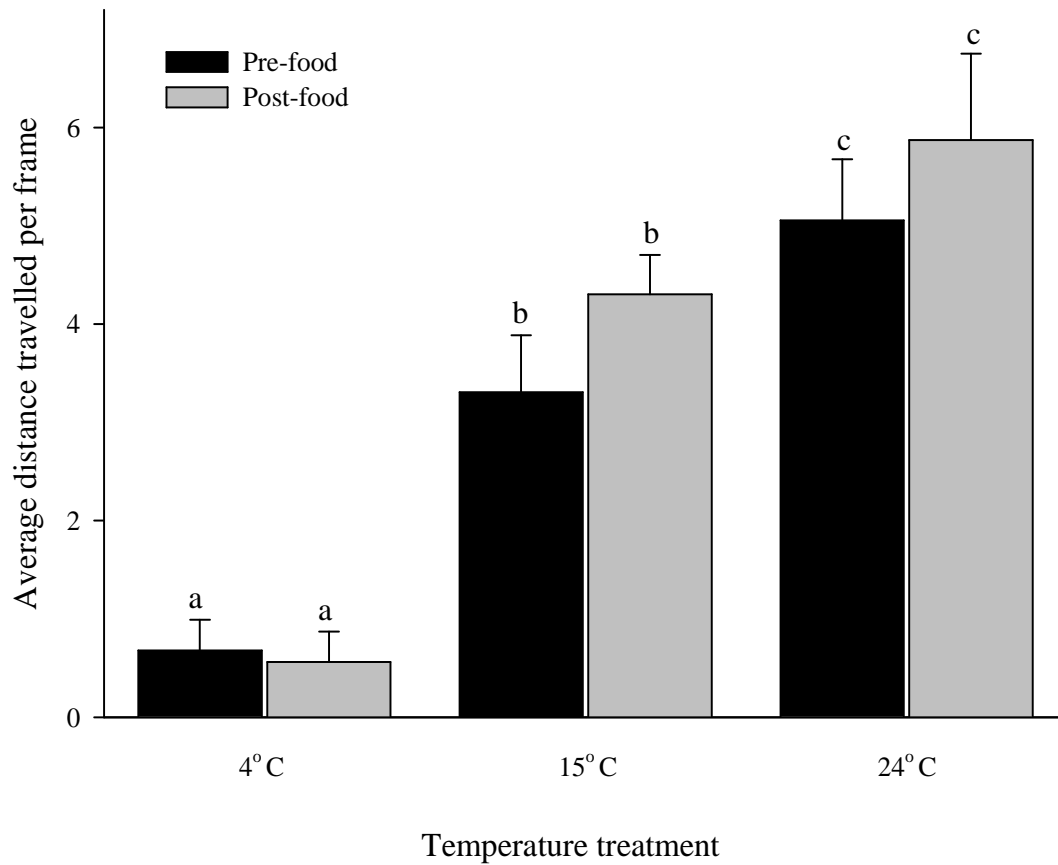
Figure 2.3: Mean distance travelled (cm) per frame of fathead minnows, pre- and post-administration of food, at three temperature regimes. Bars represent standard error around the mean. Letters above the bars represent significant differences at $\alpha = 0.05$ using Tukey post hoc tests.
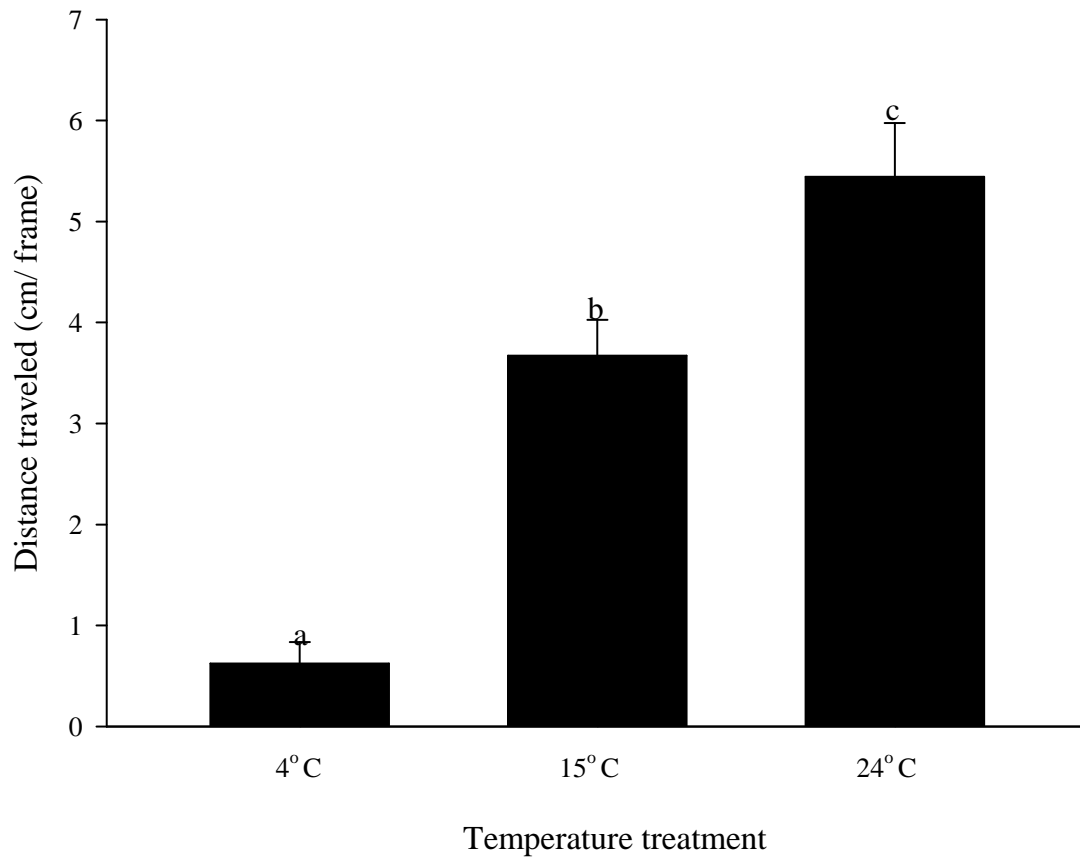
Figure 2.4: Mean (pre- and post- feeding) distance travelled (cm) per frame of fathead minnows at three temperature regimes. Bars represent standard error around the mean. Letters above the bars represent significant differences at α = 0.05 using Tukey post hoc tests.

before and after feeding, the average distance travelled/frame for the entire 30 min duration of the trial for each temperature was used in a single factor ANOVA to determine the effect of temperature on activity rates of fathead minnows. There was a significant effect of temperature on activity rates ($F_{2,15} = 81.37$, $P < 0.0001$; Figure 2.4) and a Tukey's HSD (honestly significant difference) test determined that there were significant differences between each temperature treatment (Table 2.2). There was a six-fold increase in activity rates between 4˚C and 15˚C, and a 1.5 times increase between 15˚C and 24˚C.

Discussion

In this study, both foraging and activity rates increased with increasing temperature. When compared to fishes occupying 4˚C water, fishes held at 24˚C increased their distance travelled per frame by a magnitude of nearly nine-fold. A ten-fold increase in foraging attempts was observed between fishes held at 4˚C and those held at 24˚C. In measures of both foraging and activity, fish held at 15˚C displayed intermediate foraging and activity levels. These increases in foraging as temperatures increase is similar to that observed in an herbivorous marine fish foraging under different thermal regimes (Smith 2008). Increased foraging with temperature has also been observed in juvenile brown trout, *Salmo trutta* (Ojanguren et al. 2001) and brook trout, *Salvelinus fontinalis* (Taniguchi et al. 1998). Increases in activity with temperature agrees with the results of Krause and Godin (1995) who also observed fishes held at warmer temperatures moved more rapidly and made quick turns.

Table 2.2: Summary of Tukey's HSD post hoc test of the influence of temperature on activity rates of minnows. Significant differences were observed in activity rates between all temperatures as indicated by bold values.

Treatment	4°C	15°C	24°C
4°C	-	**0.000126**	**0.000126**
15°C		-	**0.000133**

These results suggest that temperature is a driving force influencing the activity and energy budgets of fathead minnows, and that the effect of temperature may be exacerbated by positive feedback. At warmer temperatures fish are required to increase their foraging to meet their higher energetic demands. To do so, they increase their level of activity. The increased requirements for food mean they are less likely to integrate predation risk into their decision-making processes (Dill and Fraser 1984, Godin and Crossman 1994) as incorporating risk of predation into the decision to forage or not is a state-dependent decision (Magnhagen 1988, Gregory 1993). A satiated individual is less likely to take a risk to obtain food as compared to a hungry individual; the satiated individual can rely on its energetic reserves, which negates the need to forage under risk of predation. Hungry individuals are therefore more likely to take the risk and forage while predators are present which in turn may result in increased detection and capture rates by predators.

Anderson et al. (2001) found that increasing temperatures increased growth of larval anurans (*Hyla regilla*), which was expected to reduce the mortality rates of these larger individuals as their predators were gape limited; growth decreases the number of gape limited predators that can consume prey (Magnahagen and Heibo 2001) and offers a potential refuge for prey (Urban 2007). However the increase in growth of larval anurans in the study by Anderson et al. (2001) resulted in the observed increase in mortality of anurans held at higher temperatures. While activity and foraging rates were not measured in that study, it is probable that the increase in growth rates at high temperatures were a result of increased foraging and activity levels of the larval anurans, which in turn resulted in the higher morality of anurans. This in itself is likely a result of increased encounters between prey and predators as foraging/activity of prey increased with increased temperature. Increased activity has also been linked to increased mortality rates

in the damselfly, *Coenagrion hastulatum* (Brodin and Johansson 2004) and flounder, *Pseudopleuronectes americanus* (Taylor and Collie 2003) when predators are also ectothermic.

The study by Anderson et al. (2001) suggests that high temperatures results in higher predation risk. However there is a possibility that low temperatures and the resulting low activity rates as observed in this study may not necessarily result in a reduction in predation risk. Muscle function and swim speed are reduced when temperatures are low (Claireaux et al. 2006, Jones et al. 2008) and may result in a reduction in the ability to escape faster swimming predators. Johnston et al. (2004) observed the activity of young-of-year Atlantic salmon (*Salmo salar*) and determined that at low temperatures ($< 7\degree$C) salmon become less active (as observed in this study) and spend more time hiding – they also become nocturnal at low temperatures. If only the prey are ectothermic, a reduction in muscle function and swim speed may actually increase the vulnerability of fish to predation – a possible explanation for the observation of a switch to nocturnal behaviour of the salmon to avoid their endothermic predators at low temperatures (Johnston et al. 2004).

If increased temperature results in increased encounters between predators and their prey, the potential detrimental effects to prey as a result of increased temperatures will likely be beneficial to a predator. Prey are more active at higher temperatures and therefore less cryptic (Gotceitas and Godin 1991) and predators have demonstrated a preference for active prey (Krause and Godin 1995). With an increase in activity and foraging rates with temperature, it is expected that fathead minnows would experience an increase in predation risk with increasing temperature. Mitigating effects of increased predation risk might include increased mobility and escape capabilities at increased temperatures (Persson 1986) as muscle function and swim performance are temperature dependent (Logue et al. 1995).

How individual prey tradeoff increasing energy acquisition against decreased safety from predators can dictate the flow of energy within an ecosystem (Trussell et al. 2006). The energy flow within an ecosystem is itself determined by prey being consumed by predators and the rate of food consumed by these prey. Both of these factors are affected by temperature and both of these factors interact with one another. As temperature increases, food consumption and activity rates of prey increase making it increasingly difficult to meet their energetic demands. It is likely that these individuals will be less concerned with predation risk when it comes to decision making as their efforts are focused on food consumption. And not only are these individuals likely not incorporating predation risk as fully into decision making as individuals inhabiting cooler temperatures, but the increased activity observed at high temperatures likely renders these individuals more easily detected by predators. As aquatic ecosystems warm in response to climate change, prey will likely experience an increase in mortality as consumption rates by predators increase in response to their own increase in metabolic demands and in response to an increase in availability (through increased movements and therefore detection) of prey to predators.

References

Abrahams, M.V. 2006. The physiology of antipredator behaviour: what you do with what you've got. Fish Physiology. K. A. Sloman, S. Balshine, and R.W. Wilson. Elsevier Inc. **24**: 79-107.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and

indirect effects of temperature on a predator-prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Anholt, B.R., Werner, E., Skelly, D.K. 2000. Effect of food and predators on the activity on four larval ranid frogs. Ecology **81**: 3509-3521.

Baum, J. K., Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology **78**: 699-714.

Biro, P. A, Post, J. R., Abrahams, M. V. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk taking behaviour in young fish cohorts. Proceedings of the Royal Society of London Series B **272**: 1443-1448.

Brodeur, R.D., Pearcy, W.G. 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Marine Ecology Progress Series **84**: 101-119.

Brodin, T., Johansson, F. 2004. Conflicting selection pressures on the growth/predation-risk trade-off in a damselfly. Ecology **85**: 2927-2932.

Caley, M.J. 1995. Reef-fish community structure and dynamics: an interaction between local and larger-scale processes? Marine Ecology Progress Series **129**: 19-29.

Claireaux, G., Couturier, C., Groison, A.L. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). Journal of Experimental Biology **209**: 3420-3428.

Dill, L.M., Fraser, A.G.H. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioral Ecology and Sociobiology **16**: 65-71.

Eklöv, P., Werner, E.E. 2000. Multiple predator effects on size-dependent behavior and mortality of two species of anuran larvae. Oikos **88**: 250-258.

Godin, J.-G. J., Crossman, S.L. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behavioral Ecology and Sociobiology **34**: 359-366.

Gotceitas, V., Godin, J.-G.J. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behavioural Ecology and Sociobiology **29**: 255-261.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behavior of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **50**: 241-246.

Hurst, T.P., Duffy, T.A. 2005. Activity patterns in northern rock sole are mediated by temperature and feeding history. Journal of Experimental Marine Biology and Ecology **352**: 201-213.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences **58**: 157-170.

Johansson, A., Englund, G. 1995. A predator-prey game between bullheads and case-making caddis larvae. Animal Behaviour **50**: 785-792.

Johnston, P., Bergeron, N.E., Dodson, J.J. 2004. Diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity. Journal of Fish Biology **65**: 1305-1318.

Jones, E.A., Jong, A.S., Ellerby, D.J. 2008. The effects of acute temperature change on swimming performance in bluegill sunfish *Lepomis macrochirus.* Journal of Experimental Biology **211**: 1386-1393.

Krause, J., Godin, J.-G.J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour **50**: 465-473.

Larsson, S., Forseth, T., Berglund, I., Jensen, A.J., Näslund, I., Elliott, J.M., Jonsson, B. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshwater Biology **50**: 353-368.

Magnhagen, C. 1988. Predation risk and foraging in juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). Canadian Journal of Fisheries and Aquatic Sciences **45**: 592-596.

Magnahagen, C., Heibo, E. 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. Functional Ecology **15**: 754-762.

Meeuwig, M.H., dunham, J.B., G.L. Vinyard. 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. Ecology of Freshwater Fish **13**: 208-216.

Mittelbach, G.G., Chesson, P.L. 1987. Predation risk: Indirect effects on fish populations. Pages 537-555 *in* Predation: Direct and Indirect Impacts on Aquatic Communities. W.C. Kerfoot and A. Sih editors. University Press of New England, Hanover, New Hampshire, USA.

Ojanguren, A.F., Reyes-Gavilán, F.G., Braña, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. Journal of Thermal Biology **26**: 165-170.

Palkovacs, E.P., Post, D.M. 2009. Experimental evidence that phenotypic divergence in predators drives community divergence in prey. Ecology **90**: 300-305.

Persson, L. 1986. Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): Implications for coexistence between poikilotherms. Journal of Animal Ecology **55**: 829-839.

Rahel, F.J., Stein, R.A. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. Oecologia **75**: 94-98.

Schultz, E. T., Conover, D. O. 1999. The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. Oecologia **119**: 474-483.

Scott, W.B., Crossman, E.J. 1998. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada **184**:1-966.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 *in* Predation: Direct and Indirect Impacts on Aquatic Communities. W.C. Kerfoot and A. Sih, editors. University Press of New England, Hanover, New Hampshire, USA.

Smith, T.B. 2008. Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral-algal competition. Coral Reefs **27**:397-405.

Taniguchi, Y., Rahel, F.J., Novinger, D.C., Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences **55**: 1894-1901.

Taylor, D.L., Coolie, J.S. 2003. Effect of temperature on the functional response and foraging behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter flounder *Pseudopleuronectes americanus*. Marine Ecology Progress Series **263**: 217-234.

Trussell, G.C., Ewanchuk, P.J., Matassa, C.M. 2006. The fear of being eaten reduces energy transfer in a simple food chain. Ecology **87**: 2979-2984.

Urban, M.C. 2007. Risky prey behavior evolves in risky habitats. Proceedings of the National Academy of Sciences of the USA **104**: 14377-14382.

Wootton, R.J. 1990. Ecology of Teleost Fishes. Chapman & Hall, London, 404p.

Chapter 3: Risk-taking and temperature: what deviations from the ideal free distribution tell us about the influence of temperature on predator-prey interactions

Abstract. As temperatures increase, the metabolic rates of fishes increase. It was hypothesized that prey would take greater risks to achieve increased foraging payoffs to meet these increased energetic demands. To test this hypothesis, prey were provided opportunities to feed in low and high risk locations at three temperature regimes in the presence and absence of a predator held at a constant temperature. In the absence of predators, prey distributed themselves between feeding locations as predicted by the Ideal Free Distribution (IFD) at all temperatures with the highest feeding activity at 23°C. Only at 23°C did the presence of a predator not significantly alter this distribution. The behaviour of the predators was also affected by temperature with their time spent oriented towards the prey greatest at 23°C. These results suggest that increasing temperatures will generate increasing mortality rates of prey due to more prey willing to take greater risks to obtain food in combination with their predators also requiring more food to meet their elevated energy demands.

Introduction

The best-known role of predators within ecosystems is their consumption of prey; they also have indirect effects as prey modify their behaviour to avoid being consumed (Mittelbach 1984, Mittelbach and Chesson 1987, Sih 1982, Werner et al. 1983). Prey however, cannot spend all of their time avoiding predators as their energetic requirements must be met in order to avoid starvation. Habitat choices made by prey must therefore balance the benefits of avoiding predators with the net energy benefits of the food obtained (MacArthur and Pianka 1966, Werner and Gilliam 1984). Since both these parameters will vary in space and time, these decisions will constantly need to be updated (Sih 1987; Abrams 1991; Dill and Fraser 1984). Important factors affecting the prey's decisions include energetic state (Dill and Fraser 1984; Godin and Crossman 1994), predation pressure by gape-limited predators (Urban 2007) and the possibility of future foraging opportunities under reduced predation risk (Lima and Bednekoff 1999).

A large number of theoretical studies have been devoted to predicting the distribution of prey among habitat patches that have inherent risks and rewards (food) associated with them. Empirical and theoretical studies that suggest prey distribution among patches is dependent upon both resource distribution and predation risk (Gilliam and Fraser 1987, Abrahams and Dill 1989, Lima and Dill 1990, Grand and Dill 1997). In fact, Abrahams and Dill (1989) suggest that prey will use an inherently risky patch if the level of food is increased to a point at which risk of predation is offset. It is unknown if the abiotic environment will affect the distribution of fishes between habitat patches when these patches differ in risk but have equal quantities of food present.

Environmental parameters such as dissolved oxygen (Kramer et al. 1983, Wolf and Kramer 1987, Robb and Abrahams 2002), light level (see Lima and Dill 1990), turbidity

(Abrahams and Kattenfeld 1997), and temperature (Krause and Godin 1995) can have an impact on the behavioural decisions made by prey and their predators. Of particular interest in this paper is temperature, since metabolic rates of fishes will increase with temperature, (Wootton 1990). It is assumed that these increases in metabolic rates result in increased energy demands which will in turn increase the risk they are willing to incur to feed (Magnhagen 1988, Gregory 1993).

Anderson et al. (2001) found that increased temperatures increased the growth of larval anurans (*Hyla regilla*). As body size decreases the number of predators increases, (Magnahagen and Heibo 2001), meaning that a large size offers a potential refuge for prey (Urban 2007). Anderson et al. (2001) therefore expected that increased temperatures would result in a reduction in the mortality risk of the individuals reared at higher temperatures. However, they observed an increase in the number of anurans consumed by predators at higher temperatures. While activity and foraging rates were not measured in that study, it is probable that the increase in growth rates at high temperatures were a result of increased foraging and activity levels of the larval anurans, which in turn resulted in the higher mortality of anurans. This might be a result of increased encounter rates between predator and prey; foraging prey are less cryptic (Gotceitas and Godin 1991) and predators have demonstrated a preference for active prey (Krause and Godin 1995). The expectation is that as temperatures increase, in order to meet increased energetic demands, prey will increase their use of risky habitats which will in turn increase their mortality rate.

Previous work has demonstrated that fathead minnows (*Pimpehales promelas*) increase their activity levels with increasing temperature (Chapter 2), suggesting that the minnows will be more vulnerable to predators (sensu Krause & Godin 1995). The goal of this study is to determine whether prey also become more willing to take greater risks to obtain food at warmer temperatures, and whether their predators simultaneously increase their foraging behaviour as

prey become more active. Ultimately this information will allow me to determine whether the risk of predation within aquatic ecosystems will vary depending upon the temperature of the environment.

Material and Methods

Study species. Fathead minnows and yellow perch (*Perca flavescens*), a predator of the fathead minnow, were used in this experiment to determine the effect of temperature on risk taking by prey. Fathead minnows (mean ± SE weight: 2.10 ± 0.48g) for this experiment were obtained from small ponds in southern Manitoba, Canada in the fall of 2009 using minnow traps when the water temperature was approximately 7°C. The water temperature of all three aquaria was increased to 26°C for a period of two weeks. After that period, the temperature of the aquaria was decreased at a rate of approximately 1°C per day, until one aquaria was at each of three temperatures (5, 15 and 25°C). Yellow perch (mean ± SE weight: 101.01 ± 1.56g) were collected from Delta Marsh at the University of Manitoba Field Station at the southern tip of Lake Manitoba (50°11'N, 98°23'W) in 2006, again using minnow traps. Fish were held at their experimental temperatures under a 12 hour light:12 hour dark regime at the Animal Holding Facility at the University of Manitoba for at least two weeks prior to commencement of the experiment. yellow perch were housed in 200-l aquarium at 15°C. The fathead minnows were fed ad libitum Nutrafin flakes and frozen bloodworms while the yellow perch were fed squid and fish.

Experimental design. In an environment free of risk, where there is a continuous input of food, under predictions of the Ideal Free Distribution (IFD: Fretwell and Lucas 1970) it is expected that the spatial distribution of foragers will match the spatial distribution of food in the environment. The IFD assumes that individuals have "ideal" (e.g., perfect) knowledge of the resource distribution and are "free" to compete equally in any location. When these assumptions are met, deviations from the IFD can be used to quantify the impact that the risk of predation has on habitat quality (Abrahams and Dill 1989).

To determine the potential effects of temperature on predator-prey interactions, I designed an experiment to test the relative risk-taking (feeding in a risky location) by minnows held at three temperatures (5, 15 and 23°C), while the temperature of the predator remained constant. Changing the temperature of the predators would affect their metabolic rates, hunger levels, and likely their 'interest' in the prey, their potential food. This in turn could potentially alter the responses of the prey as prey can assess risk of predation based on inspection of their predators (Dugatkin and Godin 1992) and changing temperatures may change that risk. Temperature of the predators was therefore kept constant to allow for the direct effect of temperature on risk taking by the fathead minnows to be discerned without the confounding factor of changes in the riskiness of the predator.

The experimental apparatus consisted of a 40-l aquarium containing the fathead minnows and a 10-l aquarium housing the yellow perch adjacent to the end of the large aquarium. Before the experiment commenced, a solid divider was placed between the two aquaria to prevent visual contact of predator and prey (fathead minnows) and the potential habituation of the prey to a predator that is not an actual threat. Control treatments were trials with no predators; the solid divider was also placed between those two aquaria in the trials. The small aquarium was

42

randomly placed on either the right or left side of the aquarium to control for any potential side effect in both control and treatment trials. In the minnow's aquarium, two automated feeders were set up to provide equal amounts of food. One feeder was placed 5 cm from the 10-l aquarium (when predator present in the small aquarium, this was designated as the high risk location), the other 5 cm from the end of the opposite end of the aquarium (low risk). Each feeder provided 0.25 g of frozen bloodworm over an approximate 15 minute time period (see Abrahams and Dill 1989 for a description of the feeders) (Figure 3.1).

Both the predator and groups of six similar sized prey were randomly selected and placed in the apparatus 24-h before the experiment started. Once the trial was ready to begin, cameras were activated, the solid divider removed and the automated feeders were then turned on. The feeder was the only source of food for the minnows for the duration of the experiment. Upon completion of the trial, the water was changed and the aquarium cleaned. At each temperature, six replicates of each treatment (predator present or absent) were completed for a total of 36 trials. Groups of fish were used in one trial only (either predator present or predator absent). All trials were completed over 24 days with trials being performed once per day, every second day, in three aquaria.
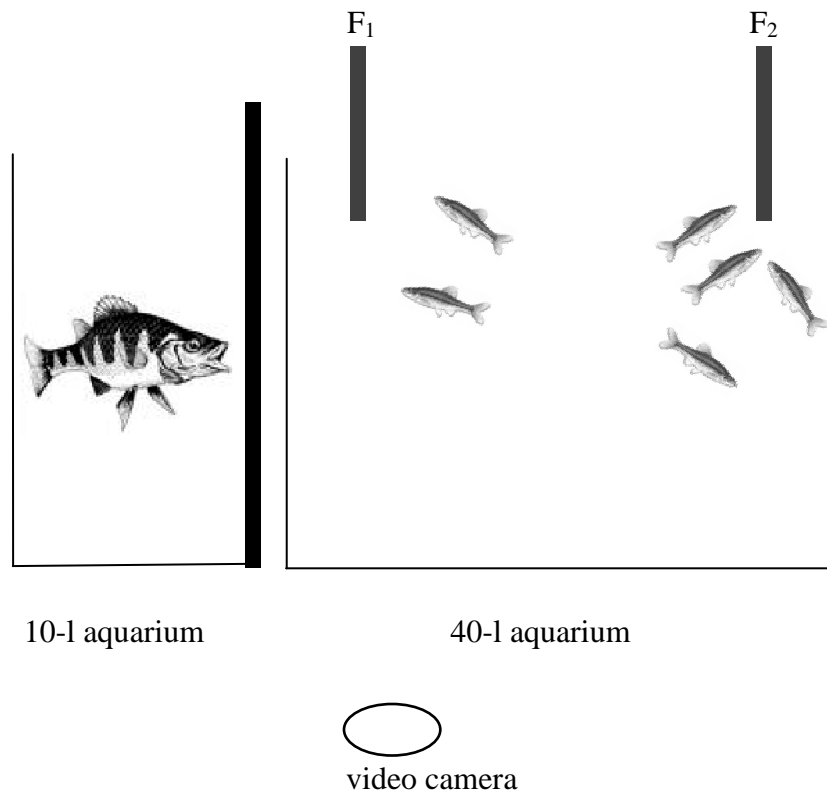
Figure 3.1: Diagram of the experimental apparatus used to determine the effects of temperature on response of minnows to a predator. F_1 represents the high-risk feeder, F_2 the low-risk feeder; they are located approximately 5 cm from the side of the 40-l aquarium. The solid divider prevented the minnows from becoming habituated to the presence of the predator.

Data collected during all trials. All trials took place between 1100 and 1130 and ran for approximately 15 minutes. The total number of minnows using the feeders and their location with respect to the feeders (whether the minnows were feeding at the high risk feeder close to the predator – the 10-l aquarium location – or the safe feeder at the opposite end of the 10-l aquarium) were observed every 30 seconds for the 15 minute duration of the trial. The mean proportion of minnows occupying the high risk location was calculated in both the predator and no predator treatments. A feeding minnow was considered to be any individual that had consumed or was consuming bloodworms within approximately 5 cm of either side of the feeder. To determine if the predators were affected by the behaviour of the prey among temperature treatments, the proportion of the time spent oriented towards the minnows in the 40-l aquaria during approximately the last 10 minutes of the 15 minute trial was assessed. Omitting the first 5 minutes of the trial allowed for any disturbances associated with the removal of the solid divider to be accounted for in the analysis.

