The Effect of Turbidity and Predation Risk on the Habitat Choice of Fathead Minnows (*Pimephales promelas*).

By Michael G. Kattenfeld

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

Master of Science

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THE EFFECT OF TURBIDITY AND PREDATION RISK ON THE

HABITAT CHOICE OF FATHEAD MINNOWS (Pimephales promelas)

BY

MICHAEL G. KATTENFELD

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba
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MASTER OF SCIENCE

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Abstract

Turbidity reduces the detection abilities of fish in aquatic communities and causes encounters between predator and prey to occur at close distances, where risk of predation is usually high. However, many planktivorous fish increase activity levels, primarily through a decrease in the use of anti-predator behavior, in turbid water. Therefore, turbidity may reduce the response of prey to predators and thus decrease the behaviorally mediated indirect effects of predation. The purpose of this thesis was to determine: 1) if turbidity reduces the behavioral response of fathead minnows to the presence of predators, 2) by which mechanism, the "Turbidity as Cover" or the "Turbidity Reduces Effectiveness" hypotheses, turbidity reduces the response of fathead minnows to predators, and 3) if the results observed in the laboratory can predict the habitat choice of fathead minnows in the field.

Turbidity reduced the response of fathead minnows to risk of predation. In clear water, the presence of a predator caused a larger proportion of the fathead minnows to forage within a refuge. In turbid water, the distribution of the fathead minnows was more even indicating that the behavioral response of the fathead minnows was reduced in turbid water. Therefore, turbidity reduced the behaviorally mediated indirect effects of predation.

The mortality rate of fathead minnows was not affected by water clarity. The same proportion of fathead minnows were consumed in both clear and turbid water. The fathead minnows did not benefit from a reduced distance to cover in turbid water, and therefore, the "Turbidity as Cover" hypothesis is refuted. Size selective predation of smaller fathead minnows occurs in clear water, because larger, faster fathead minnows are better able to avoid predators and have a more effective anti-predator behavior. In turbid water, predators consumed a more random size of fathead minnows indicating that anti-predator behavior is less effective in turbid water. These data support the "Turbidity Reduces Effectiveness" hypothesis.

In the field, the large-scale distribution (along a 16 meter transect) of fathead minnows was not affected by either the distribution of food or predation risk. Fathead minnows were most abundant near the surface of the open water habitat, an area high in predation risk and low in food abundance. Since turbidity levels did not reach high values (10 Nephelometric Turbidity Units), it was not possible to determine the affect of varying turbidity levels on the large-scale distribution of the fathead minnows. Aquatic macrophyte density and competition with young-of-the-year fish were important factors in the large-scale habitat choice of the fathead minnows. Predator exclosures were used to determine the affect of refuges to predation on the small-scale distribution (within each habitat) of the fathead minnows. High use by the fathead minnows occurred, especially in the mid and open water habitats, indicating that the minnows are able to assess the local predation risk and respond to it by selecting less risky habitats. No environmental variables measured, such as conductivity, turbidity, precipitation, water temperature, light intensity or wind speed, had any affect on the response of the fathead minnows to the local predation risk.

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Chapter 1

INTRODUCTION

INTRODUCTION

Predators play a major role in the ecosystem; by consuming prey, predators pass energy from one trophic level to the next. From this simple act of consumption, many far reaching consequences arise. Predation affects prey at the individual, population and community levels (Kerfoot and Sih, 1987). Predators exert their various effects through three different interactions: 1) the direct consumption of prey, 2) the indirect effects that arise from consumption, 3) and the indirect effects that arise as a consequence of modification (behavioral, physiological, or morphological) by the prey. By consuming prey, predators decrease the prey population size and can either limit prey numbers below the carrying capacity or drive the prey to local extinction, which occurs more frequently in aquatic than in terrestrial communities (Murdoch and Bence, 1987). The indirect effects of predation that result from consumption by predators usually manifest themselves between two or more prey species. By changing the relative abundance of several prey species, predators change the dynamics of the interaction between competitors and alter the interactions between the prey species (Miller and Kerfoot, 1987).

The indirect effects of predation that arise through modification by the prey can be of any variety. Physiological (i.e. production of distasteful or toxic chemical) and morphological modification usually result in the prey becoming a less desired food item (Havel, 1987; Kerfoot, 1982). In fish, both physiological and morphological modifications by the prey to decrease predation risk are long-

term evolutionary responses, while behavioral responses (i.e. anti-predator behaviors) are short-term changes. Behavioral modification by the prey, such as refuge use, decreased movement, or increased vigilance, to avoid predation (or predation risk) is considered to have far-reaching consequences. Werner et al. (1983) found that the presence of largemouth bass (*Micropterus salmoides*) caused the smaller, more susceptible size classes of bluegill sunfish (*Lepomis macrochirus*) to remain within a vegetated refuge. As a result, the smaller individuals showed decreased growth rates because the energetic value of the habitat was significantly lower than the more dangerous, open-water habitat. The larger bluegills, as a result of the habitat selection of the smaller fish, showed increased growth due to a decrease in intraspecific competition. Behavioral modification by the prey in response to predation risk had effects at the individual, population, and community level (Werner et al., 1983).

Anti-predator behavior is a significant ecological force because it can affect individual fitness, population structure and community dynamics. However, the extent