Statistical analysis. For descriptive statistics, each group of minnows represented a single experimental unit. For statistical analysis, each unique combination of minnows and predator at each temperature was considered an independent observation, since observations depended both upon group identity and the response of the predator to the temperature manipulation (prey behaviour at the various temperatures). A single observation for each experiment was determined by taking the mean of all sequential observations within a trial. The effects of temperature and predator on the mean number of minnows feeding and the proportion using the high-risk feeder (dependent variables) was determined using a two-way factorial ANOVA.

Finally, to determine if the temperature of the prey affected the proportion of time the predators spend oriented towards the prey a single factor ANOVA was used with temperature as the independent variable and the proportion of time the predator spent oriented towards the prey as the dependent variable. To further examine the potential relationship between the orientation of the predators toward the prey and the prey behaviour, two regression analyses were run. The first regression analysis included the average number of minnows foraging as the independent variable and the proportion of time the predator spent oriented towards the prey as the dependent variable. The second regression analysis used the mean proportion of minnows using the risky feeder as the independent variable and the proportion of time the predator spent oriented towards the prey as the dependent variable. All data were tested for normality and homogeneity of variance, and any non-normal data were transformed to meet normality standards. All data in the form of proportions were arc-sine square root transformed prior to analysis. Results were considered significant at $\alpha = 0.05$. Alpha values were set at 0.05 for all analysis which were conducted with the STATISTICA software.

Results

At 23°C, there were significantly more minnows foraging than at either of the two cooler temperatures (two-way factorial ANOVA: $F_{2, 30} = 35.31$, $P < 0.00001$, Table 3.1; Figure 3.2a; Tukey's HSD post hoc comparisons, Table 3.2); there were almost three times as many minnows foraging at 23°C as compared to both 5 and 15°C. As compared to the

Table 3.1: Results of the two-way factorial ANOVA examining the relationship between temperature and predator presence or absence (independent factors) on the mean number of minnows foraging. Significant differences are indicated with bold values.

Source of variation	*df*	F	P
Temperature	2	35.31	**0.00001**
Treatment	1	0.2464	0.6232
Temperature*Treatment	2	0.17876	0.8372

Table 3.2: Summary of Tukey's HSD post hoc test of the influence of temperature on number of

minnows feeding. Significant differences are indicated with bold values.

Treatment	5°C	15°C	23°C
5°C	-	0.858	**0.000217**
15°C		-	**0.000145**
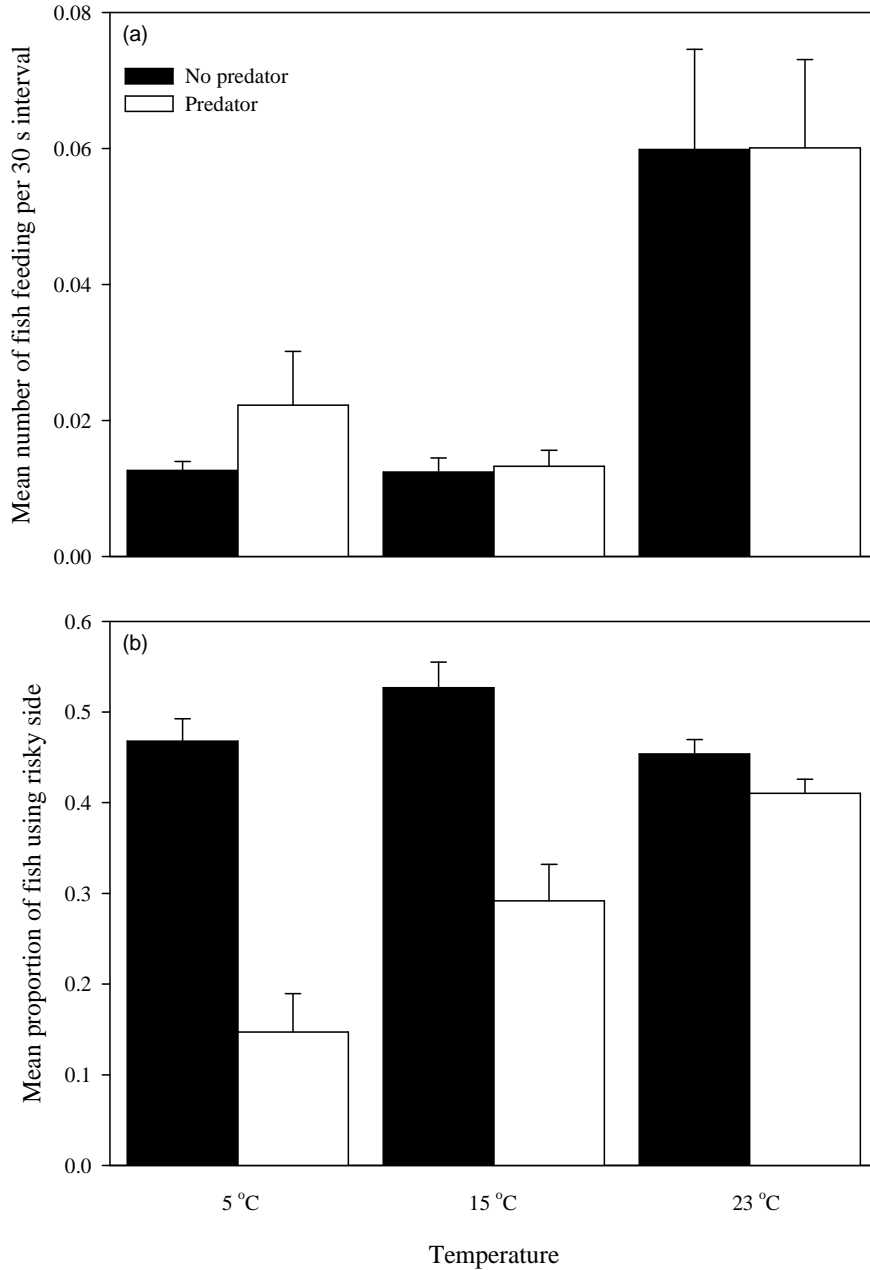
Figure 3.2: The mean response of the fathead minnows to the presence of a predator as measured

by (a) the average total number of fish feeding per trial and (b) the mean proportion of fish

feeding on the treatment (aquarium) side, at each temperature in the presence and absence of a

predator. Bars represent standard error around the mean.

number of minnows feeding in the absence of predators, the number of individuals using the feeders did not change at either of the three temperatures when predators were present (two-way factorial ANOVA: $F_{1, 30} = 0.2464$, $P = 0.6$; Table 3.3; Figure 3.2a). The proportion of minnows feeding in the presence of the predator was affected by temperature, with the predator having little influence on the spatial distribution of minnows at 23°C (Figure 3.2b). There was no effect of predator treatment on the number of minnows feeding; the interaction between predator treatment and temperature was also not significant (Table 3.1, Figure 3.2a).

As predicted by the IFD, in the absence of predators, fishes distributed themselves equally between the two feeders regardless of the temperature at which they were held (Figure 3.2b). However, there was a significant interaction between temperature and predator treatment on the proportion of feeding minnows using the risky feeder (two-way factorial ANOVA: $F_{2, 30} = 8.626$, $P = 0.001$, Table 3.3, Figure 3.2b). In the presence of a predator, minnows that were held at 5˚C used the risky feeder significantly less than minnows at every other temperature – predator present/absent combination (Tukey's HSD post hoc test, Table 3.4). As well, the proportion of feeding fish using the risky feeder at 15˚C in the presence of a predator was significantly less than the proportion of fish at 15˚C using the risky feeder in the absence of a predator (Tukey's HSD post hoc test, Table 3.4). Overall, the presence of a predator resulted in a lower proportion of the feeding minnows using the risky feeder at 15˚C. At 23˚C there were no differences in the proportion of fish using the risky feeder in the presence versus absence of the predator.

Temperature had a significant effect on predator behaviour, whereby predators spent significantly more time oriented towards the prey when the prey were at warmer

Table 3.3: Results of the two-way factorial ANOVA examining the relationship between temperature and predator presence or absence (independent factors) on the mean proportion of minnows using the risky feeder. Significant differences are indicated with bold values.

Source of variation	*df*	F	P
Temperature	2	8.451	**0.001228**
Treatment	1	40.29	**0.000001**
Temperature*Treatment	2	8.626	**0.001098**

Table 3.4: Summary of Tukey's HSD post hoc test of the influence of the interaction between temperature and predator presence on the proportion of minnows using the risky feeder. Significant differences are indicated with bold values.

Treatment Combination	Temperature	Predator Treatment	Treatment Combination				
			2	3	4	5	6
1	5˚C	Predator	**0.00014**	**0.013**	**0.00014**	**0.00019**	**0.00013**
2	5˚C	No predator	-	0.065	0.66	0.70	0.99
3	15˚C	Predator		-	**0.0082**	0.088	0.0070
4	15˚C	No predator			-	0.061	0.43
5	23˚C	Predator				-	0.89
6	23˚C	No predator					-

Table 3.5: Summary of Tukey's HSD post hoc test of the influence of temperature on the proportion of time a predator spends oriented towards its prey. Significant differences are indicated with bold values.

Treatment	5°C	15°C	23°C
5°C	-	0.980	**0.000471**
15°C		-	**0.000611**
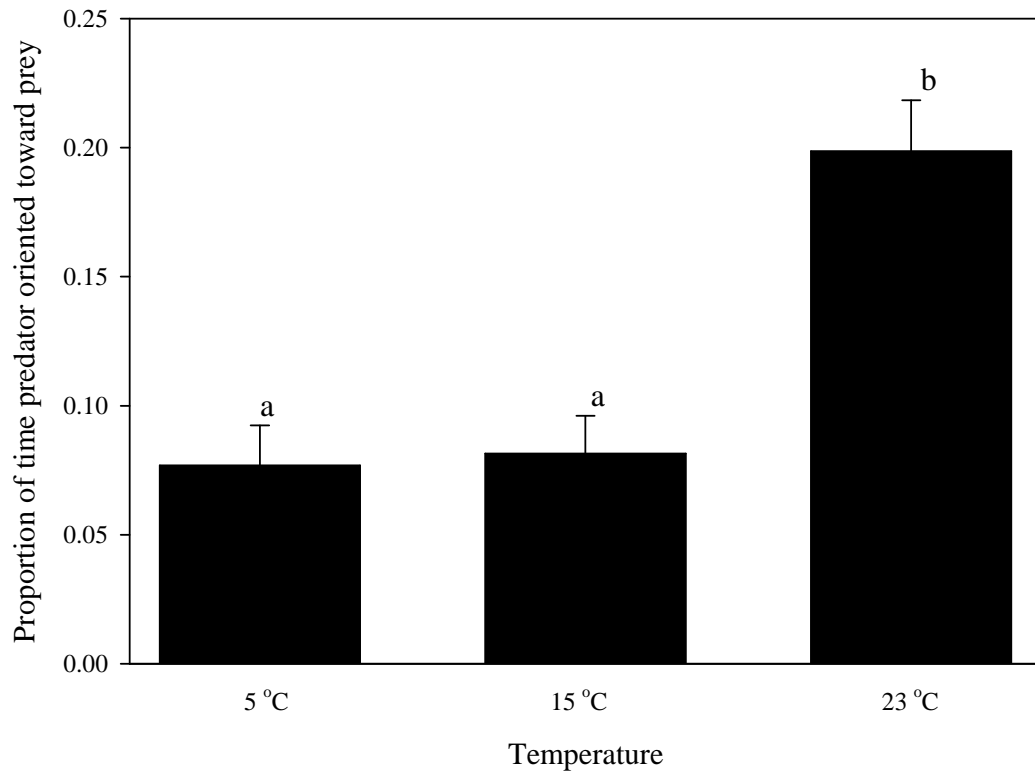
Figure 3.3: The mean response, as measure by the amount of time the predators spent oriented toward the prey, of predators to prey foraging at three temperatures. Letters above the bars represent significant differences at $\alpha = 0.05$ using Tukey post hoc tests. Bars represent standard error around the mean.
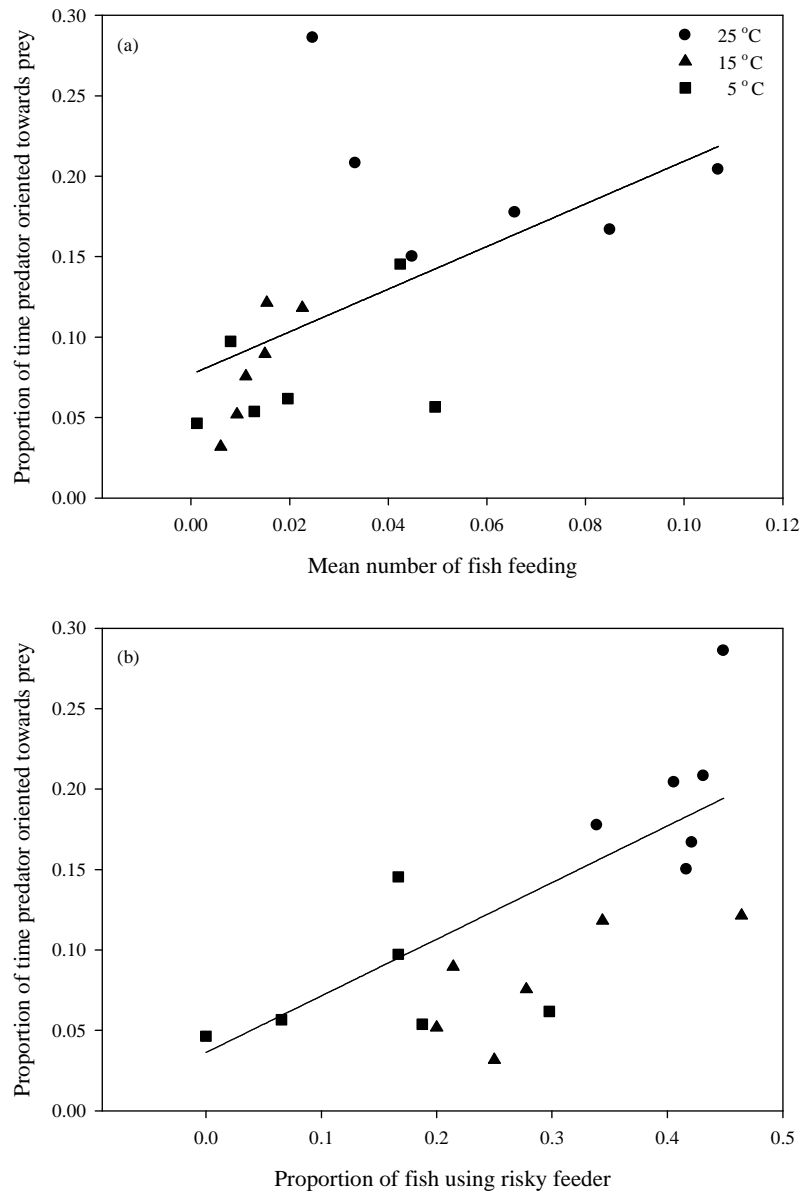
Figure 3.4: The relationship between prey activity and predator orientation towards the prey as measured by (a) the relationship between the number of fish active per trial and the proportion of time the predator spent oriented towards the prey and (b) the relationship between the proportion of fish using the risky feeder and the proportion of time the predator spent oriented towards the prey.

temperatures (one-way ANOVA: $F_{2, 17} = 60.96$, $P < 0.000001$; Figure 3.3; Tukey's HSD post

hoc test, Table 3.5). In fact, predators spent almost double the proportion of time oriented

towards the prey at 23°C than at either 5 or 15°C. Both the mean number of fathead minnows

feeding ($R^2 = 0.3063$, $F_{1, 16} = 7.064$, $P = 0.02$; Figure 3.4a) and the proportion of fathead

minnows using the risky feeder ($R^2 = 0.4242$, $F_{1, 16} = 11.79$, $P =$

0.003; Figure 3.4b) were significant predictors of the proportion of time the yellow perch spent

oriented towards their prey.

Discussion

This study has demonstrated that the temperature of prey affected the behavior of both predator

and prey, even when the water temperature in which the predator is housed remains constant.

Significantly more fathead minnows fed at warmer temperatures, even in the presence of

predators and their distribution conformed to the IFD in the absence of the predator. In the

presence of a predator, the proportion of feeding minnows using the risky feeder declined with

the greatest decrease in use of the risky feeder occurring at 5°C. In fact, at 5°C in the presence of

a predator, a significantly smaller proportion of foraging minnows use the risky feeder than any

other temperature-predator treatment combination.

As temperatures increased, the proportion of time the predator spent oriented toward the

prey also increased. This result is likely a result of the direct linear relationship between the

proportion of time a predator spends oriented toward the prey, and both the average number of

minnows foraging and the average proportion of foraging minnows using the risky habitat to

forage. Taken together, these data suggest that higher temperatures will result in increased

predation risk to prey. The increased activity and willingness to forage in risky habitats,

presumably to meet increased metabolic demands at high temperatures (Wootton 1990), will likely increase the encounters between predators and their prey. In natural ecosystems, where the temperature of the predators will also increase as prey temperatures increase, this effect will likely be exacerbated as predators increase their activity and foraging to meet their increased metabolic demands as well.

Both theoretical (Hugie and Dill 1994, Sih 1998) and empirical (Gilliam and Fraser, 1987, Abrahams and Dill 1989, Lima and Dill 1990, Bouskila 2001, Alonzo 2002) studies have suggested that habitat choice by prey is dependent upon the costs – predation risk, and benefits – foraging payoffs, of the available habitats. Prey are less likely to use risky habitats where predators are present. Abrahams and Dill (1989) suggested that prey could be encouraged to use risky locations by increasing the amount of food available in that habitat, essentially offsetting the cost of predation by increasing the benefit. In this study, at both 5° and 15°C, the potential cost of predation was enough to offset the potential foraging gains that would be acquired by using the risky habitats. However, at 23°C, minnows were as likely to use the risky feeder in the presence of a predator as they were in the absence of a predator. This suggests that the abiotic environment, specifically temperature, can affect the risk-taking decisions of the fathead minnow.

Observations of increased foraging with increased temperature have been observed in both marine (Smith 2008) and freshwater fishes (juvenile brown trout, *Salmo trutta*: Ojanguren et al. 2001; brook trout, *Salvelinus fontinalis*: Taniguchi et al. 1998; fathead minnow: Chapter 2) as well as in this study. As temperature increases, the metabolic rate of fishes increases (Wootton 1990) which increases their energetic demands. This increase in energetic demands with temperature is likely the mechanism resulting in the observed increase in foraging with

temperature in this study. At high temperatures, foraging increases to meet these energetic demands. Under risk of predation, this requirement to meet increased demands at high temperatures likely offsets the risk of predation – there was no difference in either the number of individuals feeding or in the proportion of feeding individuals that use the risky feeders.

With increasing temperature of the prey, not only did the overall number of individuals foraging increase and the proportion of individuals using the risky feeder in the presence of a predator increase, but the proportion of time the predator spent oriented towards the prey also increased. Krause and Godin (1995) observed that predatory cichlids (*Aequidens pulcher)* preferentially attacked small groups of guppies (*Poecilia reticulata)* that were held at high temperatures as opposed to large groups of guppies held at lower temperatures. In previous experiments, when groups were held at constant temperatures, predators preferentially attacked large groups of guppies. They attributed the increased attacks on smaller, warmer groups to the fact that at warm temperatures, guppies were more active and more active prey are less cryptic. In this study, similar observations were made. As number of individuals foraging increased, the proportion of time a predator spent oriented towards the prey increased. The relationship was even stronger when the proportion of individuals utilizing the risky feeder was used as the predictor of the proportion of time the predator spent oriented towards the prey. Many studies examine the role that the presence of predators and the proximity of predators to prey have on prey behaviour, growth rates, morphology and life histories (Lima and Dill 1990, Reznick et al. 1990, Lima 1998, Tollrian and Harvell 1999, Turner and Montgomery 2003). This study suggests that the actual risk to these prey by predators in close proximity to them may be affected by prey behaviour. Less active prey may experience lower mortality rates.

In Chapter 2, I demonstrated that as temperatures increased, the activity and foraging rates of the fathead minnow increased. I then suggested that in natural ecosystems, as temperatures increase, prey would experience an increase in encounter rates with predators as they attempt to meet increased energetic demands. Anderson et al. (2001) measured an increase in mortality rates of anuran larvae at increased temperatures and attributed it to increased foraging rates by individuals held at warmer temperatures (though this was not measured). My study suggests that both temperature and the presence of a predator have an effect on the number of individuals feeding and their distribution between feeders offering equal amounts of food. Temperature directly affects the number of individuals foraging and the temperature and presence versus absence of a predator interact to influence the decisions of prey to use a risky habitat. Prey are more willing to take risks and feed in the presence of a predator at warm temperatures, likely increasing their probability of being captured and consumed by a predator. If predators also increase their foraging at warm temperatures, and experience an increase in capture efficiency at warm temperatures (Persson 1986), prey are likely to experience higher rates of mortality as temperatures increase.

References

Abrahams, M.V., Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. Ecology **70**: 999-1007.

Abrahams, M.V., Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interaction in aquatic environments. Behavioural Ecology and Sociobiology **40**: 169-174.

Abrams, P.A. 1991. Life-history and the relationship between food availability and foraging effort. Ecology **72**: 1242-1252.

Alonzo, S.H. 2002. State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. Evolutionary Ecology Research **4**: 759-778.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on a predator–prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Bouskila, A. 2001. A habitat selection game of interactions between rodents and their predators. Annales Zoologici Fennici **38**: 55-70.

Dill, L.M., Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioural Ecology and Sociobiology **16**: 65-71.

Dugatkin, L.A., Godin, J.-G. J. 1992. Prey approaching predators: a cost-benefit perspective. Annales Zoologici Fennici **29**: 233-252.

Fretwell, S.D., Lucas, H.L. Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**: 16-36.

Gilliam, J.F., Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**: 1856-1862.

Godin, J.-G.G., Crossman, S.L. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behavioural Ecology and Sociobiology **34**: 359-366.

Gotceitas, V., Godin, J.-G.J. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behavioural Ecology and Sociobiology **29**: 255-261.

Grand, T.C., Dill, L.M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. Behavioral Ecology **8**: 437-447.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behavior of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **50**: 241-246.

Hugie, D.M., Dill, L.M. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology, Supplement A **45**: 151-169.

Kramer, D.L., Manley, D., Bourgeois, R. 1983. The effect of respiratory mode and oxygen concentration on the risk of aerial predation in fishes. Canadian Journal of Zoology **61**: 653-665.

Krause, J., Godin, J.-G.J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour **50**: 465-473.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior **28**:215-290.

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

Lima, S.L., Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist **153**: 649-659.

MacArthur, R.H., Pianka, E.R. 1966. On optimal use of a patchy environment. American Naturalist **100**: 603-609.

Magnhagen, C. 1988. Predation risk and foraging in juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). Canadian Journal of Fisheries and Aquatic Sciences **45**: 592-596.

Magnahagen, C., Heibo, E. 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. Functional Ecology **15**: 754-762

Mendes, T.C., Villaca, R.C., Ferreira, C.E.L. 2009. Diet and trophic plasticity of an herbivorous blenny, *Scartella cristata*, of subtropical rocky shores. Journal of Fish Biology **75**: 1816-1830.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology **65**: 689-701.

Mittelbach, G.G., Chesson, P.L. 1987. Predation risk: indirect effects on fish populations. In: Kerfoot, W.C., Sih, A., Editors. Predation: direct and indirect impacts on aquatics communities. University Press of New England, Hanover, N.H. pp 203-224.

Ojanguren, A.F., Reyes-Gavilán, F.G., Braña, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. Journal of Thermal Biology **26**: 165-170.

Persson, L. 1986. Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): Implications for coexistence between poikilotherms. Journal of Animal Ecology **55**: 829-839.

Reznick, D.A., Bryga, H., Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. Nature **346**: 357-359.

Robb, T., Abrahams, M.V. 2002. The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas.* Behavioural Ecology and Sociobiology **52**: 25-30.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni.* Ecology **63**: 786-796.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: *Predation: direct and indirect impacts on aquatics communities.* Kerfoot, W.C., Sih, A., Editors. University Press of New England, Hanover, N.H. pp 203-224.

Smith, T.B. 2008. Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral-algal competition. Coral Reefs **27**:397-405.

Taniguchi, Y., Rahel, F.J., Novinger, D.C., Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences **55**: 1894-1901.

Tollrian, R., Harvell, C.D. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.

Turner, A.M., Montgomery, S.L. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. Ecology **84**: 616-622.

Urban, M.C. 2007. Predator size and phenology shape prey survival in temporary ponds. Oecologia **154**: 571-580.

Werner, E.E., Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Reviews in Ecology and Systematics **15**: 393-425.

Werner, E.E., Gilliam, J.F., Hall, D.J., Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**: 1540-1548.

Wolf, N.G., Kramer, D.L. 1987. Use of cover and the need to breathe: the effects of hypoxia on the vulnerability of dwarf gouramis to predatory snakeheads. Oecologia **73**: 127-132.

Wootton, R.J. 1990. Ecology of Teleost Fishes. Chapman & Hall, London, 404p.

Chapter 4: Fish communities in a changing aquatic environment: implications for predator-prey interactions

Abstract. Fishes living in a shallow water ecosystem often experience a wide range of temperatures, dissolved oxygen levels, and turbidity. I tested the hypothesis that the fish community structure will vary as the aquatic environment changes and that these changes will be related to the morphology and physiology of the species. To test this hypothesis, I collected measures of temperature, dissolved oxygen and turbidity from a shallow, blind ending channel from which fishes could leave if conditions became unfavourable. I also sampled the relative abundance of predator and prey species. Regardless of whether fishes are classified as cool- or warm- water, there was a significant positive relationship between fish CPUE and temperature. CPUE of fishes with physostomous swim bladders were positively related to DO levels, while those with a physoclistous swim bladder were negatively related to DO levels. Turbidity was not a significant predictor of species that rely on either vision or chemosensory mechanisms for foraging. With respect to the role the environment plays in mediating predator-prey interactions, increases in temperature increases CPUE of all fish sampled, with the possibility of increased predator-prey interactions as a result of increased encounter rates. Periods of low DO may provide prey with a reduction in risk of predation by piscine predators as the two dominant predators of small fish, northern pike and bullhead species, have a positive relationship with measures of DO.

Introduction

Describing patterns in the structure of fish assemblages has been the focus of many ecologists with the goal of understanding the mechanisms that regulate communities (Moyle and Vondracek 1985, Jackson and Harvey 1989, Gilliam et al. 1993, Matthews et al. 1994, Jackson et al. 2001, Kennard et al. 2007, Mitchell and Knouft 2009). These studies have often focused solely on the species present (Matthews et al. 1994, Mitchell and Knouft 2009), but have also included physical habitat measures (Gilliam et al. 1993, Kennard et al. 2007), or waterbody morphology measures (Jackson and Harvey 1989). However, it is important to also consider environmental factors such as temperature, dissolved oxygen (DO) and turbidity, as these variables have the potential to mediate interactions between species and/or limit the ability of species to persist in a given area (Persson 1986, Chapman et al. 2002, Robb and Abrahams 2003, Bonner and Wilde 2002, De Robertis et al. 2003), thereby influencing the structure of fish assemblages. In a waterbody that experiences a wide range of environmental conditions it is possible that as conditions change they become more or less favourable to certain species, a factor dependent upon species-specific physiology and morphology. If changes to the aquatic environment affect predators and prey differently, understanding how the environment influences community composition may be a critical component for understanding predator-prey interactions.

   This paper has two goals: 1) to determine the role the environment plays in structuring both the species composition and the size distribution of predators within an ecosystem and to determine whether the abundances of predators can influence the abundance of the prey and 2) to determine how changes in the fish community in response to changes the environment may affect predator-prey interactions, testing the various predictions of Abrahams et al. (2007).

Abrahams et al. (2007) set out to theoretically predict the effect of a changing aquatic environment on fish communities. Specifically, the authors attempted to predict if predators or prey would benefit under changing environmental conditions.

Most fishes are poikilotherms and temperature plays a role in structuring the distribution of these fishes based on their tolerances to temperatures. Documented are species-specific upper and lower thermal limits, as well as thermal optima (Neill 1979). In North America there are three thermal guilds of fishes: cold-, cool- and warm- water with general upper lethal limits of 25, 32 and 40°C respectively although species-specific exceptions do occur (Magnuson et al. 1997). Conversely, it is not only the species of an individual that determines its temperature tolerance. The size of the individual may also affect tolerances to high water temperatures and metabolic rates of larger fish are higher at a given temperature than those of smaller fish of the same species (Hölker 2003).

Given that species and size are determinants in temperature preference and thermal optima of individuals, it is not surprising that temperature has been demonstrated to influence predator-prey interactions of poikilotherms (Persson 1986, Anderson et al. 2001). Temperature influences the energetic requirements of fish through their metabolism, (Wootton 1990) activity, (Weetman et al. 1998, Krause and Godin 1995, Chapter 2) and foraging rates (Chapter 2, Chapter 3). Temperature also influences the propensity of individuals to forage in a risky habitat to increase the amount of food received (Chapter 3). It can therefore be expected that temperature will also influence encounter rates between predators and their prey in natural ecosystems, increasing predation risk to prey. However as temperatures increase, Abrahams et al. (2007) predict that the presence of large piscivores, specifically cold-water species, will decline.

Results of their theoretical study suggest that increasing temperatures may result in a net benefit to the prey.

As with temperatures, fishes of different species and sizes will have different tolerances to dissolved oxygen levels (Robb and Abrahams 2003), which may play a role in structuring fish community composition. Unlike temperature where both extremes (highs and lows) influence physiology, the important factor influencing the ability of fishes to inhabit specific areas is the lower measure of DO - hypoxia. Hypoxia is widespread in many shallow water ecosystems and persistent extreme hypoxia (< 2 mg/l O_2) can result in extreme mortality rates (83% of fish) in small pools (Tramer 1977). Research by Fischer et al. (1987) and Chapman et al. (2002) suggest that differential tolerances to low levels of DO can influence community structure.

If DO levels become very low, there is the possibility that species that have a low tolerance for hypoxia will migrate out of the areas with low DO and into larger bodies of water that in general are more oxygenated (Chapman et al. 1996). Morphology of individuals can influence their tolerance to hypoxic conditions (Burleson et al. 2001, Robb and Abrahams 2003, Hedges 2007). Specifically, those species with physostomous swim bladders may be able to obtain oxygen with air gulped from the surface (Seymour et al. 2007). Being able to use a physostomous swim bladder in this way may enable these fishes to exploit areas with low levels of DO. With regards to size, larger individuals may be more susceptible to low levels of DO (Chapman et al. 2002) though the opposite has also been observed (see Nilsson and Östlund-Nilsson 2008 for a review). This suggests DO levels as well as the temperature of the environment may influence species composition and size distribution of individuals within a water body.

The response of both predators and prey (and therefore predator-prey interactions) to changes in measures of dissolved oxygen is predicted by Abrahams et al. (2007) to depend critically upon the specific physiology of the species present. This is because the physiology of individuals will influence their tolerance to hypoxic conditions. With smaller individuals being more tolerant of hypoxic conditions (Robb and Abrahams 2003), Abrahams et al. (2007) predicted that under periods of low oxygen levels, prey will be afforded benefits of a reduction in predation risk due to reductions in the number of piscivores present. As mentioned above however, the presence of a physostomous swim bladder in predators may alter that predicted predator-prey dynamic.

Aquatic ecosystems that experience turbid conditions are often home to fishes that use a variety of senses to detect food. Some fish, such as those that rely heavily on chemical cues while foraging, may be better than others at foraging in turbid water bodies (Bonner and Wilde 2002, De Robertis et al. 2003). For example, members of the family Ictaluridae are chemosensory feeders and are able to forage in turbid waters; they do not rely on vision to forage and as such have reduced visual acuity (Caprio 1982). With respect to fish species that do rely on vision, larger eyes imply increased visual acuity. As well, larger and longer eyes increases the distance between the cornea/lens and the retina which increases the size of the image (Howland et al. 2004). In fishes, eye size increases with the body length. It is therefore expected that fishes relying primarily on vision for foraging may be affected to a greater degree by changes in turbidity levels within an aquatic ecosystem than those that rely on chemical cues (Nilsson et al. 2009). Extrapolating responses of species to changes in turbidity levels of aquatic ecosystems to the potential effects of turbidity on predator-prey interactions, Abrahams et al. (2007) predict that as turbidity levels increase, it becomes energetically more expensive to forage. Individuals

increase their movement rates to increase encounter rates with their food in turbid conditions. However, as mentioned above, the mechanism by which individuals locate their food (chemical versus visual) may affect activity (foraging) of predators and their prey under turbid conditions, and therefore the encounter rates between predators and prey.

While looking at the role that the environment plays in structuring fish communities and predator-prey interactions, it is also important to recognize the potential dynamic between the abundances of predators and their prey. In aquatic ecosystems, the abundance of prey can fluctuate with the abundance of predators (Clark et al. 2003). During periods of high predator abundance, prey are known to increase their use of refuges and/or decline in abundance (Clark et al. 2003, Baum and Worm 2009, Vonesh et al. 2009). In a system where the abiotic environment may be a factor in structuring the predator community, any changes in the predator community may then affect the abundance of prey in the ecosystem. As this study focuses on a system in which both predators and prey can both enter and leave the study area, presence of fish in the system indicates a choice for that system. Given the preceding information the following predictions, based on the three environmental variables and the potential relationship between the abundance of predators and their prey were tested:

1) Temperature: I predicted that the two guilds of fish present (cool- and warm- water species) will respond differently to changes in temperature. As temperature increased, I expected the abundance of cool- water species (northern pike, Craig 2008) to decrease while the abundance of warm- water fishes (brown and black bullhead, freshwater drum, and fathead minnow) should not be affected by temperature (bullhead species: Richards and Ibara 1978; freshwater drum and fathead minnows: Wei et al. 2004). Temperature is also expected to influence the species-specific length of piscivorous fish. I predicted, based on the fact that metabolic costs increase

with temperature and size (large fish of a given species will have higher metabolic rates than smaller fish of the same species), that as temperature increased the size of individuals of a given species will decrease. Given the above predictions, an increase in temperature is expected to result in a reduction in predation risk to prey fish, as also predicted by Abrahams et al. (2007).

2) Dissolved oxygen: I predicted that dissolved oxygen will differentially affect those species with physostomous swim bladders (black and brown bullheads, northern pike and fathead minnows) and those who have physoclistous swim bladder (freshwater drum). Decreased DO levels should not affect the abundance of species with physostomous swim bladders; a decrease in DO is likely to result in a reduction in abundance of freshwater drum which has a physoclistous swim bladder. As well, within a given species, DO should affect individuals of various sizes differently (Robb and Abrahams 2003, Hedges 2007), though this effect is not expected to impact all species equally. A relationship between DO and body size is expected to be observed in fishes with physoclistous swim bladders, but is less likely to be observed in those individuals with physostomous swim bladders. It is predicted that larger individuals will be more susceptible to low levels of DO. While Abrahams et al. (2007) suggest that a reduction in predation risk will occur as DO levels decrease, if the primary predators in this ecosystem (northern pike) are able to utilize aerial respiration to compensate for a reduction in the DO in the water, I predict that a reduction in DO levels will not result in lowered predation pressure.

3) Turbidity: I predicted that the effect of turbidity on the abundance of fish will be dependent upon the sensory mechanism used for foraging. Visual foragers (northern pike, freshwater drum and fathead minnows) are predicted to decline in abundance as turbidity increases. Non-visual foragers such as brown and black bullheads rely primarily on chemical cues for foraging and should not be affected by turbidity. As eye size and therefore visual capabilities increase with

body length, larger visual foragers should be better able to forage under high levels of turbidity than smaller individuals. I predicted that as turbidity increases the size of visual foragers (northern pike and freshwater drum) should also increase. As predicted by Abrahams et al. (2007), as turbidity increases, the cost of foraging (increasing activity to increase encounter rates with prey) will increase. I predict that prey should experience a reduction in predation risk with increasing turbidity.

4) With the potential for predators to impact the abundance of prey and their potential predators to track the abundance of their prey, I also predicted that as the total abundance of predators increase the abundance of prey would decline.

Materials and methods

To test the predictions that fish community composition, as well as the size of the fishes present, change with changes in the abiotic properties of the aquatic ecosystem, field surveys were carried out in the summers of 2006, 2007 and 2008. During these field surveys, both predatory and prey fishes were sampled in Blind Channel, Delta Marsh, Manitoba, Canada (98°23'W, 50°11'N) (Figure 4.1). Blind Channel is a small, blind ending channel south of Lake Manitoba. Approximately 3.5 km long, the average depth of Blind Channel is 1 m. The community composition of the channel is able to change throughout the summer months as the channel is connected via one waterway to Lake Manitoba. This connection to Lake Manitoba also means that seiches in the lake (a consequence of strong winds from either the north or south) change the water levels in the channel. North winds increase water levels and a slight lowering of water temperature occurs.
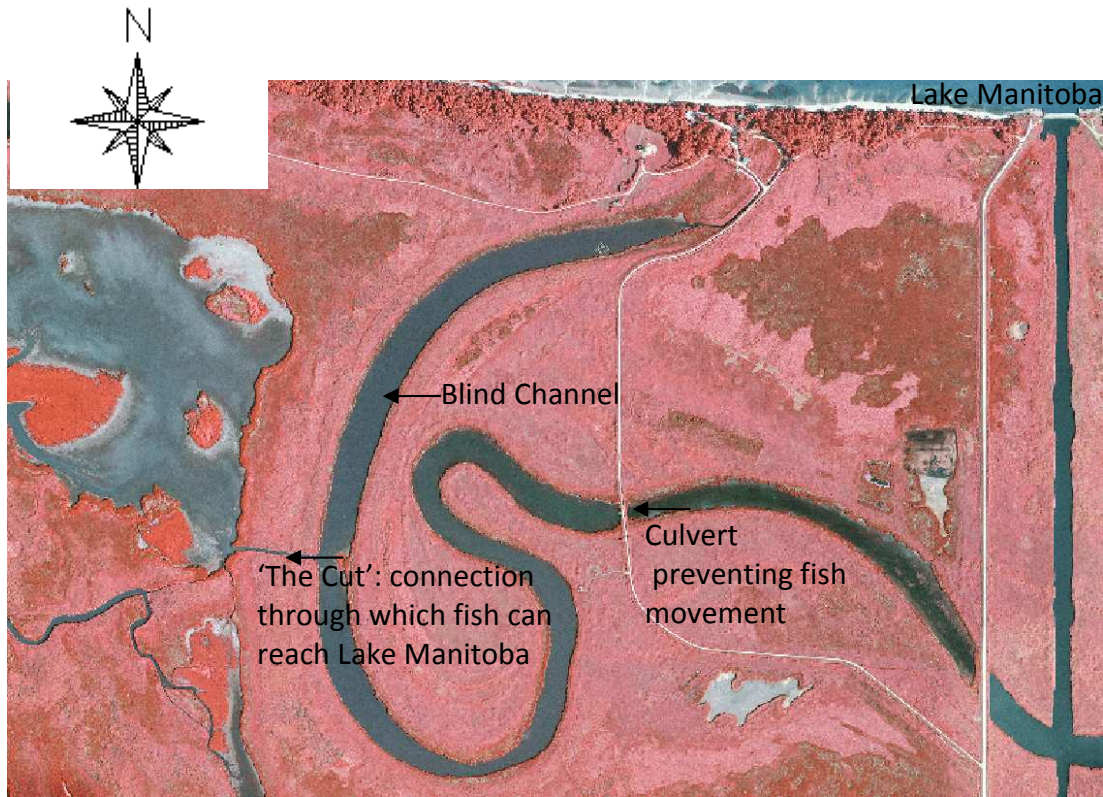
Figure 4.1: Aerial photograph of Blind Channel, Delta Marsh, Manitoba. 'The Cut' provides the connection between Blind Channel and other regions of Delta Marsh and/or from Lake Manitoba.

With the water exchange, an increase in the DO levels is also observed. A strong southerly wind will reduce water levels.

Taken with the fact that Blind Channel experiences large variation in measures of temperature, DO and turbidity, the connection between Blind Channel and Lake Manitoba renders Blind Channel an ideal system to address questions pertaining to the influence the environment has on community composition. It means that during periods of unfavourable conditions, individuals that are currently residing in Blind Channel do not have to remain there – they can exit the Channel and enter Lake Manitoba, a more stable ecosystem. It also means that if conditions become favourable within Blind Channel, individuals from Lake Manitoba can move into the system.

Measures of the aquatic environment. Over the course of the ice-free period Blind Channel experiences a wide range of turbidity (1.3 to 85 nephelometric turbidity units, NTU), temperatures (peaking at around 28-30 °C) and dissolved oxygen levels (ranging from approximately 0.1 to 10.0 mg/L). To record DO (mg/L), temperature (°C) and turbidity (NTU), three YSI 6920 data sondes were placed at the bottom, middle, and surface of the water column in Blind Channel from May through August. The sondes collected data every 30 minutes, which were then averaged to provide a daily value to correspond with measures of fish abundances. Only measures of temperature were collected for all days. DO measures were not included when the charge on the data sonde fell beyond the accepted range (below 25 or above 100 amps) and turbidity measures were not included when the measured NTU was above 500, a value indicative of debris obstructing the sensor.

Measures of fish abundance. Sampling of both large and small fishes in Blind Channel occurred from May to August in all three survey years. Large fish were sampled daily with gillnets that were set for 1.5 hours. The gillnets were 15.25 m long and 1 m in height (approximately the same depth as the water) with a stretched mesh size of 5.08 cm. Three gillnets were set per day at 0.5 hour intervals in locations that were randomly distributed throughout the channel. I recorded species and the length to the nearest cm of all captured individuals. All fish were released at their site of capture. Daily catch per unit effort (CPUE) was calculated as the average number of fish captured per hour per day. CPUE was determined for northern pike (*Esox lucius*), freshwater drum (*Aplodinotus grunniens*) and bullhead species (both black, *Ameiurus melas*, and brown, *A. nebulosus*, bullheads). While walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) were also captured, only two and four individuals, respectively, were captured over the three year study and were not included in calculations of CPUE. An average daily CPUE for total predators was also calculated.

To sample the small prey fishes in Blind Channel, 10 minnow traps were set just below the surface of the water at 10 locations within the channel. Five of these traps were deployed on the north side of the channel while the other five were set on the south side. This arrangement ensured that one side of the marsh with minnow traps would be relatively sheltered in high wind events. This study design was important as minnows were observed to aggregate in sheltered areas when winds were high and sampling only one side of the marsh would have resulted in inaccurate estimates of minnow abundance. All traps were set at permanent locations and checked after 24 hours. All captured fish were identified to species and counted. CPUE values were calculated for all species together, as the dominant fish in the traps (fathead minnows, *Pimephales promelas*) comprised over 95 % of the total number of minnows captured. CPUE

was calculated as the average (of the 10 minnow traps) number of fish captured in a 24 hour period.

Data analysis. For statistical analysis, environmental data was averaged to provide a daily measure. These data were tested for autocorrelation using Durbin-Watson tests for autocorrelation. I used parametric analyses on translated data (environmental variables as well as CPUE and length data; $y_i` = (y_i - ¯y)/s$, where s is the standard deviation of the mean of y). Quinn and Keough (2002) suggest that translations of data in regression analyses allow variables to be on similar scales. As well the translated data approached normality and met assumptions of homogeneity of variances necessary for parametric analysis of regression analysis. Quinn and Keough (2002) state that regression analyses are robust to violations of normality if data meet assumptions of homogeneity of variance. The translated data were also used in the canonical correspondence analysis as it allows comparisons between canonical weights (Hair et al. 2005). For each series of analyses pertaining to a particular environmental variable, it was first determined if there were significant differences among years in the measured variable using a single factor analysis of variance (ANOVA). If differences among years existed in any of the analyses, year was included as a categorical predictor variable and the analysis was that of a general linear model (GLM). All analyses were conducted using STATISTICA software. Alpha levels were set at 0.05 for all analysis.

To determine if temperature affected cool- and warm- water guilds of fishes differently, two separate general linear models were run. The first used northern pike (a cool- water fish) CPUE as the dependent variable and temperature as a continuous predictor variable. The second GLM used the warm- water fish species (brown and black bullheads, fathead minnows,

freshwater drum) CPUE as the dependent variable and temperature as the continuous predictor variable. The relationship between the species-specific length of predatory fish and temperature was examined using a GLM with temperature as the predictor variable. In this analysis the length of the fish was the dependent variable and each species was run separately.

A second series of GLMs were run to examine the effect of dissolved oxygen on community composition. In the first GLM, CPUE measures of species with physostomous swim bladders (northern pike, brown and black bullheads and fathead minnows) were used as the dependent variables. The second GLM used the CPUE of species with physoclistous swim bladders (freshwater drum) as the dependent variable. DO measures were the continuous predictor values in both analyses. The third GLM used DO as the continuous predictor variable and employed length of individuals as the dependent variable. Each species was analyzed separately to determine if DO levels affected the species-specific size of individuals present.

Measures of turbidity were used as the continuous predictor variables in the next series of general linear models. The first GLM included CPUE measures of visual foragers (northern pike, freshwater drum, and fathead minnows) as the dependent variable. The second GLM included CPUE measures of brown and black bullheads, foragers that rely on chemosensory cues, as the dependent variable. A second series of general linear models were employed with turbidity as the predictor variable and length of a given species as the dependent variable; each species was analyzed separately.

Lastly, to determine if the suite of environmental variables taken as a whole affected the abundance of piscine predators as well as prey fish (with daily average CPUE of predators and prey used as indices of abundance), a single canonical correlation analysis was employed. The

analysis incorporated all data from all years which were combined to determine if broad-scale patterns in fish activity could be related to their environment.

Finally, the biotic as well as abiotic environment was hypothesized to affect community structure (specifically, that the abundance of predators can affect the abundance of prey). A GLM was run using total predator CPUE as the predictor variable and prey CPUE as the dependent variable. If there were differences in CPUE measures of predators or prey among years (as determined by single factor ANOVAs), year would be included in the analysis as a categorical predictor variable.

Results

Between year differences in the abiotic environment. Daily measures of environmental data were considered independent observations in 2006, 2007 and 2008 based on Durbin-Watson tests for autocorrelation. All measures of environmental data were used in subsequent analyses. There were significant differences in measures of temperature among years; temperature differences existed between 2006 and 2008, and 2007 and 2008 with 2008 being significantly cooler than both 2006 and 2007 (single factor ANOVA: $F_{2,131} = 8.29$, $P < 0.001$; paired comparisons: significant differences occurred between 2006 and 2008, and 2007 and 2008; Figure 4.2). As differences existed among years in measures of temperature, year was used as a categorical predictor variable in further regression analyses involving temperature.

Significant differences in measures of DO levels also existed among years (single factor ANOVA: $F_{2,121} = 22.7$, $P < 0.00001$; Figure 4.3). Lowest average DO levels were measured in 2006 (1.47 ± 0.99 mg/L O_2) while highest average DO levels were measured during the sampling
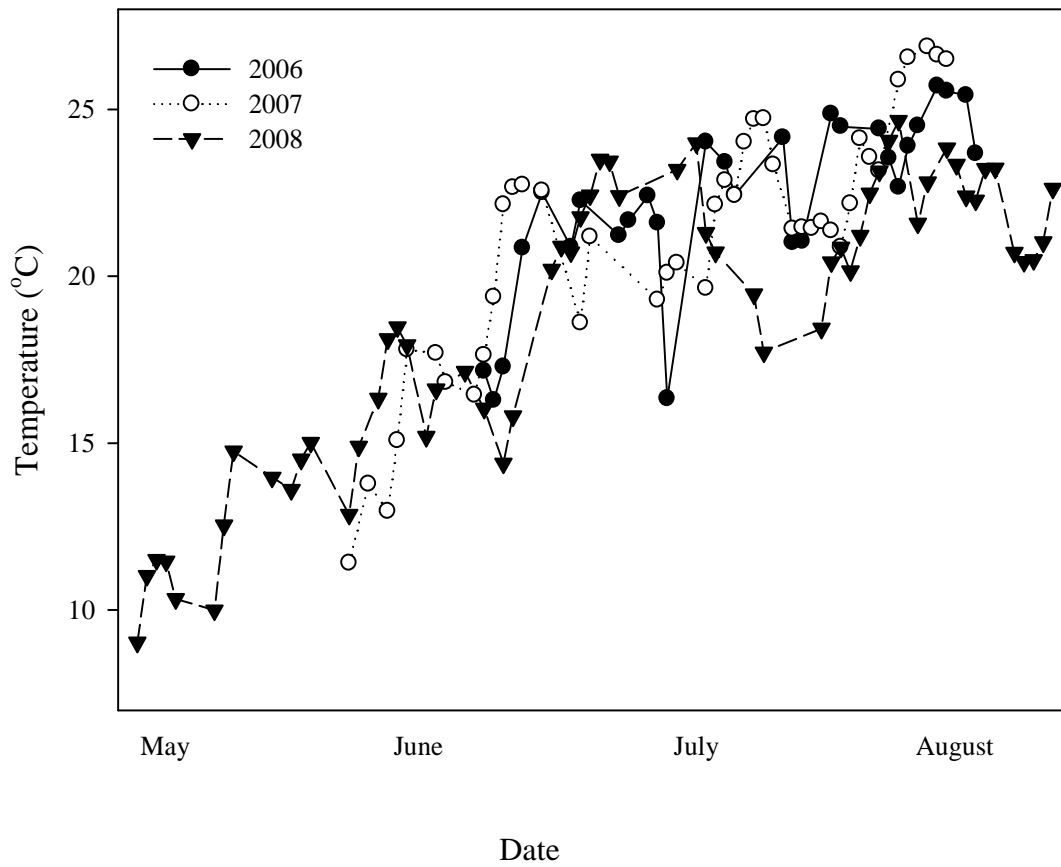
Figure 4.2: Average daily measures of water temperature in Blind Channel, Delta Marsh for the summer sampling period in 2006, 2007 and 2008.
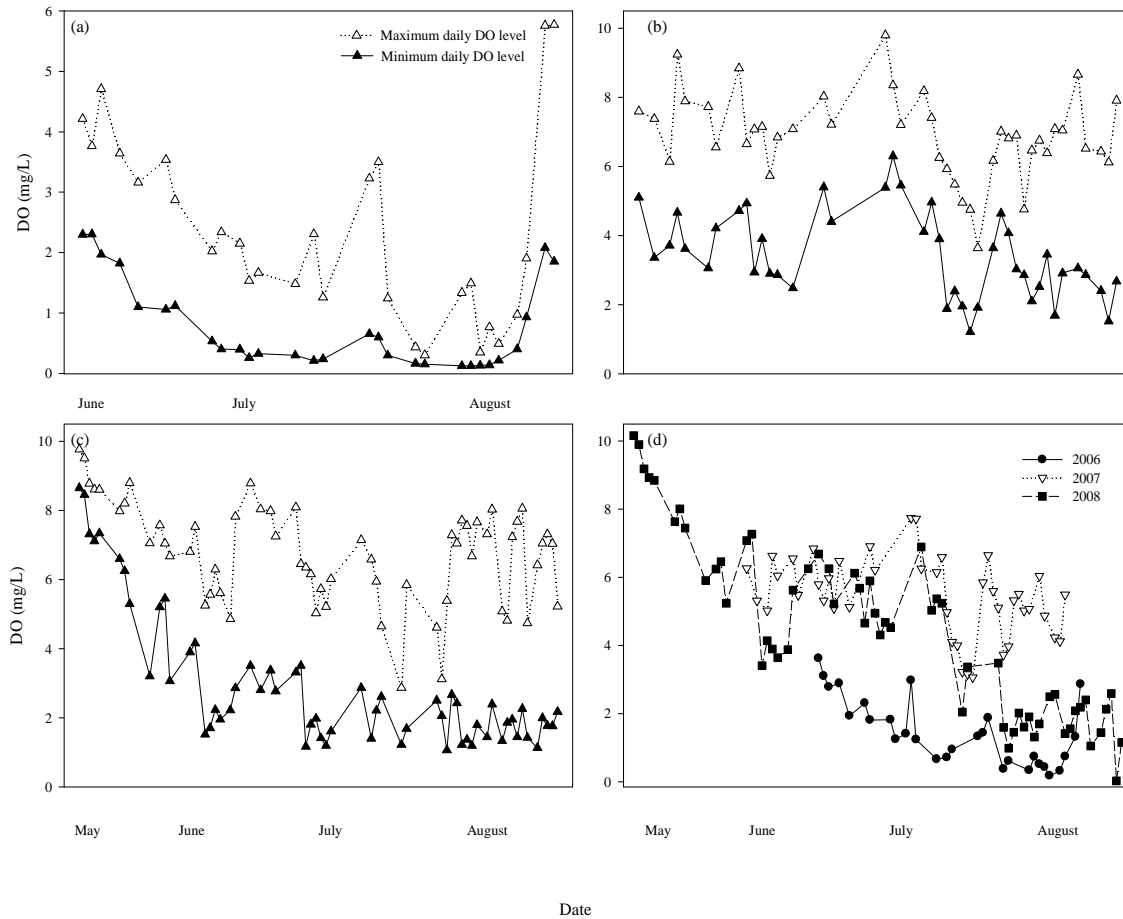
Figure 4.3: Daily minimum and maximum measures of dissolved oxygen in (a) 2006, (b) 2007, and (c) 2008 and (d) the average daily measures of dissolved oxygen by year in Blind Channel, Delta Marsh for the summer sampling period.
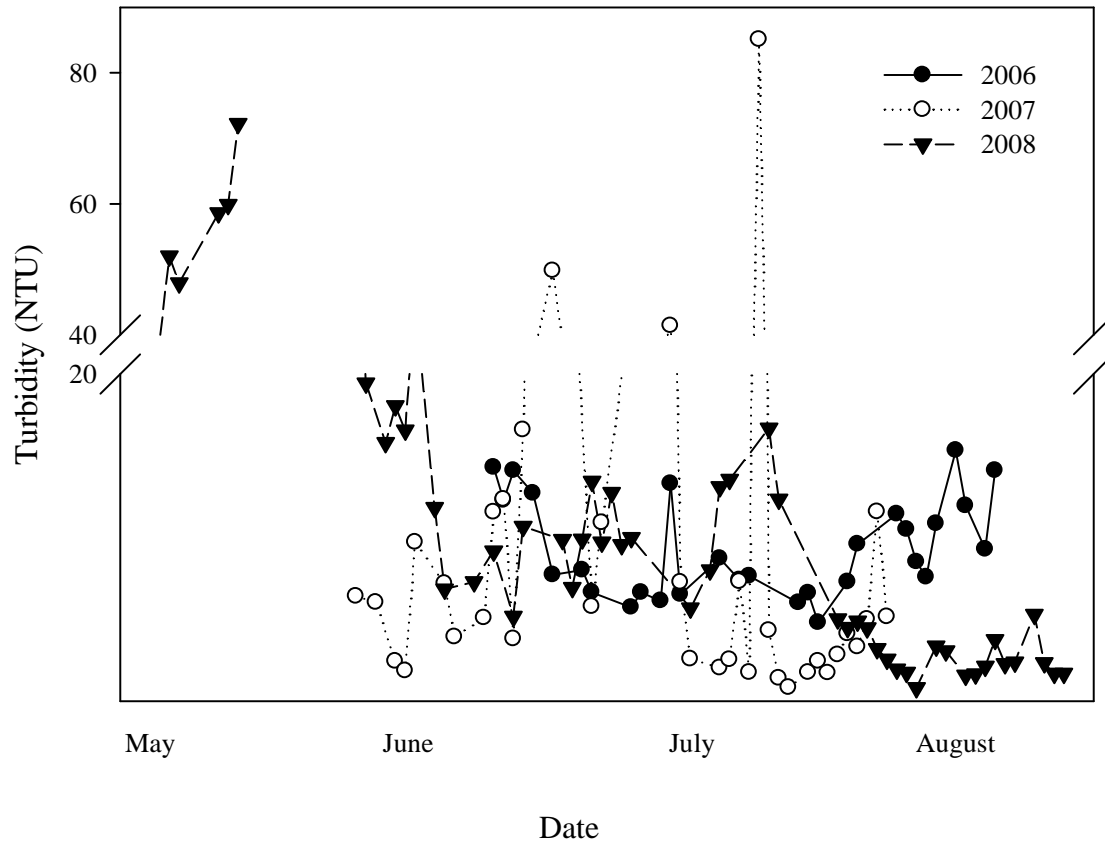
Figure 4.4: Average daily measures of turbidity in Blind Channel, Delta Marsh for the summer sampling period in 2006, 2007 and 2008.

period in 2007 (5.44 ± 1.2 mg/L O_2). As differences existed between all years in measures of

DO, year was used as a categorical predictor variable in further regression analyses involving

DO.

Differences in turbidity existed between 2006 and 2008, and 2007 and 2008 with 2006

and 2007 being significantly less turbid than 2008 (single factor ANOVA: $F_{2,120} = 4.66$, P =

0.0113; Figure 4.4; paired comparisons: significant differences occurred between 2006 and 2007

only). As a result of these yearly differences in turbidity measures, year was included as a

categorical predictor variable in regression analyses involving turbidity.

Temperature and community composition. When CPUE of northern pike, a cool-water fish, was

used in a regression analysis with year as a categorical predictor value and temperature as a

continuous predictor variable, there was a significant positive relationship with temperature; year

was not a significant predictor (Table 4.1) of pike CPUE. Temperature was also a significant

positive predictor of warm-water fish CPUE (brown and black bullhead, freshwater drum and

fathead minnows, Table 4.1). Again, year was not a significant predictor of warm water fish

CPUE. When the effect of temperature on fish length was examined, there was a significant

negative relationship between temperature and length of freshwater drum; there was no

relationship between temperature and length of any other fish species. Year was not a significant

categorical predictor of fish length for either species.

Dissolved oxygen and community structure. There was a direct significant relationship between

DO level and the CPUE of fish with physostomous swim bladders (Table 4.2); as DO levels

increased, the CPUE of fishes with physostomous swim bladders also increased. There was a

significant positive relationship between DO levels and fishes with physoclistous swim bladders; as DO levels increased, the CPUE of freshwater drum (the only fish in this study with a physoclistous swim bladder) increased (Table 4.2). However, the length of fishes with physostomous swim bladders were not significantly influenced by DO levels (Table 4.2); the length of freshwater drum was affected by DO. As DO levels increased, the size of freshwater drum captured also increased. Year was not a significant predictor in either of the regression models.

Turbidity and community structure. Turbidity levels did not significantly predict the abundance of visual foragers (fathead minnows, freshwater drum, and northern pike; Table 4.3) or the abundance of non-visual foragers (brown and black bullhead, Table 4.3). Vision is linked to eye size which in turn is a function of body size but neither year nor turbidity was a significant predictor of the body length of either of the visual predators (freshwater drum and northern pike; Table 4.3). The previous regression analysis was then repeated for non-visual foragers (bullhead species) and again, no relationship was observed between turbidity levels and length of non-visual foragers.

The abiotic environment taken as a whole. The canonical correlation analysis indicated a significant relationship between the environment and measures of fish CPUE (Canonical R = 0.6161, P < 0.0001, n = 106) with the first canonical function as the only significant function. The first canonical function is therefore the only function for which results are discussed. Given

Table 4.1: Results of regression analyses using temperature as the continuous predictor variable and year as a categorical predictor variable. Year was not a significant predictor in either regression model. Model df = 3. BH spp = bullhead species, FWD = freshwater drum, NPK = northern pike; S.E. = standard error. Significant differences are indicated with bold values.

Dependent variable	B	S.E. β	F - value	P –value	Residual df	Matches predicted relationship
Cool water fish CPUE	0.402	0.0663	16.5	**< 0.00001**	128	No
Warm water fish CPUE	0.627	0.246	6.45	**0.0003**	373	No
Length of BH spp	-0.0987	0.158	0.403	0.7	53	No
Length of FWD	-0.701	0.167	7.57	**0.00007**	297	Yes
Length of NPK	-0.128	0.0952	1.60	0.2	379	No

Table 4.2: Results of regression analyses using dissolved oxygen as the continuous predictor variable and year as a categorical predictor variable. Year was not a significant predictor in either regression model. Model df = 3. BH spp = bullhead species, FWD = freshwater drum, NPK = northern pike. S.E. = standard error. Significant differences are indicated with bold values.

Dependent variable	B	S.E. β	F - value	P –value	Residual df	Matches predicted relationship
Physostomous swim bladders	0.333	0.115	6.04	**0.0005**	373	No
Physoclistous swim bladders	0.238	0.0986	4.89	**0.003**	128	Yes
Length of BH spp	0.0355	0.157	0.213	0.9	55	No
Length of FWD	0.408	0.148	6.43	**0.0003**	279	Yes
Length of NPK	-0.000627	0.0246	0.00503	0.9	379	No

the abiotic environment, 27.9% of the variance in measured CPUE is explained. When the

measures of the simple linear correlation between the independent variables and the respective

canonical variates are determined, there is a negative correlation between the first canonical

correlation (CC1) which includes temperature, DO and turbidity, and northern pike CPUE

(canonical loading = -0.9108). Freshwater drum is positively correlated to CC1 (canonical

loading = 0.4207) while bullhead species CPUE and minnow CPUE show the lowest correlations

(canonical loadings: bullhead species CPUE = 0.1566; minnow CPUE = 0.2630). Both bullhead

species and fathead minnows are positively correlated to CC1, though the relationship is not

strong (Table 4.4). This demonstrates that the environment, as an explanatory variable, affects

the CPUE of northern pike. The environment also affects the CPUE of freshwater drum but to a

lesser degree. Based on CC1, bullhead species CPUE and minnow CPUE are essentially not

affected by the measured environmental variables.

Predators and prey. When the daily average CPUE measures were compared for individual

species of predatory fish among the sampling seasons of 2006, 2007 and 2008, northern pike and

bullhead species CPUE measures did not differ among years (single factor ANOVA: northern

pike: $F_{2, 131} = 4.37$, $P = 0.074$; bullhead species: $F_{2, 131} = 1.78$, $P = 0.173$; Figure 4.5). In the

between year comparison of total predatory fish CPUE, significant differences were only

observed between the years 2006 and 2008, with a significantly higher CPUE observed in 2008

than in 2006; no differences were observed between 2006 and 2007, 2007 and 2008 (single

factor ANOVA: $F_{2, 131} = 9.75$, $P = 0.00014$; multiple paired comparisons $P < 0.05$, Figure 4.5).

In the comparison of freshwater drum CPUE among years, significant differences were observed

Table 4.3: Results of regression analyses using turbidity as the continuous predictor variable and year as a categorical predictor variable. Year was not a significant predictor in the regression model. Model df = 3. BH spp = bullhead species, FWD = freshwater drum, NPK = northern pike. S.E. = standard error. Significant differences are indicated with bold values.

Dependent variable	B	S.E. β	F - value	P –value	Residual df	Matches predicted relationship
Visual foragers	-0.0467	0.0987	0.236	0.9	358	No
Non-visual foragers	-0.0327	0.102	0.234	0.9	105	No
Length of BH species	0.178	0.161	1.33	0.3	55	No
Length of FWD	-0.128	0.0953	0.537	0.7	297	No
Length of NPK	-0.193	0.153	0.246	0.9	379	No

Table 4.4: Results of a canonical correlation analysis examining the relationship between environmental variables (temperature, DO and turbidity) and CPUE measures of predatory and prey fish species in Blind Channel, Delta Marsh. Bold values indicate those variables with strong contributions of the canonical correlation. Only the first canonical correlation (CC1) was found to be significant and is the only canonical correlation reported here.

	Variable	CC1
	Canonical R	**0.6161**
Explanatory set	Dissolved oxygen	**-0.8447**
	Temperature	**0.9145**
	Turbidity	**-0.4556**
	Variance explained	0.5858
	Redundancy	0.2223
Response set	Total predator CPUE	**-0.5415**
	Northern pike CPUE	**-0.9108**
	Freshwater drum CPUE	**0.4207**
	Bullhead spp	0.1566
	Fathead minnow	0.2630
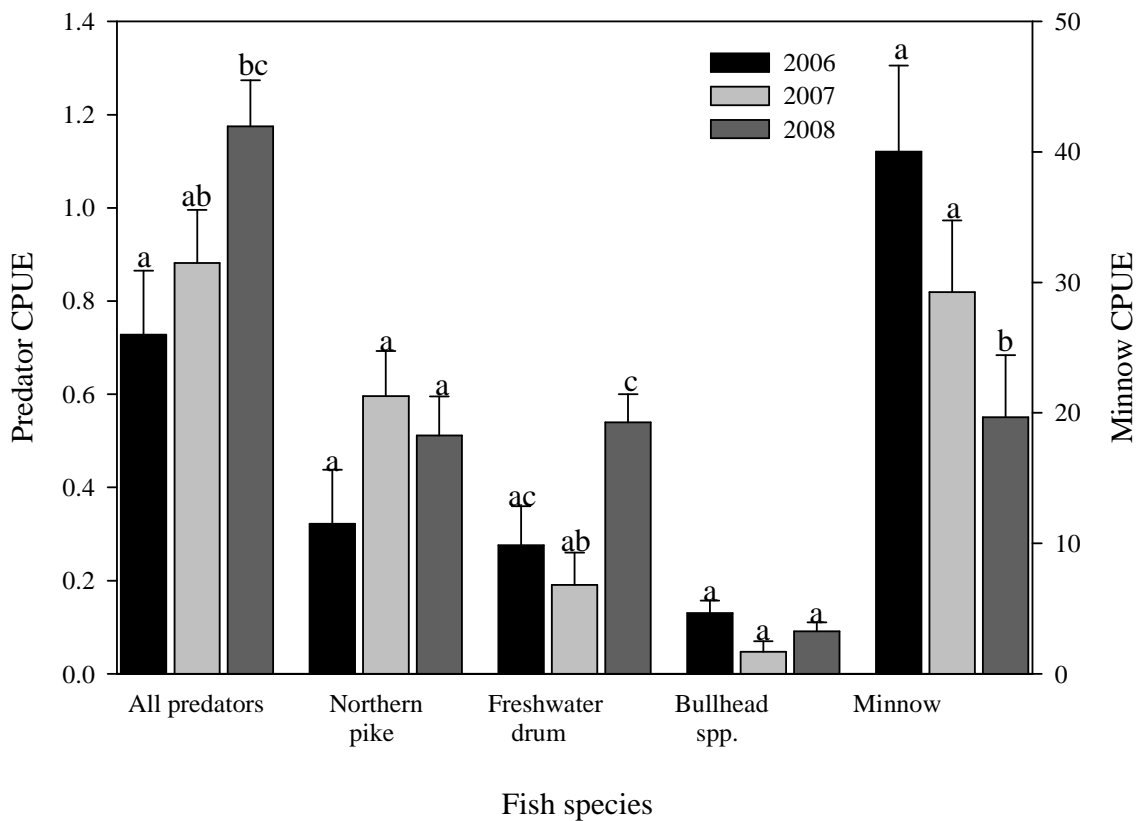
Figure 4.5: Differences in catch per unit effort for fish sampled in 2006, 2007 and 2008 from

Blind Channel, Delta Marsh. Letters above the bars represent significant differences at $\alpha = 0.05$

using Tukey post hoc tests. Bars represent standard error around the mean.

between the years of 2007 and 2008 only (single factor ANOVA: $F_{2, 131} = 11.5$, $P < 0.000026$; multiple paired comparisons between 2007 and 2008, $P < 0.05$; Figure 4.5) with significantly more freshwater drum captured per hour in 2008 than 2007. No differences were observed between 2006 and 2007, 2006 and 2008.

When the same among year comparison was made for fathead minnows, the predominant prey fish of Blind Channel, a significant difference in CPUE was observed (single factor ANOVA: $F_{2, 131} = 26.7$, $P < 0.000001$; Figure 4.5). Significantly more minnows were captured per hour in 2006 and 2007 than 2008 (multiple paired comparisons $P < 0.05$); no differences existed in fathead minnow CPUE between the years 2006 and 2007. As differences existed among years in measures of CPUE for both predators and prey, year was used as a categorical predictor variable in a regression analysis relating prey to predator abundances.

There was no relationship between total predator CPUE and prey CPUE in a regression analysis that included year as a categorical predictor variable, total predator CPUE as the continuous predictor variable and prey CPUE as the dependent variable   ($F_{3,127} = 3.19 \times 10^{-5}$, $P = 0.9$). However, there is an inverse relationship between the total predator CPUE (bullhead species, freshwater drum and northern pike) and prey (fathead minnow) CPUE when seasonal averages of CPUE were compared. In 2006 when predator abundance was the lowest of the three years, prey abundance was highest while in 2008 when predator abundance was at its highest, prey abundance was the lowest recorded for the three years.

Discussion

Linking environmental conditions that communities experience to the interactions of species within the community is a difficult task to do *in situ*. However, it is only in natural ecosystems that the effects of possible interactions of various environmental measures on multiple species can be elucidated. This study examines whether in an open ecosystem, where individuals can leave if the environmental conditions become unfavourable, the abiotic environment can be used as predictors of the abundance of various fish species. This study also examines whether predator and prey abundances are directly linked in such a system. Given the responses of these fishes to the environment, I also suggest how the environment may mediate predator-prey interactions, commenting specifically on the predictions of Abrahams et al. (2007).

The three years during which this study was undertaken experienced significantly different environmental conditions, as well as different measures of CPUE of both predatory and prey fish. This variability in environmental conditions meant that fishes experienced different combinations of temperature, DO and turbidity across the three years of study. If any relationships between environmental variable and fish CPUE or fish length were observed it would provide strong support that the particular environmental variable of interest was driving the abundance and/or length of the fish species or group of interest. It should be noted that sampling via gill net and minnow trap requires that fishes be active and swim into the net or trap. This means that it will not only be the abundance of fish that drives the observed CPUE, but also the activity of the fish present that influences fished CPUE. Both abundance and activity rates (through the relationship between activity and encounter rates) will likely have similar effects on predator-prey interactions and as such will be discussed together.

The relationship between temperature and fish CPUE was not dependent upon the temperature guild classification of fishes. For both cool- and warm- water fishes, there was a

significant positive relationship between temperature and CPUE. While it was expected that warm-water fish activity and/or abundance would increase with increasing temperature an increase in northern pike (a cool-water fish) activity and/or abundance with increasing temperature was unexpected. Cool-water fish generally have upper thermal limits of 20˚C (Magnuson et al. 1997) and Blind Channel typically reaches 20˚C in mid-June. However, temperature preferences are species-specific (Magnuson et al. 1997) and northern pike are known to tolerate a wide range of environments (Casselman and Lewis 1996); Flinders and Bonar (2008) also observed northern pike inhabiting areas outside their optimal temperature for growth (19˚C, Casselman 1978). It is probable that a cool-water species lacking in the ability to tolerate a wider range of temperatures would not have demonstrated a positive relationship with temperature, however there were no other species classified as cool-water in the system studied.

These observed positive relationships between temperature and fish CPUE could affect predator prey relationships as it suggests fish become either more active, more abundant, or both more active and more abundant when temperatures increase (minnow traps and gillnets are passive traps and increased catches suggest increased activity and/or abundance). Moore and Townsend (1998) and Anderson et al. (2001) suggest that the increase in activity of prey in response to increased temperatures (likely as prey increase foraging to meet increased metabolic demands) is responsible for the increase in mortality of prey observed at high temperatures. Taken with the observation that fathead minnows increase activity and foraging (Chapter 2) as well as their propensity to forage in risky locations (Chapter 3), temperature increases are likely to result in an increase in predation on small forage fish, a result that does not agree with predictions made by Abrahams et al. (2007). Given that predators have been observed to increase their attack rates on more active groups versus those groups who were less active (Krause and

Godin 1995) and that capture efficiency, attack coefficient, and swimming speed of fish can increase with increasing temperatures, temperature increases are likely to result in increased mortality of prey.

Temperature was also expected to influence the length of predatory fish through its impact on metabolic costs which are affected by the size of fishes. Large fish of a given species will have higher metabolic rates than smaller fish of the same species, making it more energetically costly for large fish to forage in warmer waters. In this study, only freshwater drum lengths were significantly related (negatively) to temperature. The lack of relationship between species length and temperature with the exception of freshwater drum (for either cool- or the other warm- water fish) may be a result of the ability of fishes that may be physiologically or energetically stressed to leave Blind Channel and move into Lake Manitoba, which is a large lake that is deeper and likely cooler than Blind Channel. The negative relationship between temperature and length of freshwater drum may be a result of larger, more physiologically stressed individuals leaving Blind Channel for Lake Manitoba. Any effect of temperature on predator-prey relationships will therefore be a result of the increase in activity and/or abundance of fishes with temperature, and not a result of changes to predation risk which could happen with changes in the size (length) of the potential predators (Byström and Andersson 2005).

As dissolved oxygen increased, CPUE of fishes with the ability to air breath also increased. As the ability to remove oxygen from air gulped in at the surface should negate (or reduce) the necessity of individuals with physostomous swim bladders to occupy waters of high DO levels, a relationship between CPUE of fish with physostomous swim bladders and DO was not expected. This observation might be a result of lengthy periods of time where the water was hypoxic.

When faced with periods of extreme hypoxia, it is possible that increased air breathing by these large predators would increase the risk of them being predated on by avian predators (Randle and Chapman 2004). As avian predators are present in Blind Channel, increased air breathing may increase risk of predation. Forster's terns, *Sterna forsteri*, prey upon small prey fish (Fraser 1997) such as fathead minnows and their presence over Blind Channel is directly related to DO levels (Chapter 6). American white pelicans, *Pelecanus erythrorhynchos*, and double-crested cormorants, *Phalacrocorax auritus*, have been observed to consume fish as long as 40 cm (personal observation). With the connection to Lake Manitoba, it is possible that large individuals migrate from Blind Channel to Lake Manitoba where DO levels are likely higher as a trade-off against risk of predation that they would experience exploiting surface waters in Blind Channel in periods of low DO.

With regards to the relationship between fish length and DO, if fishes have physostomous swim bladders and could air breath, there is no expectation that the length of individuals of these species would decrease with decreasing DO levels. The results of this study support the prediction that body size of species with physostomous swim bladders do not vary with DO. Observed was a positive relationship between freshwater drum length and DO. Freshwater drum have a physoclistous swim bladder and are reliant upon the oxygen content of the water for gas exchange. Smaller individuals of the same species require less oxygen to maintain body function and so the relationship was expected (Almeida-Val et al. 2000, Robb and Abrahams 2003).

Hypoxic regions have been suggested to be refuge areas for small fish (Chapman et al. 1998) and Abrahams et al. (2007) suggest that periods of low DO levels should result in a reduction in the predation risk to prey fish. This study supports that concept as the abundance and/or activity of fishes are highest when DO levels are highest and lowest when DO levels are

lowest. Predator-prey interactions may be lessened through a reduction in encounter rates when DO levels are low. As with temperature, any effects DO levels have on community structure and predator-prey relationships are expected to be a result of changes in CPUE that occur with DO levels and not with changes in predation pressure that would occur with changes in fish length and DO levels. It should also be noted however, that under periods of low DO, avian predation on these small prey will likely increase as abundance of terns is significantly, positively related to DO (see Chapter 6).

The predatory fish community of Blind Channel is comprised primarily of northern pike, a visual, ambush predator (Craig 2008). The other predator that relies primarily on vision for foraging is the freshwater drum. Fathead minnows, the primary prey in Blind Channel, also rely on vision for foraging. It was expected that as turbidity levels increased visual foragers such as northern pike, freshwater drum and fathead minnows would seek out clearer waters, potentially in Lake Manitoba, in which to forage, resulting in a negative relationship between turbidity and visual foragers. However, this prediction is based on the assumption that the decision of fish to remain in Blind Channel under given turbidity conditions is based only on foraging considerations and not on other physiological conditions resulting from changes in temperature and/or DO. Visual predators remained abundant in periods of high turbidity levels. This suggests that turbidity levels in the channel were 1) not high enough to affect foraging efficiency, 2) did not vary enough to cause changes in foraging efficiency, or 3) the abundance of forage fish within the channel was sufficient enough to offset the reduction in foraging ability of predators as turbidity increased. As well, it could be that the other option (Lake Manitoba) did not provide a decrease in turbidity levels and/or increased foraging opportunities. One final option is that under low turbidity levels fishes present that rely on vision for foraging will be able to see the

traps present and be able to avoid them. This too would result in a lack of relationship between turbidity level and CPUE of visual foragers.

Turbidity levels were also not a predictor of the length of fishes for either visual or non-visual foragers. It was expected that turbidity levels would not affect the length of non-visual foragers. Body length is related to eye size and therefore size of the sighted image; as non-visual predators are not reliant on sight for foraging, there is no expectation that increased turbidity would reduce foraging abilities, necessitating the movement out of highly turbid environments by smaller individuals. While it was expected that body size of visual foragers would increase with increasing turbidity levels (again, as smaller visual predators migrate out with increasing turbidity), given that the only location fishes can migrate is Lake Manitoba, a turbid environment, it may be that no other option is available.

In general, Blind Channel is a turbid environment. While studies have found reactive distances (Miner and Stein 1996) and antipredator behaviour (Abrahams and Kattenfeld 1997) decrease with increasing turbidity, in the range of turbidity values observed during the majority of this study, mortality of prey is expected to remain consistent (Abrahams and Kattenfeld 1997). As initially suggested by Abrahams et al. (2007), I predicted that increased turbidity should result in a reduction in predation risk to prey when predators rely on vision. However, this study found no relationship between activity and/or abundance of either visual foragers or foragers that rely on other senses to forage, and turbidity levels. This suggests that within this system it is the effects of temperature and DO on fish species that drive community composition, a fact further supported by results of the canonical correlation analysis.

Northern pike are significant predators on forage fish (He and Kitchell 1990) and have been shown to exclude small fish from small pools (Labbe and Fausch 2000). Fish also comprise

a large component of the diet of the two bullhead species as well (Keast 1985). Freshwater drum forage primarily on crustaceans and insects and rely to a much lesser extent on forage fish as a prey item (Scott and Crossman 1998). Northern pike, brown and black bullheads and freshwater drum were considered predators to small forage fish. However, unlike previous studies that determined predatory fish reduced prey abundance (Vonesh et al. 2009) there was no relationship between total predator CPUE and CPUE of prey fish in this study. This result is not entirely unexpected as a reduction in prey biomass in response to predation has not been a consistent result across studies (Åbjörnsson et al. 2002, Eitam and Blaustein 2004, Pink et al. 2007). It is possible that the densities of predators were not great enough to have an effect on prey density. It is also possible that on a small temporal scale, trends would not be evident. In this study, while daily measures of prey abundances were not related to daily measures of predator CPUE, on a larger scale (entire three month sampling period) when predator abundance (measured as average summer CPUE) was highest, prey abundance (measured as average summer CPUE) was lowest.

In summary, the results of this study suggest that in a shallow, turbid freshwater ecosystem the environmental variables that consistently influence community structure are dissolved oxygen and temperature. High temperatures may increase predation risk through increased encounter rates between predators and prey – CPUE of both predators and prey increase with increasing temperatures. Increased hypoxic conditions, which are linked to a reduction in CPUE of fishes may provide increased refuges for small fish from larger aquatic predators, though this may not carry over when aerial predators are considered and a decrease in DO results in increase predation risk.

References

Åbjörnsson, K., Brönmark, C., Hanson, L.-A. 2002. The relative importance of lethal and

non-lethal effects of fish on insect colonisation of ponds. Freshwater Biology **47:** 1489-1495.

Abrahams, M., Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioural Ecology and Sociobiology **40**: 169-174.

Abrahams, M.V., Mangel, M., Hedges, K. 2007. Predator-prey interactions and changing environments: who benefits? Philosophical Transactions of the Royal Society of London: Series B **362**: 2095-2014.

Almeida-Val, V. M. F., Val, A.L., Duncan, W.P., Souza, F.C.A., Paula-Silva, M.N., Land, S. 2000. Scaling effects of hypoxia tolerance in the Amazon fish *Astronotus ocellatus* (*Perciformes: Cichlidae*): contribution of tissue enzyme levels. Comparatve Biochemistry and Physiology Part B **125**: 219-226.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on a predator-prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Baum, J.K., Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology **78**: 699-714.

Byström, P., Andersson, J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos **110**: 523-536.

Bonner, T.H., Wilde, G.R. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society **131**: 1203-1208.

Burleson, M. L., Wilheml, D.R., Smatresk, N.J. 2001. The influence of fish size on the avoidance of hypoxia and oxygen selection by largemouth bass. Journal of fish Biology **59**: 1336-1349.

Caprio, J. 1982. High sensitivity and specificity of olfactory and gustatory receptors of

    catfish to amino acids. In: *Chemoreception in Fishes*. T.J. Hara, Editor. Elsevier,

    Amsterdam. pp 109-134.

Casselman, J.M. 1978. Effects of environmental factors on growth, survival, activity, and

    explanation of pike. American Fisheries Society, Special Publication **11**: 114-124.

Casselman, J.M., Lewis, C.A. 1996. Habitat requirements of pike (*Esox lucius*). Canadian

    Journal of Fisheries and Aquatic Sciences **53**: 161-174.

Chapman, L.J., Chapman, C.A., Chandler, M. 1998. Wetland ecotones as refugia for

    endangered fishes. Biological Conservation **78**: 263-270.

Chapman, L.J., Chapman, C.A., Nordlie, F.G., Rosenberger, A.E. 2002. Physiological

    refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake

    Victoria region. Comparative Biochemistry and Physiology Part A **133**: 421-437.

Chapman, L.J., Chapman, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L., Keiter, A.E.

    1996. Refugia for endangered fishes from and introduced predator in Lake Nabugabo,

    Uganda. Conservation Biology **10**: 554-561.

Clark, K.L., Ruiz, G.M., Hines, A.H. 2003. Diel variation in predator abundance, predation risk

    and prey distribution in shallow-water estuarine habitats. Journal of Experimental Marine

    Biology and Ecology **287**: 37-55.

Craig, J.F. 2008. A short review of pike ecology. Hydrobiologia **601**: 5-16.

De Robertis, A., Ryer, C.H., Veloza, A., Brodeur, R.D. 2003. Differential effects of turbidity on

    prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and

    Aquatic Sciences **60**: 1517-1526.

Eitam, A., Blaustein, L. 2004. Oviposition habitat selection by mosquitoes in response to

predator (*Notonecta maculate*) density. Physiological Entomology **29**: 188-191.

Fishcer, W. U. Jr., Standora, E.A., Spotila, R. 1987. Predator-induced changes in thermoregulation of bluegill, *Lepomis macrochirus*, from a thermally altered reservoir. Canadian Journal of Fisheries and Aquatic Sciences **44**: 1629-1634.

Flinders, J.A., Bonar, S.A. 2008. Growth, condition, diet, and consumption rates of northern pike in three Arizona reservoirs. Lake and Reservoir Management **24**: 99-111.

Fraser, G. 1997. Feeding ecology of Forster's terns on Lake Osakis, Minnesota. Colonial Waterbirds **20**: 87-94.

Gilliam, J.F., Fraser, D.F., Alkins-Koo, M. 1993. Structure of a tropical stream fish community: A role for biotic interactions. Ecology **74**: 1856-1870.

Hair, J.F., Black, B., Babin, B., Anderson, R.E., Tatham, R.L. 2005. Multivariate Data Analysis 6th Edition. New Jersey, U.S.A. Prentice Hall.

He, X., Kitchell, J.F. 1990. Direct and indirect effects of predation of a fish community: a whole-lake experiment. Transactions of the American Fisheries Society **119**: 825-835.

Hedges, K.J. 2007. Effects of abiotic factors on predator-prey interactions in freshwater fish communities. Ph.D. Thesis, University of Manitoba.

Hölker, F. 2003. The metabolic rate of roach in relation to body size and temperature. Journal of Fish Biology **62**: 565–579.

Howland, H.C., Merola, S., Basarab, J.R. 2004. The allometry and scaling of the size of vertebrate eyes. Vision Research **44**: 2043-2065.

Jackson, D.A., Harvey, H.H. 1989. Biogeographic associations in fish assemblages: Local vs. regional processes. Ecology **70**: 1472-1484.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences **58**: 157-170.

Keast, A. 1985. Implications of chemosensory feeding in catfishes: an analysis of the diets of *Ictalurus nebulosus* and *I. natalis*. Canadian Journal of Zoology **63**: 590-602.

Kennard, M.J., Olden, J.D., Arthington, A.H., Pusey, B.J., Poff, N.L. 2007. Multiscale effects of flow regime and habitat and their interaction on fish assemblage structure in eastern Australia. Canadian Journal of Fisheries and Aquatic Sciences **64**: 1346-1359.

Krause, J., Godin, J.-G. J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour **50**: 465-473.

Labbe, T.R., Fausch, K.D. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications **10**: 1774-1791.

Magnuson, J.J., Webster, K.E., Assel, R.A., Browser, C.J., Dillon, P.J., Eaton, J.G., Evans, H.E., Fee, E.J., Hall, R.I., Mortsch, L.R., Schindler, D.W., Quinn, F.H. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambriam Shield region. Hydrological Processes **11**: 825-871.

Matthews, W.J., Harvey, B.C., Power, M.E. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a Midwestern stream (U.S.A.). Environmental Biology of Fishes **39**: 381-397.

Miner, J.G., Stein, R.A. 1996. Detection of predators and habitat choice by small Bluegills: Effects of turbidity and alternative prey. Transactions of the American Fisheries Society **125**: 97-103.

Mitchell, A.L., Knouft, J. H. 2009. Non-native fishes and native species diversity in freshwater fish assemblages across the United States. Biological Invasions **11**: 1441-1450.

Moore, M.K., Townsend Jr., V.R. 1998. The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos **81**: 329-336.

Moyle, P.B., Vondracek, B. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology **66**: 1-13.

Neill, W.H. 1979. Mechanisms of fish distribution in heterothermal environments. American Zoologist **19**: 305-317.

Nilsson, P.A., Jacobsen, L., Berg, S., Skov, C. 2009. Environmental conditions and intraspecific interference: unexpected effects of turbidity on pike (*Esox lucius*) foraging. Ethology **115**: 33-38.

Nilsson, G.E., Östlund-Nilsson, S. 2008. Does size really matter for hypoxia tolerance in fish? Biological Reviews **83**: 173-189.

Persson, L. 1986. Temperature induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. Journal of Animal Ecology **55**: 829-839.

Pink, M., Fox, M.G., Pratt, T.C. 2007. Numerical and behavioural responses by cyprinids to the introduction of predatory brook trout in two oligiotrophic lakes in northern Ontario. Ecology of Freshwater Fish **16**: 238-249.

Quinn, G.P., Keough, M.J. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Randle, A.M., Chapman, L.J. 2004. Habitat use by the African anabantid fish *Ctenopoma muriei*: implications for the costs of airbreathing. Ecology of Freshwater Fish **13**: 37-45.

Richards, F.P., Ibara, R.M. 1978. The preferred temperatures of the brown bullhead, *Ictalurus nebulosus*, with reference to its orientation to the discharge canal of a nuclear power plant. Transactions of the American Fisheries Society **107**: 288-294.

Robb, T., Abrahams, M.V. 2003. Variation in tolerance to hypoxia in a predator and prey species: and ecological advantage of being small? Journal of Fish Biology **62**: 1067-1081.

Scott, W.B., Crossman, E.J. 1998. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada **184**:1-966.

Seymour, R.S., Farrell, A.P., Christian, K., Clark, T.D., Bennett, M.B., Wells, R.M.G., Baldwin, J. 2007. Continuous measurement of oxygen tensions in the air-breathing organ of Pacific tarpon (*Megalops cyprinoides*) in relation to aquatic hypoxia and exercise. Journal of Comparative Physiology B **177**: 579-587.

Tramer, E.J. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. American Midland Naturalist **97**: 469-478.

Vonesh, J.R., Kraus, J.M., Rosenberg, J.S., Chase, J.M. 2009. Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. Oikos **118**: 1219-1229.

Weetman, D., Atkinson, D., Chubb, J.C. 1998. Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulta.* Animal Behaviour **55**: 1361-1372.

Wei, A., Chow-Fraser, P., Albert, D. 2004. Influence of shoreline features on fish distribution in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences **61**: 1113-1123.

Wootton, R.J. 1990. Ecology of Teleost Fishes: Fish and Fisheries Series 1. Chapman & Hall, London.

Chapter 5: Using a dynamic state variable model to predict the effect of temperature on survival probabilities of fathead minnows over an ice-free season

Abstract. In shallow water ecosystems, fathead minnows (*Pimephales promelas*) experience temperatures ranging from near 0 to above 30˚C over the ice-free season, which ranges typically

from March to November in temperate regions. Over this period there is an annual survival rate of approximately 65%. Since these fish are poikilothermic, their energetic demands will be strongly driven by their thermal environment. High temperatures increase energetic demands and understanding the role of temperature in behavioural decisions made by prey may play an important role in understanding how survival rates are driven by the temperature of the environment. At high temperatures, individuals may be more likely to starve, resulting in them taking greater risks to obtain more food. To better understand this process I developed a state-dependent optimization model that required individuals to make foraging decisions that balanced the risk of starvation against the risk of predation in a dynamic thermal environment. Results from this model predict that temperature increases will have a detrimental outcome on the survival probabilities of adult fathead minnows, at least in the short term, regardless of the relationship between probability of receiving food and the amount of food present and irrespective of a reduction in predation risk with temperature. With many climate change predictions suggesting rising temperatures across the prairies, the results from this study suggest that populations of minnows may experience a reduction in numbers. As fathead minnows are a dominant forage fish in many shallow water ecosystems, any reductions in population size will affect community dynamics.

Introduction

For a poikilothermic animal such as a fish, the temperature of the environment it inhabits will influence rates of biological processes at scales from the molecular-level to the whole organism (Logue et al. 1995). The influence of temperature can be observed as changes in metabolic, assimilation and consumption rates of fishes (Wootton 1990) as well as in changes in activity

(Krause and Godin 1995, Johnston et al. 2004, Chapter 2), foraging (Chapter 2 and Chapter 3) and swimming performance (Logue et al. 1995). This relationship between temperature and metabolic processes is not a direct linear relationship, but instead fishes have a temperature optimum (Huey and Kingsolver 1989) outside of which performance of the individual is reduced. Treating temperature as an ecological condition, thermal habitats should therefore be selected to optimize physiological performance. However, with the thermal conductivity of water 24.5 times that of air (Hammel 1955), the availability of thermal microhabitats within a shallow body of water will be limited and changes in environmental temperature will rapidly change body temperature.

The temperature of the environment in which a fish resides is related to the metabolic rates of the fishes, and therefore their energetic demands (Elliott 1976). Increasing energetic demands should therefore result in an increased requirement for food. Because of this relationship between temperature and energetic demands, temperature can drive many aspects of the decision making and behaviour of small fishes: foraging to meet energetic demands are balanced against risk of predation. Larval anurans respond to increasing temperatures (and therefore energy requirements) by increasing their foraging rates (Anderson et al. 2001). A similar response was observed in studies of the fathead minnow (Chapter 2, Chapter 3). If these increased energetic demands can be met, increased temperatures should also lead to increases in growth rates (Elliott 1976, Keast 1984, Anderson et al. 2001). With body size and risk of predation being inversely related (Nilsson and Brönmark 2000) individuals may experience a reduction in predation risk at increased temperatures. As well, Abrahams et al. (2007) described, via a model, changes in population abundance of brown trout (*Salmo trutta*) as a result of temperature increases. They described an overall reduction in risk of predation through a

reduction in the number of large bodied individuals, and an overall general reduction in the

abundance of these trout. Predation risk may therefore decrease with increases in temperatures.

As long as temperatures remain below the lethal limit and energetic demands are met, increases

in temperature should be linked to increases in the probability of survival of prey. However,

there is a caveat. In the study by Anderson et al. (2001), accompanying the increase in foraging,

consumption and growth rates of prey, were increased mortality rates at higher temperatures. As

movement rates increase, it becomes more likely that an encounter occurs between predator and

prey. Coupled with an observed decrease in capture and handling time of prey by predators as

temperature increases (Persson 1986), it becomes less clear if increases in temperature will result

in an increase or decrease in the probability of survival.

Adding to the uncertainty of the relationship between temperature and survival is the

amount of available food and the probability of consuming that food. Food availability is linked

to temperature and the probability of encountering and consuming that food is linked to the

amount of food available. As mentioned above, if temperature increases cause excess food

availability growth rates also increase (Elliott 1976, Keast 1984, Person-Le Ruyet et al. 2004).

However, if high temperatures do not coincide with high abundances of prey, weight loss will

occur (Gibbons et al. 1978). Starvation is therefore of concern if an increase in metabolic

demand cannot be met via consumption of food.

For a small minnow, prey abundance is linked to temperature (Goldman and Carpenter

1974, Walls and Ventelä 1998, Gillooly 2000, Gillooly et al. 2002, Savage et al. 2004, Verbitskii

et al. 2009). The doubling time for both algae and zooplankton, primary foods for fathead

minnows (Scott and Crossman 1973), decrease as temperatures increase (Goldman and Carpenter

1974, Gillooly et al. 2002). The overall result is that while increasing temperatures may increase

energetic demands of small fish, if their prey abundance increases at a rate that allows them to meet energetic demands, growth and possibly survival will likely increase. However, if the rate of increase in prey abundance and availability does not match that of the rate of metabolic increase, an increased probability of starvation may occur. The goal of this paper is to examine the possible changes in the probability of survival over the ice-free period of a typical, non-breeding fathead minnow, *Pimephales promelas*. The fathead minnow is an ideal model as it is a fish that experiences a wide range of thermal variation over the course of the ice-free season. Further manipulations of the state-dependent optimization model will allow for predictions regarding survival of the fathead minnow to be made when the overall environment warms, including whether there will be changes in probabilities of starvation and predation.

Methods

The model overview. A dynamic state variable model examining the probability of survival over the ice-free season was constructed for a typical, non-breeding, fathead minnow under a normal temperature regime (see Clark and Mangel 2000, McNamara and Houston 1986, for the principles of stochastic dynamic programming). This model describes the role temperature variation plays on habitat selection decisions of the fathead minnow through the development of rules necessary for decision making. The environment that was modeled was Blind Channel, Delta Marsh, MB, a location that has been used to study fathead minnows for approximately 20 years. To address the question of the role of temperature on the survival of fathead minnows, it was first necessary to model a temperate environment that experiences variability in temperatures. This variation in temperature allows for the role of temperature variation on habitat selection to be determined via a state-dependent optimization model.

Blind Channel is a small, turbid, shallow water ecosystem located just south of Lake Manitoba, Manitoba, Canada (98°23'W, 50°11'N). Approximately 3.5 km long, its average depth is 1 m and recorded summer temperatures have reached 29°C. Temperatures can fluctuate up to 4°C daily (personal observation). It is the thermal environment of Blind Channel that is the basis for the temperatures of the habitats present in the model. By modifying the overall temperature (i.e. the temperature of all patches), the responses, as measured by changes in survival probabilities of the fathead minnow, can be elucidated. The fish community of Blind Channel is comprised of large piscivores (northern pike, *Esox lucius*, dominate; brown and black bullhead, *Ictalurus nebulosus* and *I. melas* and freshwater drum, *Aplodinotus grunniens* are also common) as well as small forage fish, of which fathead minnows dominate numerically. Common across central North America, the fathead minnow, in Canada, is distributed east to New Brunswick and west into Alberta and averages 51 mm total length (Scott and Crossman 1998). Across their range, including within Blind Channel, fathead minnows experience a wide range of temperatures seasonally.

With bioenergetics and risk of predation linked to temperature, it is expected that changes in temperatures will alter the behaviour of fish through their habitat selection decisions as individuals try to meet increasing energetic demands. The development of a state-dependent optimization model allows for manipulation of model parameters such as available food and predation risk while keeping all other parameters and rules of habitat selection unchanged. This allows for the development of rules necessary for making decisions under the state-dependent optimization model. The use of these rules can then be used to better understand sources of mortality over the ice-free period, assuming that animals continue using the same rules. Overall,

the model allows for the effect of changes in parameters such as predation, amount of food, probabilities of finding food, as well as temperature, to be uncovered.

The model parameters.

Temperature of patches:

Temperatures of patches were based on measured temperatures at Delta Marsh, MB, Canada, and were constant within patches for the duration of one time step in the model, one 24 hour day. As water temperatures were directly measured only from 11 May through 07 August I determined the water temperature for the remainder of the ice-free season using the relationship between water temperature (T_W) and air temperature (T_A), which were both measured at Delta Marsh, using:

$$T_W = 0.6414T_A + 10.794 \tag{1}$$

(regression analysis: $R^2 = 0.8175$, $P < 0.00001$)

This initial temperature calculation corresponds to the temperature (EnvTemp) of Patch 1. Temperature of Patch 2 is equal to EnvTemp + 2˚C, and the temperature of Patch 3 equals EnvTemp – 1˚C. For all descriptions of the model parameters, the use of the term temperature refers to the patch specific temperature. To understand how thermal variation affects the survival of fathead minnows due to the impact of temperature upon state-dependent parameters, I increased the temperature of the ecosystem by 2C˚ (+2˚C Increased Temperature Regime, +2ITR) and 4 C˚ (+4˚C Increased Temperature Regime, +4ITR).

Metabolic cost of residing in a patch (α_i):

The metabolic cost of inhabiting a patch is based on the temperature of that patch as the metabolic rate of poikilotherms is directly related to temperature. Metabolic rates of fathead minnows at a variety of temperatures were obtained from MacLeod and Smith (1966) and Klinger et al. (1982). These data were then graphed and a log function was used to produce the equation used to predict metabolic cost (α_i) from water temperature ($R^2 = 0.9992$, $P < 0.00001$).

$$\alpha_i = 2.0141 * Ln(T_W) - 0.0217 \qquad (2)$$

This equation was rounded to the nearest whole number within the model to describe the role of temperature on the energetic state of the individual. There are always metabolic costs associated with the occupied patch and therefore if a fish fails to find food, its energetic state declines by the calculated cost of metabolism associated with the patch.

Probability of death due to predation, β_i

The equation describing probability of death due to predation was based on work by Persson (1986) who determined capture rate of prey by the Eurasian perch, *Perca fluviatilis*, over a range of temperatures. The Eurasian perch is a cool-water fish (Persson 1983), as is northern pike, *Esox lucius*, the dominant predator in Blind Channel, the system after which this model is based. It is therefore expected that the effect of temperature on the capture efficiencies of pike in Blind Channel would be similar to those of the Eurasian perch. The data from Persson (1986) described the relationship ($R^2 = 0.8172$, $P < 0.001$) between mortality rate of prey in a patch (β_i) and water temperature as:

$$\beta_i = 1.415^{-4} \, TW + 2.25^{-3} \qquad (3)$$

A model derived by Abrahams et al. (2007) suggests that as temperatures increase, the abundance of piscivorous fishes decrease. In their model, temperature increases of 3 and 7˚C

resulted in a reduction in the population of predatory brown trout (*Salmo trutta*) by approximately 0.78 and 2.3% respectively. Given those results, I was also interested in the probability of survival of fathead minnows over the ice-free season if predation risk decreased with temperature, instead of increased. To do this I simulated a reduction in predator population size similar to that observed by Abrahams et al. (2007) by reducing the probability of prey capture by predators (β_i) by 1.5%. As the dominant predator in Blind Channel is a cool water fish (northern pike, *Esox lucius*) and a 4°C increase in temperature could result in temperatures of nearly 34°C, I also reduced the probability of prey capture by 10% and determined the probability of fathead minnow survival in response to these changes in predation risk.

Probability of consuming food, λ_i

The probability that a fish consumes food is related to the density of the available food (Mols et al. 2004, Ruxton 2005, Ioannou et al. 2008). Using published data (Ioannou et a. 2008), the relationship between the probability of consuming food in patch *i* (λ_i) and prey density in that patch (Y_i) ($R^2 = 0.6810$, $P < 0.01$) is:

$$\lambda_i = 0.0783Y_i^{-0.663} \tag{4}$$

While Ioannou et al. (2008) determined that the probability of consuming the first encountered prey decreases with increasing density, it would be expected that in times of increased energetic demands, these initially encountered prey items would be consumed. A second equation based on data from Kawabata et al. (2006) was also used in the model ($R^2 = 0.3536$, $P < 0.025$):

$$\lambda_i = 4Y_i^{0.5038} \tag{5}$$

Under both scenarios, if a fish receives food, its energetic state increases by the amount of food it receives. The use of these two equations allowed me to determine if the pattern of survival

between temperature regimes would remain the same given different relationships between the amount of food present and the probability of receiving that food. These equations were used in two separate versions of the model and the outcomes compared.

Amount of food received if found, Y_i

Scott and Crossman (1998) suggest that fathead minnows primarily eat algae but also consume zooplankton and detritus (Herwig and Zimmer 2007). To incorporate multiple prey items into the model, I arbitrarily assigned 75% of the diet of the minnows to be algae; the other 25% was assumed to be zooplankton. As the population size of both algae (Goldman and Carpenter 1974) and zooplankton (Verbitskii et al. 2009) vary with temperature, I again used published data relating population doubling times to temperature to generate an equation to predict the amount of food available in the patches for algae (Y_{ia}) ($R^2 = 0.9261$, $P < 0.00001$):

$$Y_{ia} = 0.75 * (5.9085 * (2.7183^{0.0644Tw})) \tag{6}$$

and zooplankton (Y_{iz}) ($R^2 = 0.9998$, $P < 0.000001$) :

$$Y_{iz} = 0.25 * (5.95T_w - 6.9715) \tag{7}$$

The model assumes that algae and zooplankton have equal energetic content. These equations were rounded to the nearest whole number within the model. If temperature increases resulted in an increase in the probability of starvation, the model was used to determine how much food would be necessary to offset this risk of starvation.

Backward iteration. State-dependent optimization models are based on maximizing a measure of fitness. In this model, patches are selected to maximize the probability of survival for the fathead minnow. The model then moves backwards 181 time steps (each time step is a day), the calculated number of ice-free days in the study system. The backward iteration equation (a

stochastic dynamic programming equation) used in this model is based on patch selection to maximize survival, where $V_i(x, t)$ is a measure of fitness associated with visiting patch i on day t. $F(x, t)$ is the maximum expected survival probability between day t and the end of the ice-free season (or the end of the organisms life), given that $X(t) = x$.

$$V_i(x, t) = (1 - \beta_i)\{\lambda_i F(x - \alpha_i + Y_i, t + 1) + (1 - \lambda_i) F(x - \alpha_i, t + 1)\} \quad (8)$$

Forward iteration. The probabilities of being eaten by a predator and receiving food based on the previously described patch parameters are calculated (see Table 5.1 for model parameters) during the forward iteration based on the patch selection rules arising from the backward iteration. If the fish survives the first time step, at the next time period (i.e. the next day) the next patch is selected based on the new state of the fish. At states below 30, the fish is considered to not have enough energy for survival and dies. One hundred is the maximum state of the fish, which represents the greatest amount of energy reserves a fish can have. The forward iteration allows for a direct calculation of survival probabilities of fathead minnows over the ice-free season. Overall, the use of the dynamic state optimization model allows for a better understanding of sources of mortality that fathead minnows experience over the course of the ice-free season.

Table 5.1: Definitions of model parameters and variables.

Parameter	Definition
λ_i	Probability of receiving food in patch i
Y_i	Amount of food in patch i
α_i	Metabolic cost of residing in patch i

β_i	Probability of predation in patch i
x_crit	Critical energetic state necessary for survival; if x_crit < 30 the fish dies
x_max	Maximum energetic state; no fish can exceed an energetic state of 100
T	Time period over which the model runs; it is the total number of ice-free days = 181

Model output. I used the model to determine the survival rate of a population of 10 000 fathead during the ice-free period within Delta Marsh. Because I tracked sources of mortality and kept the decision making rules of the minnows in the backward iteration the same, I could also determine the relative impact of predation (and changes in risk of predation) and starvation on the population. I could also determine the effect of temperature on predation and starvation. Finally, if increased temperature indeed increased risk of starvation, both the amount of food

necessary to offset the energetic cost of increased temperature could be estimated in the model. The effect of temperature (both +2ITR and +4ITR), changes in overall predation risk, and the relationship between food density and the probability of receiving food on the probability of predation, probability of starvation and overall probability of survival are discussed.

Sensitivity analysis. Sensitivity analyses were conducted on the key parameters used in this model. Each parameter (λ_i, Y_i, β_i, and α_i) was increased by 5% and the resulting change in the probability of survival, calculated as a percent change, was determined. The percent change in the survival probability, was then divided by 5%, the change in the parameter value, and a dimensionless elasticity was calculated. I also determined that the model was not sensitive to my arbitrary assignment of 75% of the forage of the fathead minnows being comprised of algae with the other 25% of the forage arising from zooplankton (elasticity = -0.18) Elasticities were calculated for one parameter at a time; all other model parameters were kept unchanged while the parameter of interest was varied (Clark and Mangel 2000). The results of this analysis were used to determine which parameters were the most important to model predictions as well as to determine whether model predictions are heavily reliant upon parameters that are estimated and uncertain (Clark and Mangel 2000). As well, parameters that were determined to have large calculated elasticities were further manipulated to determine how changing these parameters would affect the model outcome.

Results

Sensitivity analysis. The parameter that had the largest calculated elasticity was β_i, the risk of predation. A 5% increase in the risk of predation reduced the probability of survival

approximately 2.25%. When β_i was then increased in the increased temperature regime iterations of the model, the resulting increase in probability of death was exacerbated – a 5% increase in risk of predation decreased the probability of survival by as much as 5% under the +2ITR and nearly 10% under the +4ITR. This reduction in survival was primarily a result of an even greater impact on mortality due to predators. The results of changing predation risk (specifically a reduction in risk) were further examined with respect to temperature. The parameter with the smallest calculated elasticity was α_i, the metabolic rate of the fish. A 5% increase in the metabolic cost, resulted in the smallest change in the probability of survival, a 0.35% decrease. All calculated elasticities were less than 0.5 and ranged from -0.47 to 0.23 (Table 5.2).

Model output and the natural ecosystem (normal temperature regimes)

Under the current temperature regime, the model predicts that the fathead minnow has between a 64 and 67% probability of surviving the ice-free season given the probability of consuming food decreases or increases, respectively, with food density. In both

Table 5.2: Calculated elasticities for the probability of survival when the indicated model parameter is increased by 5%. Changes to the risk of predation result in the greatest change in the probability of survival.

Model parameter	Elasticity
λ_i	0.18^1
	0.23^2
β_i	-0.47
α_i	-0.06
Y_i	0.137

Starvation	0.64^3

[1]From *Equation 5(a)*

[2]From *Equation 5(b)*

[3]Starvation combines Y_i, α_I and λ_i
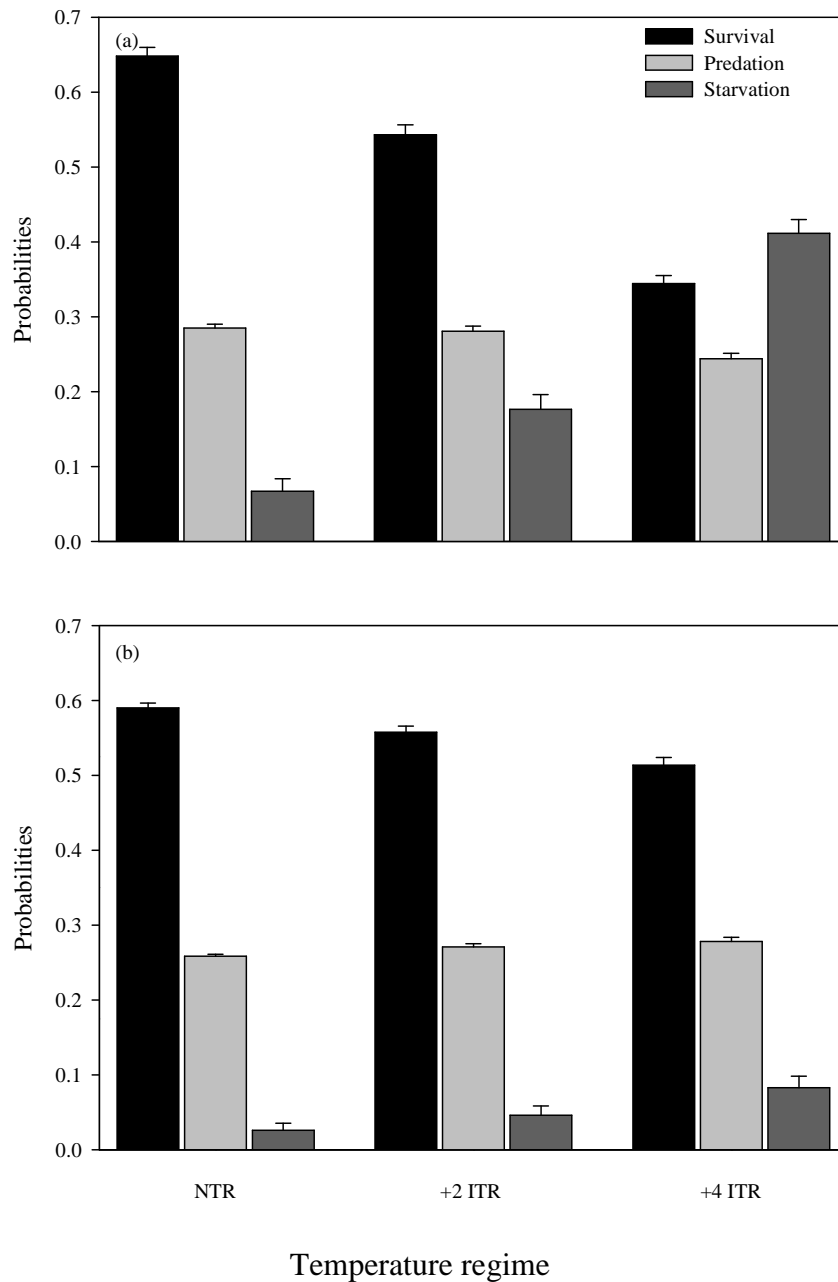
Figure 5.1: The average probability of surviving, dying due to predation and dying due starvation during the ice-free season regardless of initial state under three different temperature regimes (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density. Error bars represent the standard error around the mean.

scenarios, the primary cause of mortality is predation (28.5 and 29.5% chance of predation) while less than 7% of the population will succumb to starvation (Figure 5.1). Even at the lowest energetic state when the probability of receiving food declines with food density, the probability of surviving the ice-free season is 30%. When the probability of receiving food increases with food density, the probability of survival increases to approximately 45% (Figure 5.2) when individuals are at their lowest energetic state. The probability of death due to starvation approaches 60% at the lowest energetic states when the probability of receiving food decreases with food density. When the probability of receiving food increases with food density the probability of starvation declines to approximately 40% (Figure 5.3). Under the current temperature regime, the minimum probability of death due to predation occurs when there is a positive relationship between the probability of receiving food and food density. When this occurs, there is approximately a 10% probability of death due to predation (Figure 5.4). For all energetic states, risk of predation is lower when individuals have a greater probability of receiving food as food density increases – these individuals do not have to occupy the most risky patches to meet energetic demands.

Temperature and survival. Regardless of the iteration of the model compared, more fish die as temperature increases (Figures 5.1 and 5.2). The probability of survival declines from approximately 64% under the normal temperature regime to 34% under +4ITR when there is an inverse relationship between prey density and probability of consuming food. The probability of survival under a +4ITR when prey density and probability of consuming food are positively linked does not decrease as much; fathead minnows have a
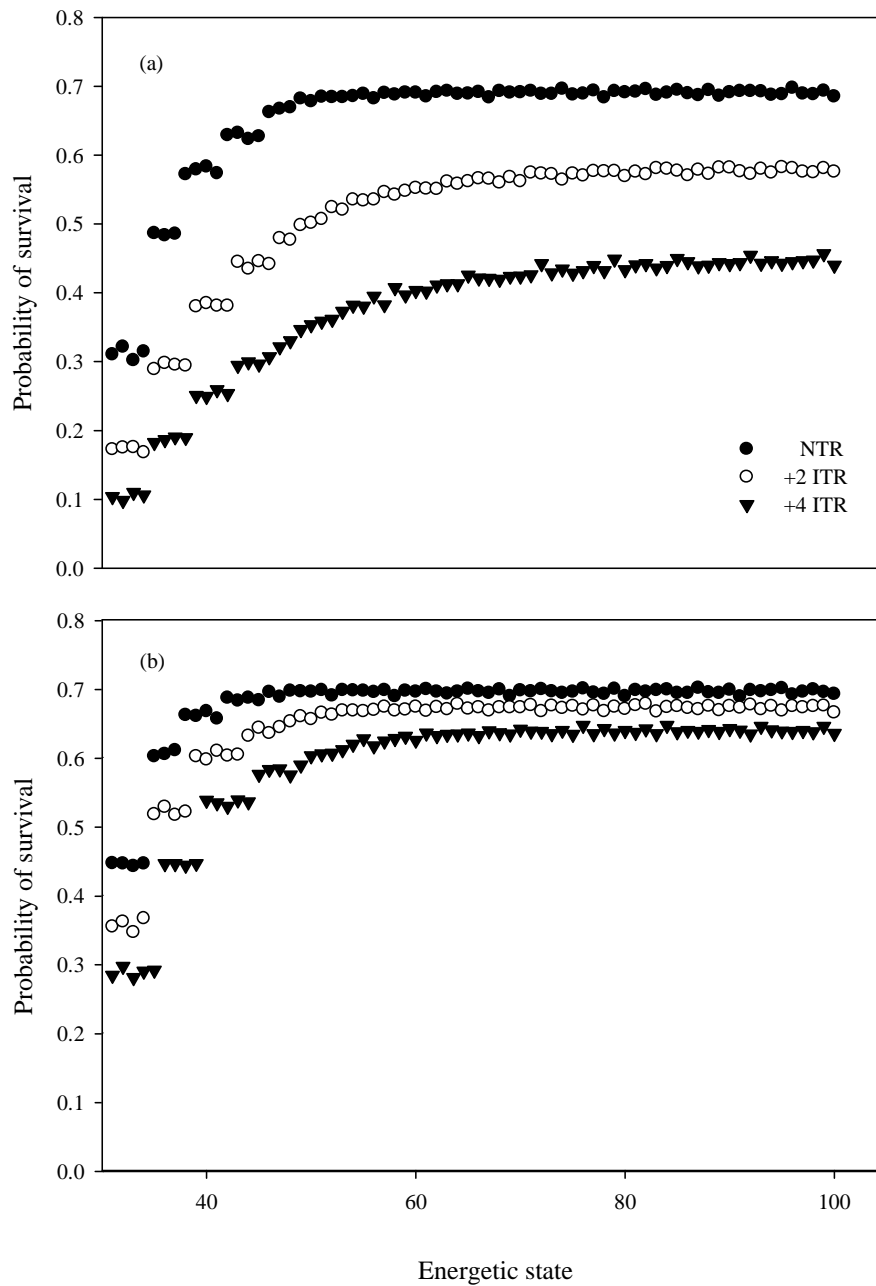
Figure 5.2: The probability that an individual fish survives the ice-free season, given the initial energetic state of the individual and the temperature regime (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density.
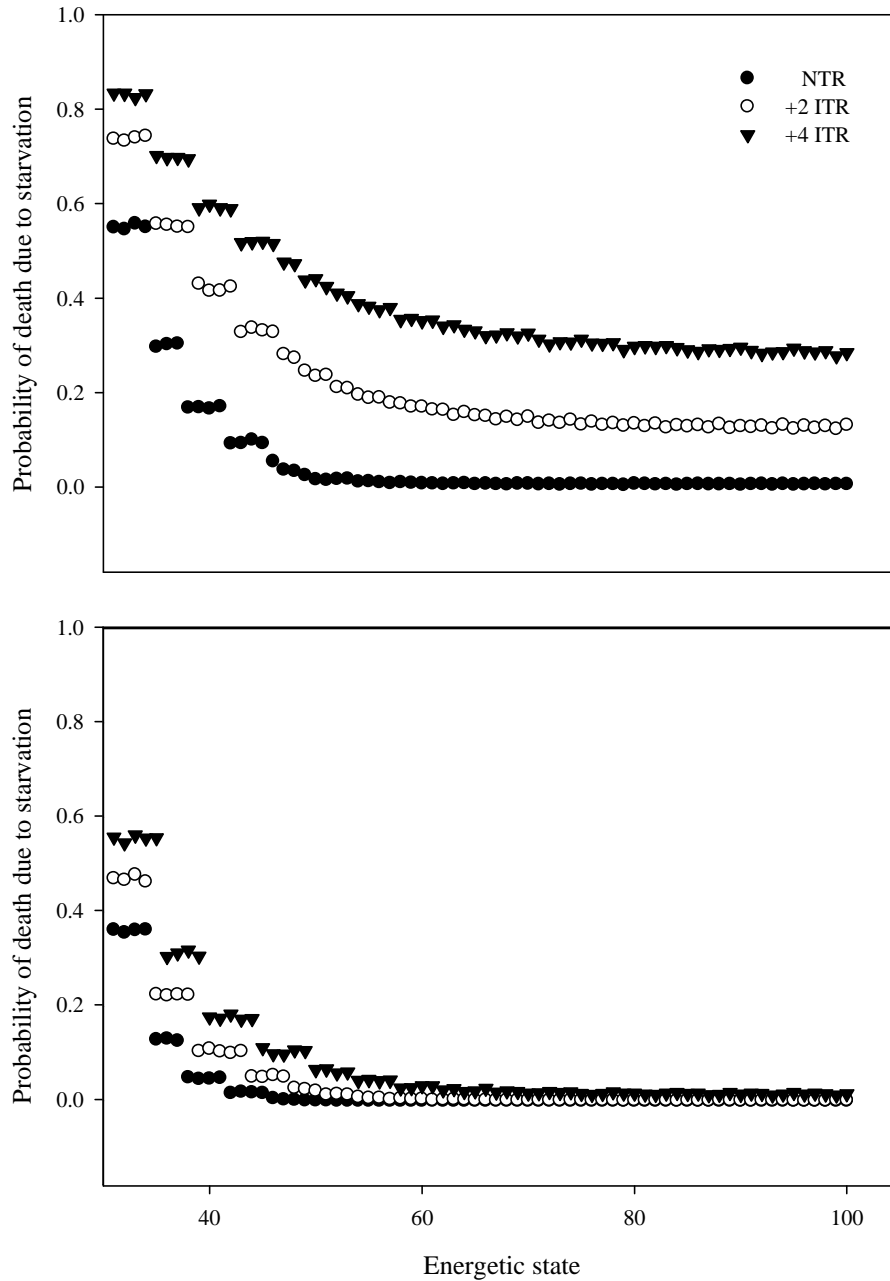
Figure 5.3: The probability that an individual fish dies due to starvation given the initial energetic state of the individual and the temperature regime (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density.
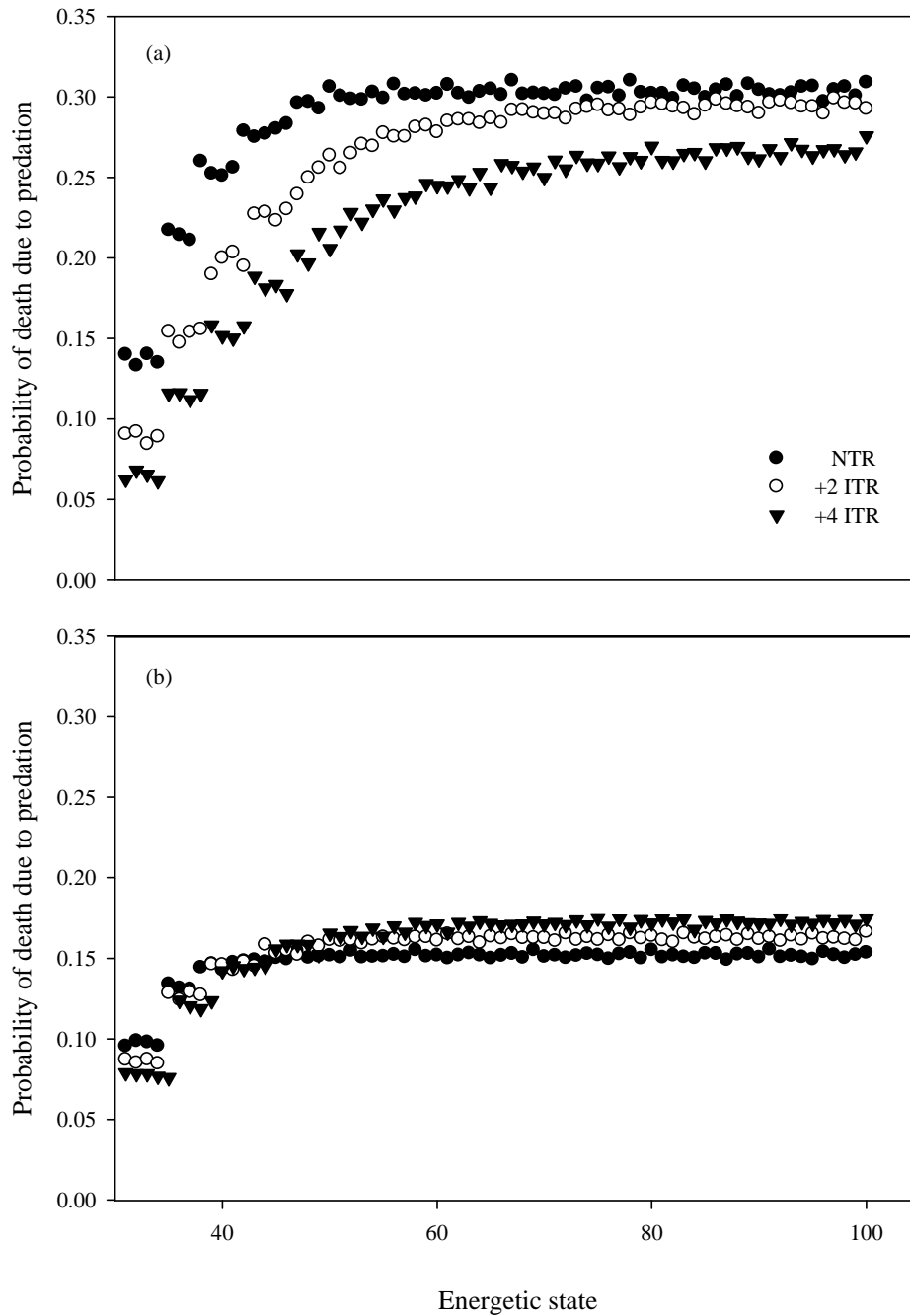
Figure 5.4: The probability that an individual fish dies due to predation given the initial energetic state of the individual and the temperature regime (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density.

59% probability of survival under those conditions. In fact, the probability of survival decreased more under the +2ITR (54%) when there was a negative relationship between food density and probability of consumption than under the +4ITR when food density and consumption probabilities were positively related.

The change in probability of survival when there is an inverse relationship between prey density and the probability of consuming food reflects the increase in the probability of dying due to starvation (Figures 5.1 and 5.3). Under NTR, the probability of death due to starvation is less than 7%; under the +2ITR, this probability increases to approximately 18%. With a doubling of the temperature increase (+4ITR), there is over a doubling of the probability that an individual fish will die due to starvation (41%). This increase in probability of death as temperature increases is greater than the reduction in the risk of death due to predation that occurs with an increase in temperature. When there is an inverse relationship between prey density and probability of consumption of the prey, the probability of survival increases through the decrease in risk of death as a result of a predation event (Figures 5.1 and 5.3).

Comparing the results of the second iteration of the model (where there is a positive relationship between prey density and the probability of consuming prey) to the iteration where there is a negative relationship between prey density and the probability of consuming prey suggests that while the probability of survival still decreases with temperature, the mode of death responsible for this observed drop in survival probability changes. The probability that an individual will die due to starvation still increases as temperature increases (+4ITR) under the iteration with a positive relationship between food availability and probability of consuming it (Figures 5.1 and 5.3). The extent of the increase in probability of starvation however, is much less (less than 10%, as compared to 41%). There is an increased risk of death with temperature

increases as a result of a slight increase in risk of predation (2% overall). The risk of predation

under the NTR is similar between the two iterations of the model but when there is a positive

relationship between the density of food and the probability of consuming food, the probability

of death due to predation increases with a 2°C increase and further increases when the

temperature is increased by 4°C.

When mode of death is explored and there is a negative relationship between the

probability of consuming food and prey density, in the NTR and +2ITR more individuals die due

to predation than starvation. Risk of starvation outweighs risk of predation almost 2:1 under the

+4ITR. When the relationship between successful foraging and forage density is positive, more

fish again succumb to predation versus starvation, this time under all temperature regimes.

When there is an inverse relationship between the probability of consuming food and the

amount of available food, there was an increase in probability of death due to starvation as

temperature increased. In order to offset this risk, the amount of food available to individuals

would have to increase by nearly 3.5 times. This would reduce the probability of starvation when

the probability of consuming food decreases with increasing density under the +4ITR to similar

values (near 10%) as in the other model outputs. If the probability of consuming food increases

with increasing food density, an increase in the amount of food by approximately two and a half

results in a further reduction of the probability of starvation to less than 2%.

Temperature and survival when predation risk is reduced. If predation risk declines slightly

(1.5%) as temperatures increase (through a reduction in the number of predators present), the

survival probabilities of the fathead minnow increase approximately 3% under a +2ITR

regardless of the relationship between consuming food and the amount of food available (Figure

5.5). An approximate 10% reduction in risk increases by approximately 20% the survival probabilities of the fathead minnow over the ice-free season (18% when the relationship between consuming food and amount of available food is negative, 22% when that relationship is positive) (Figure 5.6). A slight reduction in predation risk under the +4ITR, results in an overall increase in the probability of survival for the fathead minnow. This includes a 2% reduction in mortality risk when the relationship between amount of food and the probability of finding food is negative and a 4% reduction when the relationship between amount of food and the probability of finding food is positive. Given a 10% reduction in predation risk, under the +4ITR there is an approximate 13% and 22% increase in the probability of survival when the relationship between the amount of food present and the probability of consuming the food is negative and positive respectively.

Discussion

The results of the sensitivity analysis suggest that changes in β_i, the risk of predation, results in the greatest amount of change in survival. As this variable is estimated from published data on the Eurasian perch (Persson 1986) and influences the overall survival probabilities of the fathead minnow, it is important that future research examines the specific influence of temperature on risk of predation for a variety of predators. A better estimate of how risk of predation changes with temperature would increase the accuracy of the model. The influence of temperature on the probability of finding food (λ_i) ranks second in importance based on elasticities. Again, these variables were estimated from published data and are not specific for the probability of fathead
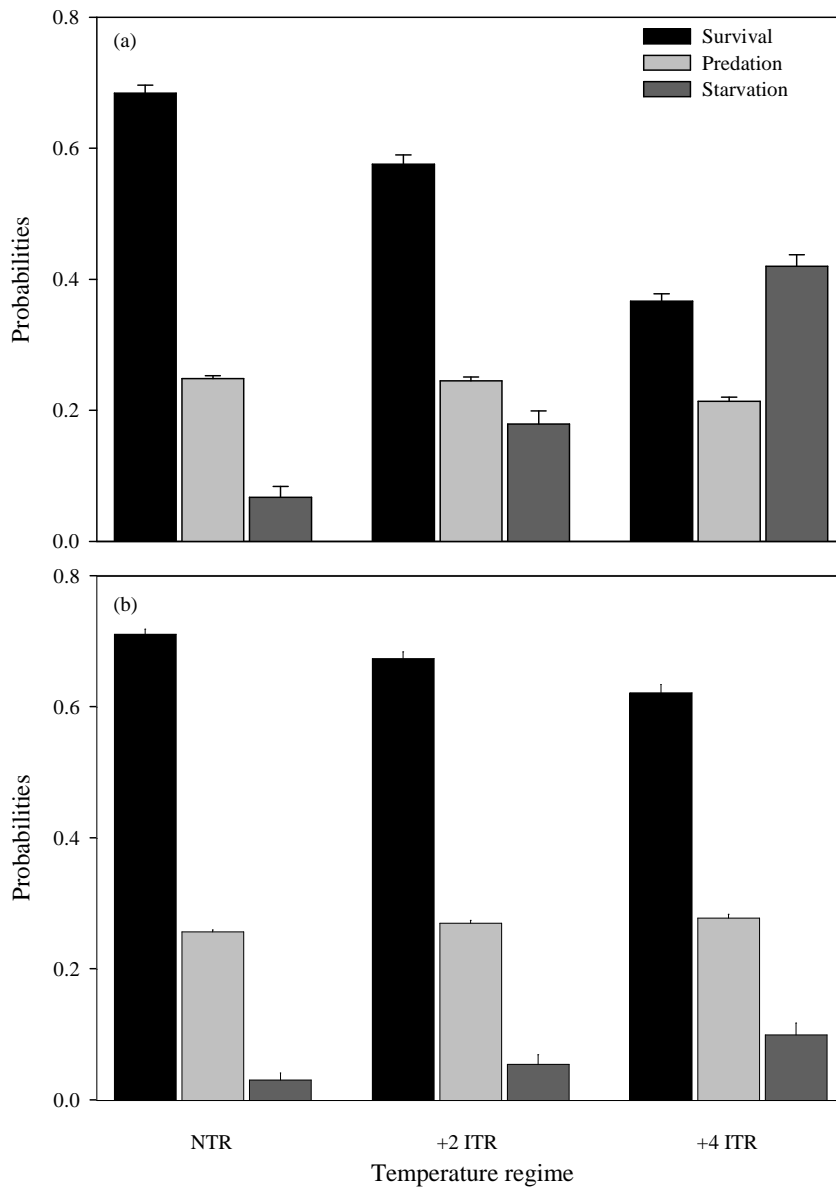
Figure 5.5: The average probability of surviving, dying due to predation and dying due to starvation during the ice-free season regardless of initial state under three different temperature regimes assuming the risk of predation declines slightly (1.5%) with temperature (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density. Error bars represent the standard error around the mean.
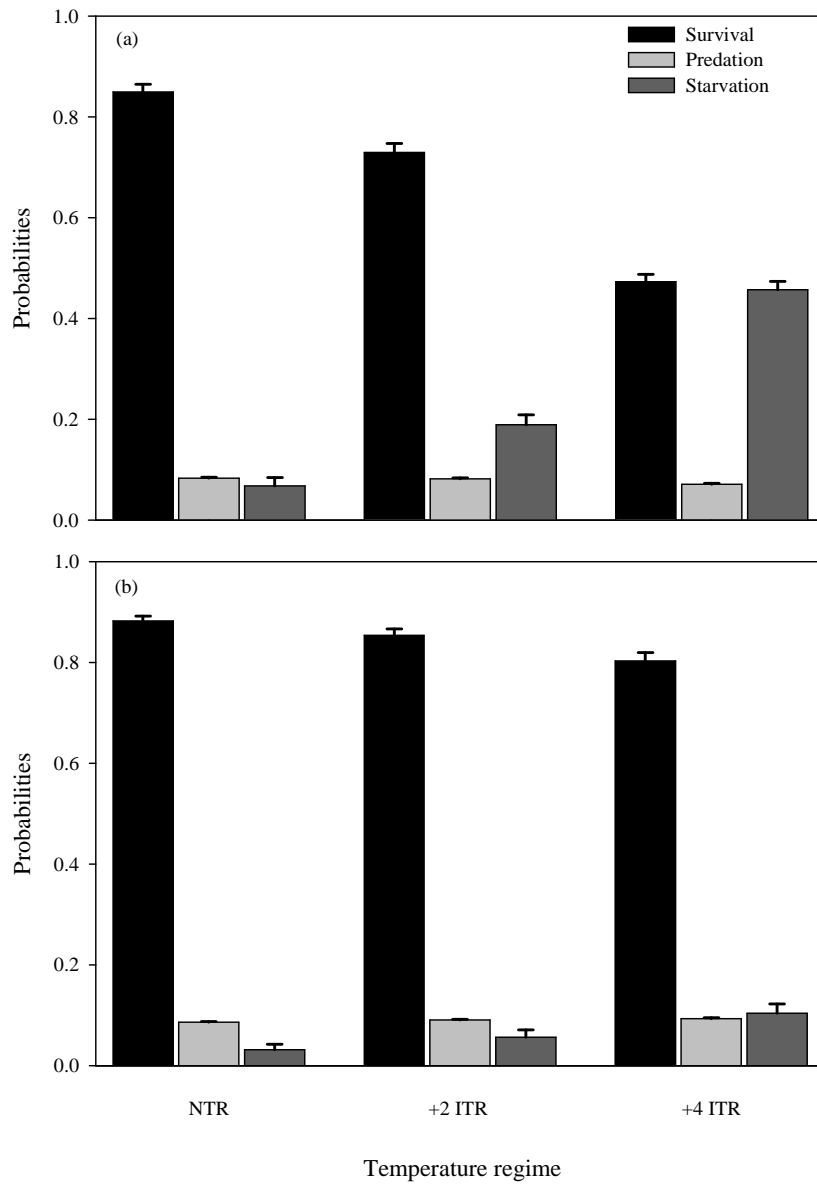
Figure 5.6: The average probability of surviving, dying due to predation and dying due to starvation during the ice-free season regardless of initial state under three different temperature regimes assuming the risk of predation declines 10% with temperature (current, NTR; +2°C increase, +2 ITR; and +4°C increase, +4 ITR) with (a) negative, and (b) positive relationship between probability of finding food and food density. Error bars represent the standard error around the mean.

minnows consuming food given the density of available food in the environment and suggest future research is necessary.

Under the current temperature regime, the dynamic state dependent model constructed to examine survival probabilities of a small minnow predicts that a typical, non-breeding fathead minnow has an approximate probability of survival of 64%. This survival probability is similar to survival probabilities published from field data (58-73%) on a population of fathead minnows in Alberta, Canada that experience a similar temperature regime as those used in the model (Divino and Tonn 2007). The fact that the model output is in agreement with published data gives support to the model's ability to predict responses to changing environment.

The results of this study suggest that an average daily temperature increase as low as 2 C° over the course of the ice-free season results in a reduction in the probability of survival for fathead minnows. Depending on the iteration of the model (there can be either a positive or negative relationship between density of prey items and the probability of consuming prey), the range of reduction in survival is 4-10%. A more significant temperature increase reduces the probability of survival another 4-20%. While it is unrealistic to expect the model to have the accuracy to predict, to a specific percentage, the result of increasing temperature on the probability of survival of the fathead minnow over the ice-free season, what the model does demonstrate is the fact that increasing temperature by 2 C° decreases the likelihood of survival of a fathead minnow, and an additional increase of 2 C° further decreases the minnow's probability of survival.

In temperate climates where bodies of water freeze during the winter months, survival during the ice-covered period depends on lipid content of fishes, a measure correlated with size of the fish (Biro et al. 2004). For poikilotherms, in both field (Anderson et al. 2001) and

laboratory (Keast 1984, Vigg and Burley 1991, Person-Le Ruyet et al. 2004) studies increased temperature results in increased growth rates and therefore larger fish. An increase in temperature could be thought to increase the probability of survival not only over the ice-covered period, but also during the ice-free season as larger fish have increased energetic reserves and can afford to refuge at the expense of feeding if predation risk is high. In the model described in this paper, an increase in predation risk with temperature is observed when probability of consuming food is positively related to temperature. When the relationship between the probability of finding food and food density is negatively related, there is a slight decrease in predation risk with temperature however, risk of starvation appears to be the driving factor in the overall reduction in likelihood of survival.

In this model, fish have a choice of three patches that differ in temperature. When there is a negative relationship between temperature and the probability of consuming food, the patch that will be energetically superior will be the patch that is coolest. As risk of predation increases with temperature, this cool patch will also be the patch that is less risky. Examining the outcomes of the model under increased temperature regimes it is observed that the fish consistently chose the low risk patch with the greatest amount of food and the lowest probability of death due to predation. Risk of predation decreases as temperature increases. Yet probability of survival continues to decrease even though fish are occupying the patch with the highest probability of receiving food and the lowest risk of predation. In this iteration of the model, the increase in the probability of death is due to the increase in the probability of death due to starvation. In much the same way as fishes without adequate food stores do not survive the winter even though they have eaten (Biro et al. 2004), under an increased temperature regime even though fish are eating, they are not consuming enough to meet metabolic demands. Further examination of the model

suggests that the predicted amount of food available would have to increase three and one half times in order for fish to reduce the probability of survival to those predicted under the normal temperature regime.

If food availability increased with temperature it might be expected that survival rates would also increase as metabolic demands would be met. Nevertheless, in the second iteration of this model where there is an increased probability of receiving food with increased temperature, the probability of survival still decreased with increasing temperature, though to a lesser degree than in the first iteration of the model. In this second iteration, the result of an increased likelihood of receiving food with increasing temperature can be observed in the model output. The probability of death due to starvation increases 6% over the 4°C temperature increase (versus a 34% increase when the relationship between the amount of food and the probability of consuming that food is negative). The probability of predation increases with increasing temperature. While fish can meet energetic demands through the use of the warmest patches doing so puts them at an increased risk of predation. It is this increase in risky behavior (selecting patches with both high food and high risk) that causes the overall reduction in survival probabilities.

The use of a state dependent stochastic dynamic model to predict survival probabilities under different temperature regimes has the benefit of not only being able to predict general survival patterns and overall averages of probabilities of death due to starvation and predation, but it also demonstrates the role of state in decision making processes. At low energetic states, very few fish die as a result of a predation event. Death at low energetic states is most often the result of starvation. However, if an individual can increase their energetic state so that they enter the ice-free period with large amounts of energetic reserves the probability of death due to

starvation decreases to almost zero in the NTR. Under all temperature regimes, when prey density is positively related to probability of obtaining food, the probability of death due to starvation is again almost zero. When there is an inverse relationship between prey density and probability of receiving food, fish must be at higher energetic state in order to reduce their risk of starvation to essentially zero under the + ITR. Under the +4ITR, regardless of the state at which the fish begins the ice-free season, there is always the probability of dying as a result of starvation.

Abrahams et al. (2007) suggest that an increase in temperature will result in a reduction in the predator population, as well as a reduction in the number of large predators present. Taking this result into consideration, I reduced the risk of predation in the model. Overall survival for fathead minnows over the ice-free season increased to over 80% when the risk of predation was reduced approximately 10%. When risk of predation is reduced, the probability of death due to both predation and starvation is reduced as compared to initial model iterations. The reduction in risk of predation allows the fish to exploit the more energetically profitable patches while not incurring a greater risk of predation thereby increasing their overall probability of survival.

This paper highlights the importance of temperature to the survival of poikilotherms, and specifically fathead minnows. Temperature is an ecological condition in that it can drive the underlying habitat selection decisions of individuals. When choosing patches, individuals must balance the costs and benefits of each habitat and select the one that best suits its current state and potential future success. Under environmental conditions predicted by climate change models (Meehl et al. 2007), the future success of minnows as measured by survival over the ice-free season declines under both the conservative temperature increase estimate and the more

extreme temperature increase predictions. The results from this study suggest that populations of minnows may experience, at least initially, a reduction in numbers. As fathead minnows are a dominant forage fish in many shallow water ecosystems, any reductions in population size may affect community dynamics.

References

Abrahams, M.V., Mangel, M., Hedges, K. 2007. Predator-prey interactions and changing environments: who benefits? Philosophical Transactions of the Royal Society B: Biological Sciences **362**: 2095-2104.

Anderson, M. T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on a predator–prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Biro, P. A., Morton, A.E., Post, J.R., Parkinson, E.A. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences **61**: 1513-1519.

Clark, C.W., Mangel, M. 2000. Dynamic State Variable Models in Ecology: Methods and Applications. New York: Oxford University Press. 289 pp.

Divino, J.N., Tonn, W.M. 2007. Effects of reproductive timing and hatch date on fathead minnow recruitment. Ecology of Freshwater Fish **16**: 165-176.

Elliott, J.M. 1976. The energetic of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature, and ration size. Journal of Animal Ecology **45**: 923-948.

Gibbons, J.W., Bennett, D.H., Esch, G.W., Hazen, T.C. 1978. Effects of thermal effluent on body condition of largemouth bass. Nature **274**: 470-471.

Gillooly, J.F. 2000. Effect of body size and temperature on generation time in zooplankton. Journal of Plankton Research **22**: 241-251.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M., Brown, J.H. 2002. Effects of size and temperature on developmental time. Nature **417**: 70-73.

Goldman, J. C., Carpenter, E.J. 1974. A kinetic approach to the effect of temperature on algal growth. Limnology and Oceanography **19**: 756-766.

Hammel, H.T. 1955. Thermal properties of fur. American Journal of Physiology **182**: 369-376.

Herwig, B.R., Zimmer, K.D. 2007. Population ecology and prey consumption by fathead minnows in prairie wetlands: importance of detritus and larval fish. Ecology of Freshwater Fish **16**: 282-294.

Huey, R.B., Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology and Evolution **4**: 131-135.

Ioannou, C.C., Payne, M., Krause, J. 2008. Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk. Oecologia **157**: 177-182.

Johnston, P., Bergeron, N.E., Dodson, J.J. 2004. Diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity. Journal of Fish Biology **65**: 1305-1319.

Kawabata, K., Narita, T., Nishino, M. 2006. Predator-prey relationship between the landlocked dwarf ayu and planktonic Crustacea in Lake Biwa, Japan. Limnology **7**: 199-203.

Keast, A. 1984. Growth responses of the brown bullhead (*Ictalurus nebulosus*) to temperature. Canadian Journal of Zoology **63**: 1510-1515.

Klinger, S.A., Magnuson, J.J., Gallepp, G.W. 1982. Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) for low oxygen in winter. Environmental Biology of Fishes **7:** 113-120.

Krause, J., Godin, J.-G.J. 1995. Predator preference for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behavior **50**: 465-473.

Logue, J., Tiku, P., Cossins, A.R. 1995. Heat injury and resistance adaptation in fish. Journal of Thermal Biology **20**: 191-197.

MacLeod, J.C., Smith, L.L. Jr. 1966. Effect of pulpwood fiber on oxygen consumption and swimming endurance of the fathead minnow, *Pimephales promelas.* Transactions of the American Fisheries Society **95:** 71-84.

McNamara, J.M., Houston, A.I. 1986. The common currency for behavioral decisions. The American Naturalist **127**: 358-378.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C. 2007. Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis.Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S.,D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller, Editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Mols, C.M.M., van Oers, K., Witjes, L.M.A., Lessells, C.M., Drent, P.J., Visser, M.E. 2004. Central assumptions of predator-prey models fail in a semi-natural experimental system. Proceedings of the Royal Society of London Series B: Biological Sciences **271**: S85-S87.

Nilsson, P.A., Brönmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos **88**: 539-546.

Person-Le Ruyet, J., Mahé, K., Le Bayon, N., Le Delliou, H. 2004. Effects of temperature on growth and metabolism in a Mediterranean population of European sea bass, *Dicentrarchus labrax.* Aquaculture **237**: 269-280.

Persson, L. 1983. Effects of intraspecific and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. Oikos **41**: 126–132.

Persson, L. 1986. Temperature induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. Journal of Animal Ecology **55**: 829-839.

Ruxton, G.D. 2005. Increasing search rate over time may cause a slower than expected increase in prey encounter rate with increasing prey density. Biology Letters **1**: 133-135.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., Charnov, E.L. 2004. Effects of body size and temperature on population growth. The American Naturalist **163**: 429-441.

Scott, W.B., Crossman, E.J. 1998. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada **184**:1-966.

Verbitskii, V.B., Verbitskaya, T.I., Malysheva, O.A. 2009. Population dynamics of

Daphnia longispina (O.F. Müller, 1785) and *Diaphanosoma brachyurum* (Lievin, 1948) (Crustacea, Cladocera) under stable and graded temperature regimes. Biology Bulletin **36**: 66-73.

Vigg, S., Burkley, C.C. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish *Ptychocheilus oregonensis* from the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences **48**: 2491-2498.

Walls, M., Ventelä, A.-M. 1998. Life history variability in response to temperature and *Chaoborus* exposure in three *Daphnia pulex* clones. Canadian Journal of Fisheries and Aquatic Sciences **55**: 1961-1970.

Wootton, R.J. 1990. Ecology of Teleost Fishes. London: Chapman and Hall. 404 pp.

Chapter 6: Can the abiotic environment of a shallow water ecosystem influence the dynamics of avian predation on prey fishes?

Abstract. Shallow water aquatic ecosystems may be considered discrete feeding patches for foraging terns. A unique feature of these ecosystems are that their physical conditions can change dramatically in a short period of time, particularly temperature, turbidity, and dissolved oxygen. Based on previous research I predicted that increasing turbidity will reduce the availability of fish (minnows) to plunge diving terns through reduction of visibility of the fish, while increasing temperature and decreasing dissolved oxygen will increase their availability through increases in activity and movement towards the more oxygenated surface areas respectively. I also predicted that overall abundance of minnows should increase feeding activity by terns. I measured these environmental variables, tern activity, and minnow abundance from May to August from 2006 to 2008 in a marsh in southern Manitoba. My results demonstrated that only variation in dissolved oxygen levels affected tern feeding activity. Since there was no relationship between tern and minnow abundance either within or among years, these results suggest that it is the availability of prey (i.e. the movement by prey fishes up into the water column) and not their abundance that influences the number of predators present and hence the risk of predation.

Introduction

The dynamic interactions between predators and their prey have the ability to structure aquatic environments (Paine 1966). Predators consume prey thus controlling populations, altering relative abundances, and changing the size structure of prey populations (Crowder and Cooper 1982, Tonn and Magnuson 1982, Werner and Gilliam 1984, He and Kitchell 1990). Predators can also exert indirect effects on prey populations; the risk of predation can affect prey morphology, physiology, life history traits and behaviour (see Mittelbach and Chesson 1987 for a review). Prey faced with a risk of predation can have reduced growth rates and survivorship (Werner and Anholt 1996) because they may trade-off food rich habitats for food poor habitats that offer cover from predators (Werner et al. 1983).

In freshwater ecosystems, the study of predator-prey interactions, from small scale experiments to large scale manipulations, has focused primarily on piscivorous fish and their prey (Tonn and Magnuson 1982, Crowder and Cooper 1982, Werner et al. 1983, Turner and Mittelbach 1990, Eklöv and Persson 1996, Wazenbock et al. 2006). The study of the effects of avian predation on prey communities in a completely natural setting has been widely overlooked even though some research has demonstrated that the presence of avian predators can change the size structure, behaviour and abundance of prey populations (Milinski and Heller 1978, Harvey and Stewart 1991, Allouche and Gaudin 2001, Collis et al. 2001, Hodgens et al. 2004, Steinmetz et al. 2008). More importantly, the effects of prey populations on the abundance and/or presence of avian predators in these freshwater ecosystems has not been studied as much of the research has focused on changes in abundance of fishes as a result of avian predation. This research has been focused primarily in hatcheries or stocked ponds or streams (Collis et al. 2001, Hodgens et al. 2004).

The purpose of this study is to address whether changes in the abiotic aspects of the aquatic environment (i.e. temperature, dissolved oxygen and turbidity) can influence the avian predator population through the effect of the environment on prey behaviour. It is thought that changes in the aquatic environment may lead to changes in the behaviours of prey fishes or, as with changes in turbidity may lead to direct changes in the visibility of the prey to the predators, which would then mediate the presence of predators through changes in prey conspicuousness and/or availability. As presence of avian predators have been used as indicators of available prey in marine ecosystems (Monaghan et al. 1989, Weimerski et al. 2005), it is reasonable to expect that avian predators will respond in the same manner in a freshwater ecosystem by becoming more abundant in areas where prey are available.

Experiments examining the role of dissolved oxygen (DO) in risk of waterbird predation to their fish prey has demonstrated that in times of low oxygen, use of surface waters by fish increases their risk of capture by green heron, *Butorides striatus* (Kramer et al. 1983) and pied kingfisher, *Ceryle rudis* (Randle and Chapman 2004). In periods of low DO the movement of fish up into the water column to areas close to the surface to meet oxygen demands (Kramer 1987) is the probable factor that increases the vulnerability of the fish to predators, both avian (Randle and Chapman 2004) and piscine (Wolf and Kramer 1987), as prey are more easily detected while active (Krause and Godin 1995) and near the surface of the water. While these small scale experiments provide useful information as to possible responses of prey to predators and how the habitat of the prey can influence predation risk it is important to determine how these results translate on a large scale where prey are not constrained to a small area. It is predicted that in response to low DO levels there will be the potential for movement of prey fishes to positions higher in the water column where DO levels are higher (Kramer 1987), avian

predators will react to an increase in prey availability by increasing their presence in the area during that time.

The role that environmental variables other than DO play in the risk of avian predation to small bodied fishes is not well studied in either small or large scale experiments or observational studies (though see Eriksson 1985, Gwiazda and Amirowicz 2006 for studies incorporating turbidity with risk of avian predation). The effects of temperature and turbidity on fish behaviour and mortality under piscivorous predation risk are studied to a greater extent (turbidity: Gregory 1993, Abrahams and Kattenfeld 1997, Reid et al. 1999, Bonner and Wilde 2002, Snickars et al. 2004, temperature: Krause and Godin 1995, Weetman et al. 1998, Weetman et al. 1999). Through the results of these studies it is possible to predict how the changing environment will directly affect probability of detection of the prey by the predators (and therefore presence of predators), or how the changing environment indirectly influences the risk of predation through the behavioural responses of prey fish to the changes in temperature and turbidity.

Studies of the influence of turbidity on piscivory has suggested that moderate turbidity levels (11 and 20 NTU) do not affect capture of prey by predators (Reid et al. 1999, Abrahams and Kattenfeld 1999), while a study on great cormorants, *Phalacrocorax carbo sinensis*, found that their probability of detecting a prey fish declined significantly as turbidity increased (Strod et al. 2008). Observations of grey heron, *Ardea cinerea*, predation among water bodies that differed in turbidity levels demonstrated favourable foraging in highly turbid areas (Gwiazda and Amirowicz 2006). Given that the predators in this study are plunge divers and take prey from the top 30 cm of the water column (Forster's terns, *Sterna forsteri*, hereafter referred to as terns), it is predicted that turbidity will be less important in moderating availability of prey to predators than

low dissolved oxygen levels which may result in prey fishes moving up into the water column to exploit waters with higher levels of DO.

The direct role of temperature in studies of aquatic predator-prey interactions has received little attention (Krause and Godin 1995, Moore and Townsend 1998, Weetman et al. 1998, Weetman et al. 1999, Anderson et al. 2001, Lass and Spaak 2003, Taylor and Collie 2003). In a study on anurans and their invertebrate predators, Anderson et al. (2001) suggest that increased temperatures may lead to increase capture rates and decreased handling times. With respect to the behavioural responses of fish to changing temperatures, it is expected that fish will become more active with increasing temperatures (Atkinson 1994, Krause and Godin 1995, Chapter 2). As well, with metabolic rates of fishes increasing with temperature (Clarke and Johnston 1999) there is an increase in the rate at which fish consume energy, likely resulting in an increased willingness to risk exposure to predators to gain access to food (Godin and Crossman 1994). Increased activity increases the probability of being selected for attack by a piscine predator (Krause and Godin 1995) and it is likely true for avian predators as well. Therefore increased water temperature should provide more productive feeding areas for avian predators.

Four predictions were tested in this study: 1) the number of terns observed will increase as the abundance of their prey increase, 2) an increase in water temperature will result in an increase in the number of observations of terns, 3) a decrease in dissolved oxygen content will increase observations of terns and 4) a decrease in turbidity will result in an increase in the number of terns observed. The last three predictions arise from the interaction between environmental variables and prey fish behavior (which is not measured) and it is the resulting changes in the behaviours of minnows that the terns would in fact be responding to. It was

hypothesized that DO, turbidity and temperature would influence abundance of terns through either direct effects that alter the ability of the predators to observe their prey (turbidity) or via indirect effects of the aquatic environment on prey fish behaviour (temperature and DO). DO was hypothesized to have the greatest affect since hypoxic conditions would force minnows to shallow depths making them available to plunge diving terns. Since fathead minnows are the most abundant species in this location, and they are known to tolerate moderate hypoxia (defined as oxygen concentrations ranging from 2.35 – 2.74 mg/L) (Robb and Abrahams 2003), I predicted that the effect of DO on tern abundance would be most pronounced with extreme hypoxia (< approximately 2 mg/L DO).

Materials and Methods

To test the aforementioned predictions the environmental variables of interest were measured and averaged on a daily basis. These measures were then related to the presence of terns which was established via recordings of the study area during the same time period as the environmental variable measurements were collected.

The aquatic environment. Measures of DO, temperature and turbidity were taken in Blind Channel, Delta Marsh, Manitoba, Canada (98°23'W, 50°11'N) from May to August of 2006 to 2008. Blind Channel is a shallow (~1.5 m), turbid, slow moving blind ending channel. The marsh itself is a 21 870 hectare wetland located on the southern shore of Lake Manitoba with a single narrow passageway connecting the lake to Blind Channel. Blind Channel is a relatively protected area, and many piscivorous fishes use the channel for spawning and feeding during the spring and summer months (Suthers and Gee 1986). Water levels in Blind Channel are primarily controlled by seiches as a result of prevailing winds; a strong northerly wind rising and a strong

143

southerly wind lowering water levels. As the water entering Blind Channel does so from Lake Manitoba, temperatures generally decrease with a northerly wind bringing cooler, more oxygenated lake water into the channel. Over the course of the ice-free period Blind Channel experiences a wide range of turbidity, temperatures (peaking at around 28-30 °C) and dissolved oxygen levels (ranging from normoxia to extreme hypoxia) (Robb and Abrahams 2003).

To record DO, temperature and turbidity YSI 6920 data sondes were placed at the bottom, middle, and surface of the water column in Blind Channel. The sondes collected data every 30 minutes that was averaged to provide a daily value to correspond with measures of predator and prey abundances.

Measures of prey abundance. The primary prey for Forster's terns in Blind Channel is the fathead minnow, the numerically dominant forage fish in the Channel. Common across central North America, the fathead minnow, in Canada, is distributed east to New Brunswick and west into Alberta and averages 51 mm total length (Scott and Crossman 1998). Prey abundance (primarily fathead minnows, *Pimephales promelas*) was measured using ten minnow traps set just below the surface of the water. Five of these traps were deployed on the north side of the channel while the other five traps were set on the south side. This arrangement ensured that one side of the marsh with minnow traps would be relatively sheltered in high wind events. This was important as minnows were observed to aggregate in sheltered areas when winds were high and sampling only one side of the marsh would have resulted in inaccurate estimates of minnow abundance. All traps were set at permanent locations within the area that was surveyed for avian predators.

Minnow traps were checked every morning from May to August in all three study years. All captured fishes were identified to species and a count of the number of individuals of the species present was recorded. The number of fish captured among all traps at each location was averaged to provide a single measure of catch per unit effort (CPUE) that represented the abundance of fish during that 24 h period.

Measures of risk of avian predation. The most common avian predator in this system is the Forster's terns. Forster's terns are plunge divers and generally take fish in the top 30 cm of water. They capture one fish approximately once every 3 to 6 dives (Salt and Willard 1971), and so must dive often to feed on small fish. At least six known locations within Delta Marsh are used as tern colonies, though not every site is used each year (McNicholl 1971). Previous studies of Forster's terns in Delta Marsh have suggested that the number of nests at a given colony may vary year to year, though on average, the number of nests in the marsh is relatively stable between years (McNicholl 1971). During this study, no colonies were observed within Blind Channel itself, or Forster's Bay, the known location closest to Blind Channel. Given that Forster's terns are known to forage for distances averaging over 6 km (Bluso-Demers et al. 2008), terns from colonies throughout Delta Marsh are likely to forage within Blind Channel.

To measure presence of these predators, three Panasonic CCTV WV-CP484 SDIII cameras with Pentax 3.5-8mm F/1.4 CS auto iris lenses were set up overlooking portions of the southern end of Blind Channel. I used this portion of the channel as it allowed me to film without worry of glare from either the setting or rising sun.

Cameras recorded to a March Networks mobile digital video recorder (MDVR) during daylight hours from May to August during all three years of the study. For each camera's

recording, the daylight hours were broken down into 15 minute sections. From each 15 minute block, two minutes were randomly chosen for viewing (the same two minutes of each camera were chosen for each day) and the number of Forster's terns present in each two minute block was recorded. The number of birds observed in each two-minute block were totaled and then divided by the number of hours of daylight recorded for that day. The number of terns observed per hour was then averaged across the three recordings. These daily averages were then used as measures of predator abundance in further analysis.

Data analysis. For statistical analysis, data averaged to provide a daily measure (the average of 48 measures of each environmental variable – one measure every 30 min) were considered independent observations in 2006, 2007 and 2008 based on Durbin-Watson tests for autocorrelation. Periodic technical issues, primarily in the first year of study, meant that there were not equal observations of daily averages of environmental variables, tern and minnow abundance across years. In 2006, there were 13 sets of data; in 2007, 55 and in 2008, 33.

I used parametric analyses on transformed data (Box – Cox transformations for environmental data and $\log_{10}(x +1)$ for both minnow and tern observations) as the transformed data met assumptions for normality and homogeneity of variances necessary for parametric analysis. All analyses were conducted using STATISTICA software. Alpha levels were set at 0.05 for all analysis.

To test the prediction that increases in prey abundance would result in increased observations of terns I used a generalized regression model. Due to perceived high interannual variation in the CPUE of minnows between the three years I first compared tern and minnow abundance between years using an ANOVA. If differences between years were observed, year

would be included as a categorical predictor variable in the generalized regression model. The model itself included tern abundance as the dependent variable and minnow abundance as the continuous predictor variable. If there were no differences in minnow and tern abundance between years the regression model would be run without year as a categorical predictor variable.

To test the prediction that the environmental variables measured would influence tern observations through changes in prey fish behavior, I first determined if there were differences in DO, temperature and turbidity between years using an ANOVA. If differences existed, I would include year as a categorical predictor model in a generalized regression model using tern abundance as the dependent variable and dissolved oxygen, temperature, and turbidity as continuous predictor variables. If no differences existed between years, the regression model would be run without year as a predictor variable.

The final prediction of this study was that it will be during periods of extreme hypoxia that prey fish will increase their use of surface waters (that have higher levels of DO than the underlying water) resulting in an increase in the observation of terns when conditions are hypoxic as compared to when conditions are normoxic. To test this prediction a student's t-test using data from periods of extreme hypoxic (< 2.0 mg/L) and normoxic (> 4.0 mg/L) values of DO was conducted. If the previously mentioned ANOVA determined that differences existed between years in tern abundance, this analysis would be conducted for each year separately. Otherwise, data from all three years would be combined.

Results

Prey abundance as a predictor of predator abundance. The abundance of minnows differed

significantly between years (ANOVA: $F_{2, 97} = 22.13$, $P < 0.0001$). Minnow abundance in 2006

was significantly greater than the abundance in either 2007 or 2008 while no differences in

abundances existed between 2007 and 2008 (Tukey's HSD post hoc test was significant for the

comparison between 2006 and 2008, 2006 and 2007). Tern abundance also differed significantly

between years with number of terns observed per hour in 2006 and 2008 significantly greater

than the number observed in 2007; no differences were observed between 2006 and 2008

(ANOVA: $F_{2,95} = 7.301$, $P < 0.00001$; Tukey's HSD post hoc tests significant for 2006 and 2007,

2007 and 2008; no differences between 2006 and 2008). On the scale of the study period, tern

abundance did not mirror minnow abundance. In 2008, when minnows were on average the

lowest recorded, tern abundance was at its highest.

Within the generalized regression model, which included year as a categorical predictor

variable and minnow abundance as the continuous predictor variable, only year was a significant

predictor of tern abundance (Table 6.1). Comparing tern and minnow abundance on a seasonal

scale, it can be observed that summers that have high abundances of prey fish do not necessarily

have high abundances of terns (Figure 6.1). On a smaller scale, a scatterplot of daily minnow

CPUE and daily averages of the number of terns observed again indicate that there is no

relationship between the two (Figure 6.2). Predatory terns are therefore not tracking abundance

of prey on either a small (daily) or large (annual) scale, suggesting that prey abundance is not a

good predictor of tern presence, counter to earlier predictions.

Conformity at broad scales: Environmental variables across years. Significant differences were observed in daily average measures of DO when compared between years (ANOVA; DO: $F_{2,106}$ = 8.937, P = 0.0003); while no differences were found when temperature and turbidity measures were compared (ANOVA: temperature: $F_{2,109}$ = 2.726, P = 0.07; turbidity: $F_{2,102}$ = 0.1809, P = 0.8). Dissolved oxygen differed between 2006 and 2007, 2007 and 2008; no differences were found between 2006 and 2008 (Tukey's HSD post hoc test significant for comparisons between 2006 and 2007, 2007 and 2008; no difference between 2006 and 2008). DO levels were significantly lower in 2006 and 2008 when compared to 2007 (Figure 6.3). The warmest year during the three year study period was 2006 followed by 2007 and then 2008 which was, on average, approximately 4°C cooler than 2006 and 2°C cooler than 2007 (Figure 6.3). No significant differences existed in average turbidity levels across years, though 2006 was slightly more clear than 2007 which was slightly more clear than 2008 (Figure 6.3).

Impacts within years: Dissolved oxygen, temperature and turbidity as predictors of predator abundance. Results of the generalized multiple regression model with year as the categorical predictor variable, environmental variables (DO, temperature and turbidity) as the continuous predictor variables and $\log_{10}$ (average number of terns + 1) as the dependent variable suggest that only year and dissolved oxygen were significant predictors of tern abundance (Table 6.2). As DO levels decreased an increase in tern abundance was observed. To further examine the role of DO in structuring the relationship between predators and prey, given the physiological significance of extreme hypoxia (versus moderate hypoxia) for the primary prey species in the system (i.e. testing prediction 5), student's t-test using only using tern abundances associated with extreme hypoxia (< 2 mg/L DO) and normoxia (> 4 mg/L DO) separated by year was conducted.

149

Table 6.1: Results of generalized regression model with year as the categorical predictor variable, $\log_{10}$ (minnow abundance +1) and $\log_{10}$ (mean number terns observed/hr + 1) as the dependent variable. Generalized regression results: Adjusted $R^2 = 0.198$, $F_{2,88} = 8.49$, P = 5.2 x 10^{-6}. S.E. = standard error. Significant differences are indicated with bold values.

Predictor variable	β	S.E. β	F-value	P-value
Year			12.72	**0.00002**
Minnow abundance	0.0578	0.102	0.3199	0.5731
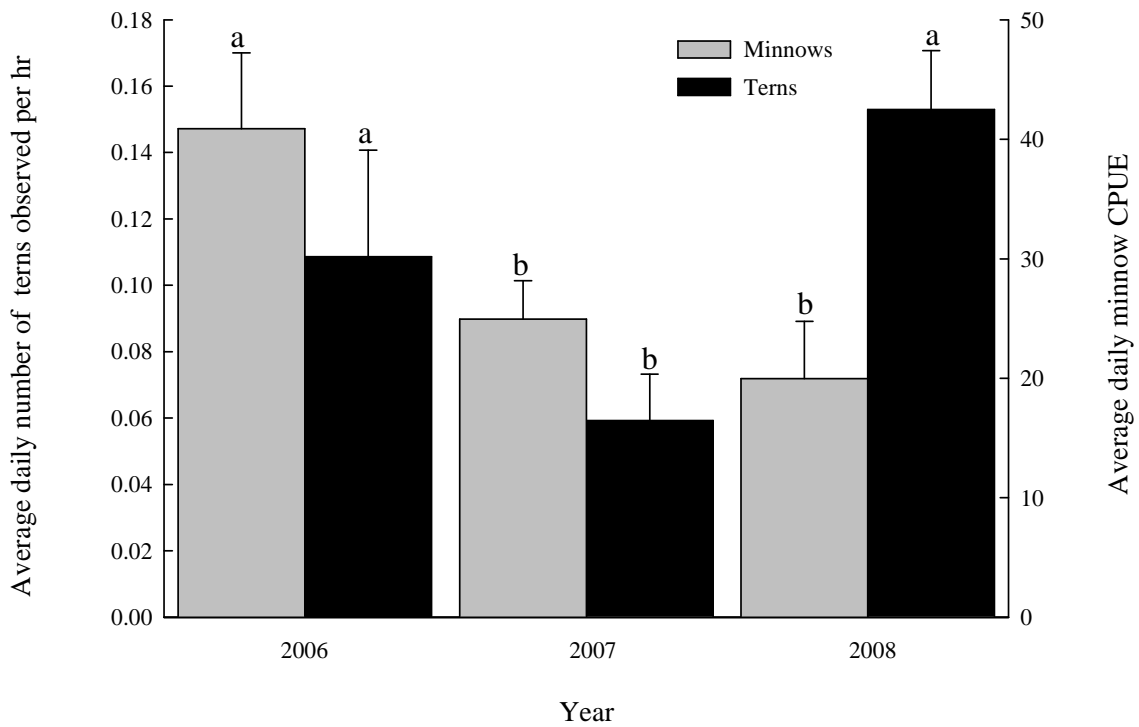
Figure 6.1: Average minnow abundance (CPUE) and measures of tern abundance across the three sampling years. Error bars represent measures of standard error. When measures of minnow CPUE are compared across years 2008 is significantly different from both 2006 and 2007. A comparison of number of terns observed/hr across years found 2007 to differ from both 2006 and 2008.
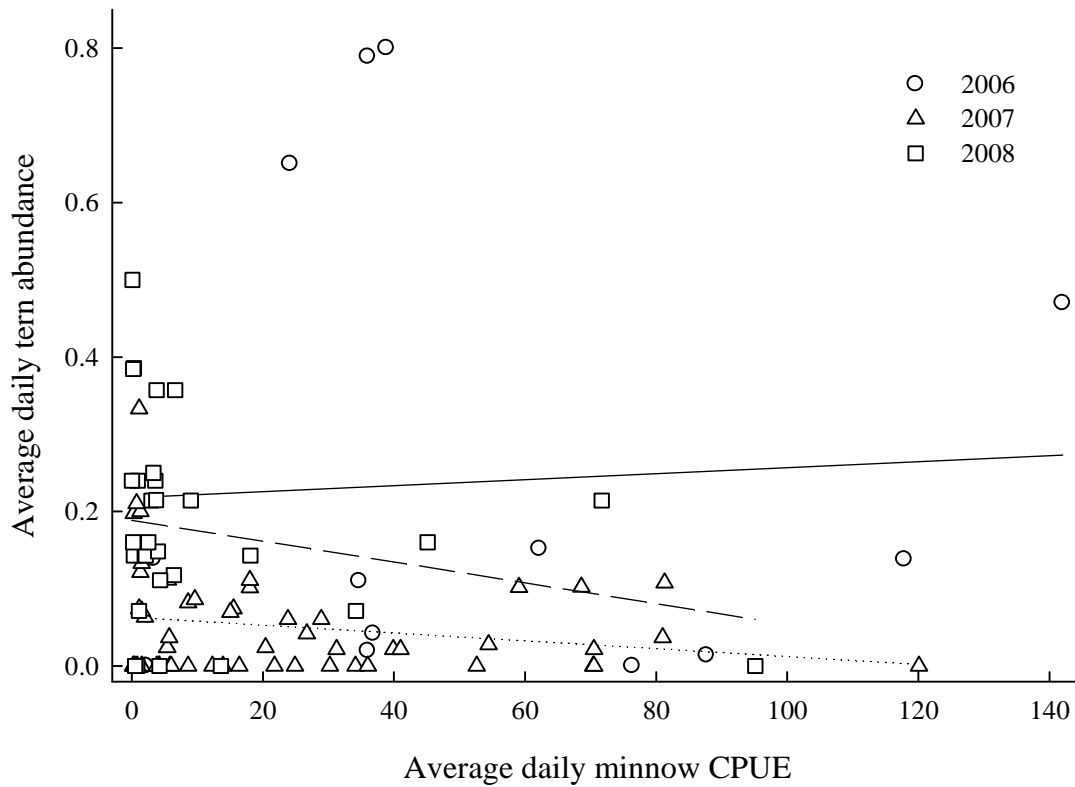
Figure 6.2: Daily average measures of minnow CPUE and tern abundance across all three years. The solid line represent the trendline for 2006 data, dotted line represents the trendline for 2007 and the dashed line represents the trendline for 2008 data. Significant differences occur between years with respect to average number of terns observed per hour, but there is no relationship between minnow CPUE and tern abundance.
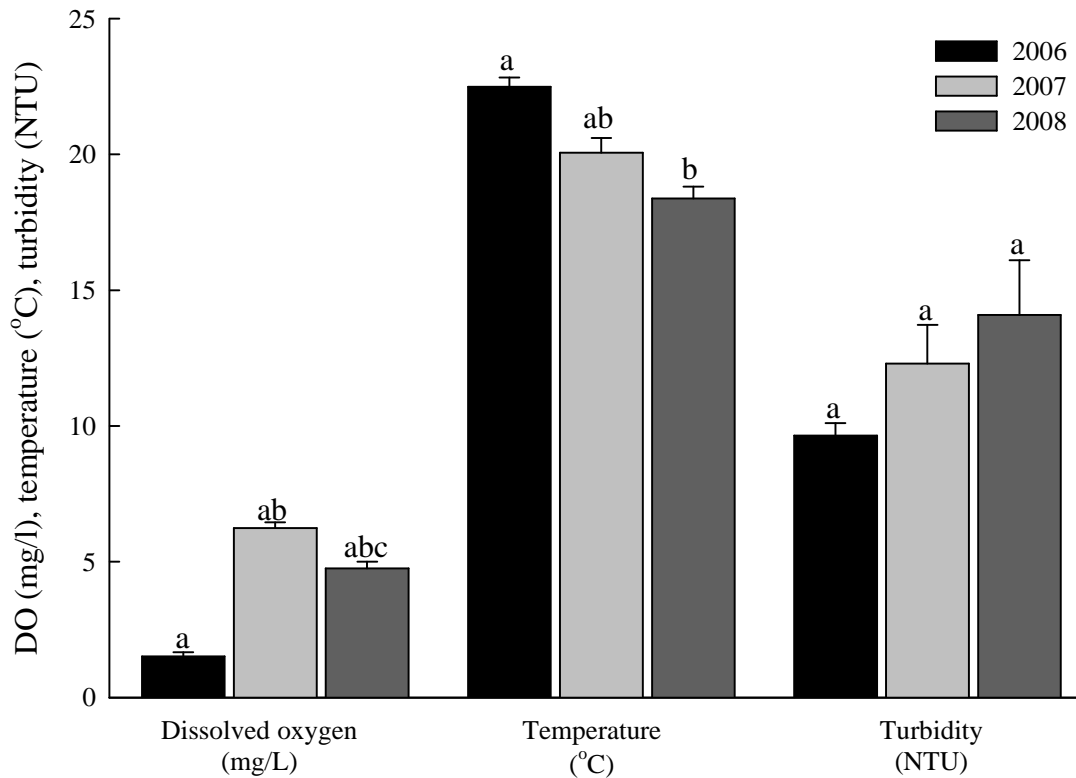
Figure 6.3: Interannual variation in three measures of the abiotic aquatic environment: summer averages of dissolved oxygen (mg/L), temperature (°C) and turbidity (NTU). Error bars represent measures of standard error. There is a significant difference between each of the three years when DO values are compared while no differences exist in turbidity levels between years. When temperature is compared across the three years only 2006 and 2008 significantly differ.

Table 6.2: Results of the generalized multiple regression model with year as the categorical predictor variable and $\log_{10}$ (tern abundance + 1) as the dependent variable. Measured environmental variables (dissolved oxygen, temperature and turbidity) are continuous predictor variables (generalized regression model: Adjusted $R^2 = 0.3486$, $F_{4, 97} = 11.49$, P < 0.000001). S.E. = standard error. Significant differences exist in the tern abundance between years. Dissolved oxygen is the only significant continuous predictor variable. Significant differences are indicated with bold values.

Predictor variable	β	S.E. β	F-value	P-value
Year			10.28	**0.00009**
Dissolved oxygen	-0.532	0.136	15.38	**0.0002**
Temperature	-0.263	0.106	2.204	0.06
Turbidity	0.0748	0.102	0.5340	0.5
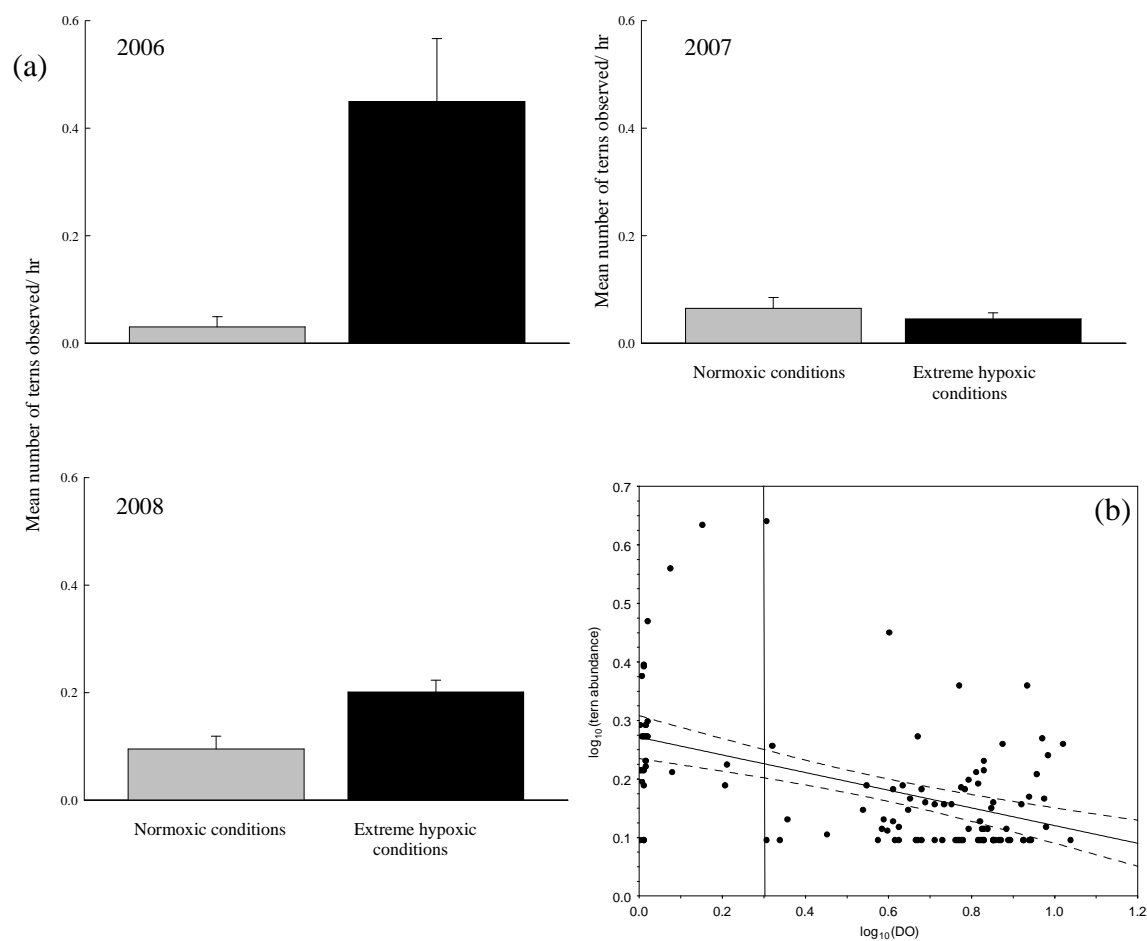
Figure 6.4: A comparison of tern abundance, in each year of the study, on days when the water had high levels of dissolved oxygen (normoxic conditions are those days > 4mg/L DO) to the number observed per hour during times of low dissolved oxygen levels (extreme hypoxic conditions are those days < 2 mg/L DO); 2006 was a low DO level year, 2007 a high DO level year and 2008 a moderate DO level year. Error bars represent standard error (a). Relationship between DO and tern abundance across all years and all DO levels (b); solid horizontal line represents 2 mg/l DO levels.

Significant differences existed in tern abundance during periods of hypoxia as compared to periods of normoxia in 2006 and 2008 (t-test; 2006: t = -3.74, P = 0.003, df = 12; 2007: t = -0.161, P = 0.874. df = 52; 2008: t = -3.82, P = 0.00046, df = 31; Figure 6.4) with significantly more terns observed during periods of extreme hypoxia. When DO levels are compared across years, 2006 and 2008 have the lowest average DO levels, with the average DO level in 2006 falling in the hypoxic range (1.914 ± 0.15 mg/L, lowest DO level recorded was 0.23 mg/L); 2006 is also the year in which tern abundance was highest in times of low DO. In 2007 there was no difference in tern abundance in times of hypoxia as compared to times of normoxia; 2007 was the year in which the average summer DO levels reached hypoxic conditions for the fewest number of days and the average summer DO levels was the highest (6.235 ± 0.21mg/L).

Discussion

Changes in the aquatic environment are linked to changes in the abundance of avian predators in a predator-prey system where the predators are plunge divers and the prey are small minnows. While DO, temperature and turbidity were thought to potentially alter the availability of prey fishes to their avian predators, and in turn influence the presence of these avian predators, only DO was a significant predictor of tern abundance.

Low levels of dissolved oxygen have been linked to both increases (Pihl et al. 1992) and decreases (Nestlerode and Diaz 1998) in predation risk in fish – invertebrate predator-prey interactions; in predator-prey systems that involve only fish, decreases in dissolved oxygen level result in an increase in predation in experimental manipulations (Wolf and Kramer 1987). In small scale experiments, hypoxic conditions resulted in greater consumption of prey by avian predators (Randle and Chapman 2004). In this study where both predators and prey are free to

move about in the environment, hypoxia increased the number of avian predators. As predation events require detection and encounters of the prey by the predators, increasing the numbers of predators will likely increase the predation risk of minnows.

Demonstrating that the increased risk of predation is a direct result of behavioural changes in the prey fish as a result of changing DO levels and not the absolute number of prey fish, this study measured CPUE of the minnows throughout all levels of DO and found no relationship between CPUE and number of terns present. Further support for this hypothesis is evident in data collected in the same channel in 2005 where the position within the water column where minnows forage under differing oxygen levels were analyzed. In that study, at times of low (hypoxic) DO levels, minnows feed primarily at the extremes of the water column (surface and near bottom, ANOVA: surface $F_{1,27} = 18.08$, $p < 0.0014$; bottom $F_{1,27} = 4.735$, $p < 0.038$; $p > 0.1$ for the two middle depths; (Hedges 2007), with more foraging occurring near the air water interface than elsewhere in the water column. This provides a direct link between a change in fish behaviour as a result of decreased oxygen levels, which in turn made the fish more available to their avian predators; fish are more easily taken by avian predators when they inhabit shallow waters or areas close to the surface (Whitfield and Blaber 1978, Kramer et al. 1983).

Temperature, as well as dissolved oxygen, has been shown to influence predation risk in fish predator-prey interactions (Krause and Godin 1995) as well as invertebrate -anuran tadpole predator-prey interactions (Anderson et al. 2001, Moore and Townsend 1998). In these studies, as temperature increased attack rate by predators on their prey increased (Krause and Godin 1995) and/or mortality rate of the prey increased (Anderson et al. 2001, Moore and Townsend 1998). In this study however, no relationship was observed between temperature and abundance of predators. It was hypothesized that as temperature increased the activity and foraging levels of

the minnows would increase in response. This increase in activity would make them more easily observed by their avian predators, resulting in an increase in abundance of these predators. However, if the response of the minnows in response to lowered DO is taken into consideration it is understandable why an increase in temperature does not result in an increased risk of avian predation; there may be an increase in activity level of the fishes but if they are not active at surface they are not available to their predators. This same rationale can also be applied to the lack of response by the avian predators to reductions in turbidity levels.

Previous work has demonstrated the variable affects of turbidity on predator-prey interactions. Gregory and Levings (1998) found a decrease in predation risk in fish predator-prey interactions while Abrahams and Kattenfeld (1997) demonstrated that at moderate turbidities, there was no difference in risk of predation. The same variability in risk of predation under differing turbidities can also been found in literature pertaining to avian predation; both increases (Strod et al. 2008) and decreases (Gwiazda and Amirowicz 2006) in predation risk were observed. In this study, no relationship between turbidity and predator abundance, and hence predation risk, was observed. Blind Channel is a turbid environment throughout the summer, though variation does arise. Again, unless the prey are occupying areas close to the air water interface they will not be available to their avian predators.

The risk of predation by Forster's terns to minnow prey, as determined by the abundance of terns is not directly related to either abundance of prey, temperature or turbidity of aquatic environment. There is a relationship between dissolved oxygen and tern abundance with an increase in dissolved oxygen resulting in a decrease in the abundance of terns present. When only physiologically significant levels of dissolved oxygen are considered the relationship between DO levels and tern abundance becomes even more apparent. Another interesting trend

occurs when DO levels over the course of the three sampling years are considered. In 2007, when Blind Channel became hypoxic for only seven days during the sampling period, tern abundance was lowest overall and there was no relationship between DO and tern abundance. In 2006 and 2008 when hypoxic conditions occurred for 32 and 19 days respectively, the relationship between tern abundance and DO was obvious. This suggests that it is not only the daily level of DO that is important in predator-prey relationships but also the trend in DO over the course of a longer time frame. This observation is likely a result of availability of prey; if the prey are available to predators for only a short period of time, energetically it is not feasible for predators to continually search in areas where prey are not available. In times when DO levels are routinely low, prey are available more often, and for a predator the food source becomes more reliable. Overall tern abundances are higher during periods when dissolved oxygen levels are hypoxic for extended period of time; this occurs regardless of the number of prey present. The abundance of the prey does not matter if prey are not available to the predator.

In larger lakes, use of these shallow littoral zones by forage fish would make them available to plunge diving predators such as Forster's terns. In areas such as Delta Marsh, water bodies generally do not have gently sloping shorelines that may be occupied by small bodied fish. In these instances, there is the potential for the DO content of the water to have important effects on energy budgets for adult Forster's terns, as well the success of their fledglings. This is a result of the observation in this study: that it appears as if it is not the abundance of prey, but their availability to predators that is important. Under normoxic conditions, if prey are using deeper waters as a refuge from predation and are not physiologically stressed because DO levels are high, terns may have to increase their search area as these prey are not available in this location. Increased searching and travel distance to a new food patch increases the terns own

energetic requirement for food. This could lead to a reduction in the amount of food provisioned to their fledglings, and a potential reduction in successful fledging. Future research examining the effects of dissolved oxygen levels on foraging success (not just presence) of terns, as well as its impact on the amount of food provisioned to young chicks would provide further insight into the consequences of a variable environment of the overall success of tern colonies.

References

Abrahams, M.V., Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioural Ecology and Sociobiology **40**: 169-174.

Allouche, S., Gaudin, P. 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. Oikos **94**: 481-492.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on predator-prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? Advances in Ecological Research **25**: 1-58.

Bluso-Demers, J., Colwell, M.A., Takekawa, J.Y., Ackerman, J.T. 2008. Space use by Forster's terns breeding in South San Francisco Bay. Waterbirds **31**: 357-364.

Bonner, T.H., Wilde, G.R. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society **131**: 1203-1208.

Clarke, A., Johnston, N.M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Ecology **68**: 893-905.

Collis, K., Roby, D.D., Craig, D.P., Ryan, B.A., Ledgerwood, R.D. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary: vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society **130**: 385-396.

Crowder, L.B., Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**: 1802-1813.

Eklöv, P., Persson, L., 1996. The response of prey to the risk of predation: proximate cues for refuging juvenile fish. Animal Behaviour **51**: 105-115.

Eriksson, M.O.G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. Ornis Scandinavica **16**: 1-7.

Godin, J.-G. J., Crossman, S.L. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behavioural Ecology and Sociobiology **34**: 359-366.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **50**: 241-246.

Gregory, R.S., Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society **127**: 275-285.

Gwiazda, R., Amirowicz, A. 2006. Selective foraging of Grey Heron (*Ardea cinerea*) in relation to density and composition of the littoral fish community in a

submontane dam reservoir. Waterbirds **29**: 226-232.

Harvey, B.C., Stewart, A.J. 1991. Fish size and habitat depth relationships in

headwater streams. Oecologia **87**: 336-342.

He, X., Kitchell, J.F. 1990. Direct and indirect effects of predation on a fish community: a

whole-lake experiment. Transactions of the American Fisheries Society **119**: 825-835.

Hedges, K.J. 2007. Effects of abiotic factors on predator-prey interactions in freshwater fish

communities. Ph.D. Thesis, University of Manitoba.

Hodgens, L.S., Blumenshine, S.C., Bednarz, J.C. 2004. Great blue heron predation on stocked

rainbow trout in an Arkansas tailwater fishery. North American Journal of Fisheries

Management **24**: 63-75.

Kramer, D.L. 1987. Dissolved oxygen and fish behaviour. Environmental Biology of Fishes **2**:

81-92.

Kramer, D.L., Manley, D., Bourgeois, R. 1983. The effect of respiratory mode and oxygen

concentration on the risk of aerial predation in fishes. Canadian Journal of Zoology **61**:

653-665.

Krause, J., Godin, J.-G. J. 1995. Predator preference for attacking particular prey group sizes:

consequences for predator hunting success and prey predation risk. Animal Behaviour **50**:

465-473.

Lass, S., Spaak, P. 2003. Temperature effects on chemical signalling in a predator-prey system.

Freshwater Biology **48**: 669-677.

McNicholl, M.K. 1971. The breeding biology and ecology of Forster's tern (*Sterna forsteri*) at

Delta, Manitoba. Ph.D. thesis, University of Manitoba.

Milinski, M., Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature **275**: 642-644.

Mittelbach, G.G., Chesson, P.L. 1987. Predation risk: indirect effects on fish populations. Pages 537-555 *in* W.C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Monaghan, P., Uttley, J.D., Okill, J.D. 1989. Terns and sandeels: seabirds as indicators of changes in marine fish populations. Journal of Fish Biology **35**: 339-340.

Moore, M.K., Townsend, V.R. Jr, 1998. The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos **81**: 329-336.

Nestlerode, J.A., Diaz, R.J. 1998. Effects of periodic environmental hypoxia on predation of a tethered polychaete, *Glycera Americana*: implications for trophic dynamics. Marine Ecology Progress Series **172**: 185-195.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist **100**: 65-75.

Pihl, L., Baden, S.P., Diaz, R., Schaffner, L. 1992. Hypoxia induced structural changes in the diet of bottom feeding fish and Crustacea. Marine Biology **112**: 349-361.

Randle, A.M., Chapman, L.J. 2004. Habitat use by the African anabantid fish C*tenopoma muriei*: implications for costs of air breathing. Ecology of Freshwater Fish **13**: 37-45.

Reid, S.M., Fox, M.G., Whillans, T.H. 1999. Influence of turbidity on piscivory in largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences **56**: 1362–1369.

Robb, T., Abrahams, M.V. 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? Journal of Fish Biology **62**: 1067-1081.

Salt, G.W., Willard, D.E. 1971. The hunting behavior and success of Forster's tern. Ecology **52**: 989-998.

Snickars, M., Sandstrom, A., Mattila, J. 2004. Antipredator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. Journal of Fish Biology **65**: 1604-1613.

Steinmetz, J., Soluk, D.A., Kohler, S.L. 2008. Facilitation between herons and smallmouth bass foraging on common prey. Environmental Biology of Fishes **81**: 51-61.

Strod, T., Izhaki, I., Arad, Z., Katzir, G. 2008. Prey detection by great cormorant (*Phalacrocorax carbo sinensis*) in clear and in turbid water. Journal of Experimental Biology **211**: 866-872.

Suthers, I.M., Gee, J.H. 1986. Role of hypoxia in limiting diel spring and summer distributions of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Canadian Journal of Fisheries and Aquatic Sciences **43**: 1562-1570.

Taylor, D.L., Collie, J.S. 2003. A temperature- and size- dependent model of sand shrimp (*Crangon septemspinosa*) predation on juvenile winter flounder (*Pseudopleuronectes americanus*). Canadian Journal of Fisheries and Aquatic Sciences **60**: 1133-1148.

Tonn, W.M., Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology **63**: 1149-1166.

Turner, A.M., Mittelbach, G.G. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores and plankton. Ecology **71**: 2241-2254.

Wanzenbock, J., Mikheev, V.N., Pasternak, A.F. 2006. Modification of 0+ perch foraging behaviour by indirect cues of predation risk. Ecology of Freshwater Fish **15**: 118-124.

Weetman, D., Atkinson, D., Chubb, J.C. 1998. Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulta.* Animal Behaviour **55**: 1361-1372.

Weetman, D., Atkinson, D., Chubb, J.C. 1999. Water temperature influences the shoaling decisions of guppies, *Poecilia reticulata*, under predation threat. Animal Behaviour **58**: 734-741.

Weimerskirch H., Le Corre M., Jaquemet S., Marsac, F. 2005. Foraging strategy of a tropical seabird, the red footed booby, in a dynamic marine environment. Marine Ecology Progress Series **288**: 251-261.

Werner, E.E., Anholt, B.R. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology **77**: 157-169.

Werner, E.E., Gilliam, J.F. 1984. The ontogenetic niche and species interactions in a size-structured populations. Annual Reviews in Ecology and Systematics **15**: 393-425.

Werner, E.E., Gilliam, J.F., Hall, D.J., Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology: **64**: 1540-1548.

Whitfield, A.K., Blaber, S.J.M. 1978. Feeding ecology of piscivorous birds at Lake St. Lucia, Part I: Diving birds. Ostrich **49**: 185-198.

Wolf, N.G., Kramer, D.L. 1987. Use of cover and the need to breath: the effects of hypoxia on vulnerability of dwarf gouramis to predatory snakeheads. Oecologia **73**: 127-132.

Chapter 7: General Discussion

In ecological studies of aquatic systems, our attempts to understand the role that the abiotic environment plays in both the composition of the fish community present are complicated. While it is not always possible to disentangle the role that each environmental variable exerts on the structure of the community in isolation, measuring each variable and attempting to find patterns between the abiotic environment and measures of the fish community is one method available. The laboratory provides a means to determine the effect of a single variable on species interactions. While many of the intricacies of the natural ecosystem are removed, the direct effect of that one variable can be determined. Another tool that ecologists can implement as a means to determine the influence of the environment on the aquatic community is theoretical modeling. In a mathematical model, parameters are included that incorporate findings from both the field and laboratory experiments, essentially allowing a simulation of the role these parameters have on the outcome of interest.

This thesis implements all of the aforementioned techniques in an attempt to uncover how the abiotic environment both structures the natural community and influences the interactions between species, specifically between predators and their prey. Within this thesis, the field research focuses on temperature, dissolved oxygen and turbidity and the role that these environmental factors play in community structure – specifically interactions between predators and their prey. The laboratory work, as well as the theoretical model, both focus on the role that temperature plays in aquatic ecosystems. However, the focus of the two studies differ: the laboratory studies allow for the determination of the direct effect of temperature of the activity and foraging rates of small fish. The laboratory experiments also allowed me to determine the effect of temperature, via its effect on metabolic rates and therefore energy consumption, on risk-

taking (propensity to forage in the face of predation risk). The theoretical study is more broad in that it incorporated the role temperature plays on metabolic rates, food acquisition and risk of predation to predict the overall survival probabilities of the fathead minnow over the course of the entire ice-free period.

Results of the work conducted for this dissertation demonstrate that the environment does play a role in both structuring aquatic communities and in mediating the interactions between predators and their prey. As demonstrated in the lab, with an increase in temperatures, fathead minnows increase their distance travelled over a given time period (Chapter 2) and increase their foraging (Chapter 2, Chapter 3). The fathead minnows also were more likely to use risky habitats to increase their foraging returns at warm (23°C) versus cooler (5 and 15°C) temperatures (Chapter 3). Likely as a result of increased overall foraging and increased use of risky feeders, as temperatures increased so to did the proportion of time the predator spent oriented towards their prey. The driving force behind these observations is likely the relationship between temperature and metabolic rates and therefore energetic demands (Wootton 1990). As temperatures and energetic demands increase, individuals increase their activity, likely as they increase their search efforts for food. Foraging increases as individuals attempt to meet increases in energetic demands. Risk taking also increases as the potential gains (food required to offset higher metabolic rates) are weighed against potential costs (probability of being consumed by a predator). As predators are more interested in more active prey (Krause and Godin 1995, Chapter 3) as temperatures increase encounter rates between predators and prey are likely to increase. Therefore under increased temperature conditions, predation risk to prey is expected to increase.

Results of field work where I sampled temperature, dissolved oxygen and turbidity and related those variables to the CPUE of fishes provide further evidence that temperature plays a

role in species interactions, this time in a natural ecosystem. Regardless of the thermal guild classification of fishes, as temperatures increase the CPUE of fishes also increase. Whether this is a result of an increase in the abundance of fishes present (including predatory fishes) or a result of increases in the activity and movement rates of fishes (as was observed in laboratory studies: Chapter 2), it suggests that encounter rates between predators and prey will increase. Further support for this was observed in the propensity of prey to forage in risky habitats under the warmest temperature treatments (Chapter 3). If there are increased encounter rates between predators and their prey, it should also be expected that mortality rates of prey will also increase. This would be similar to what was observed by Anderson et al. (2001) when they studied the effect of temperature on growth and mortality rates of anuran larvae and their insect predators. In their study, Anderson et al. (2001) observed an increase in growth rates with temperature, but also mortality rates of the anuran larvae increased. This likely was a result of increased foraging, and therefore activity rates by these larvae, which in turn increased their encounters with their predator.

Previous laboratory (Abrahams and Kattenfeld 1997) and field (Gregory and Levings 1998) studies suggest that turbidity will reduce predation risk by piscivorous predators on their piscine prey. However, my research suggests that turbidity does not affect measures of CPUE of either visual predators as expected, or those that rely on chemical cues were influenced. It is possible that this is a result of confounding effects that happen as turbidity levels increase. An increase in turbidity levels reduces the foraging efficiency of fishes (Gregory and Northcote 1993). In a turbid environment, in order to meet energetic demands, it is expected that individuals will have to increase their foraging rates. This should therefore be expected that CPUE of visual foragers should increase with turbidity as CPUE is reflective of both the

abundance and activity of individuals. However, if the increase in activity is coupled by an emigration into Lake Manitoba where conditions may be more favourable, there might not be any perceivable relationship between turbidity and CPUE of visual foragers.

Research has suggested that hypoxic areas may provide a physiological refuge for small fish (Randle and Chapman 2004). Large fishes generally have a lower tolerance to hypoxic conditions than smaller fishes (Robb and Abrahams 2003, Hedges 2007) and as a result, under hypoxic conditions, spend less time interested in their prey when DO levels are low (Robb and Abrahams 2002). Fishes with physostomous swim bladders were positively related to DO levels, while freshwater drum, with a physoclistous swim bladder were negatively related to DO levels. Periods of low DO may provide prey with a reduction in risk of predation as the two dominant predators of small fish, northern pike and bullhead species, have a positive relationship with measures of DO. Taken with an observed increase in the presence of avian predators with a decrease in DO levels (Chapter 6) periods of low dissolved oxygen may reduce the piscine predator pressure, but that may be offset by an increase in the avian predator pressure.

An increase in mortality rates as a result of increased temperature was also the outcome of the state-dependent optimization model that I created using Visual Basic (Chapter 5). Increasing temperature is not always the result of increased predation rates, in general risk of predation also increase with temperature (Chapter 5). Increasing metabolic demands results in an increased requirement for energy. If individuals cannot meet this increased demand either because the food they require is not available or because they cannot acquire energy at the pace necessary to meet demands, individuals succumb to starvation. Regardless of the mode of death, an increase in temperature appears to be detrimental to small prey fishes. This effect may be

exacerbated further by the fact that prey fishes are more likely to take risks and forage in the presence of predators as temperatures increase (Chapter 3).

It is obvious from the results of the studies conducted as part of this dissertation that the abiotic environment influences fishes. In the field, temperature and dissolved oxygen were related to CPUE measures of fishes present, suggesting that these variables play a role in the structuring of aquatic environment. The relationship between temperature, dissolved oxygen and the CPUE of various fishes suggests that these factors can influence interactions, including predator-prey interactions, of species. The results from Chapter 6 suggest that these effects extend past aquatic predator-prey interactions. In periods of hypoxia, aerial predators become more common. Given that fathead minnows increase their use of surface waters under periods of hypoxia, it is likely that the behavioural responses of these small fish put them at increased risk of predation. The interaction between behaviour of individuals and temperature can also play a role in predator-prey interactions. Temperature affects activity rates and foraging rates of the fathead minnow. It also affects their propensity to take risks. Taken together, dissolved oxygen and temperature are likely to play a large role in structuring predator-prey interactions in aquatic environments.

References

Abrahams, M.V., Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interaction in aquatic environments. Behavioural Ecology and Sociobiology **40**: 169-174.

Anderson, M.T., Kiesecker, J.M., Chivers, D.P., Blaustein, A.R. 2001. The direct and indirect effects of temperature on a predator-prey relationship. Canadian Journal of Zoology **79**: 1834-1841.

Gregory, R.S., Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society **127**: 275-285.

Gregory, R.A., Northcote, T.G. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences **50**: 233-240.

Hedges, K.J. 2007. Effects of abiotic factors on predator-prey interactions in freshwater fish communities. Ph.D. Thesis, University of Manitoba.

Krause, J., Godin, J.-G. J. 1995. Predator preference for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour **50**: 465-473.

Randle, A.M., Chapman, L.J. 2004. Habitat use by the African anabantid fish *Ctenopoma muriei*: implications for the costs of airbreathing. Ecology of Freshwater Fish **13**: 37-45.

Robb, T., Abrahams, M.V. 2002. The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. Behavioural Ecology and Sociobiology **52**: 25-30.

Robb, T., Abrahams, M.V. 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? Journal of Fish Biology **62**: 1067-1081.

Wootton, R.J. 1990. Ecology of Teleost Fishes. London: Chapman and Hall. 404 pp.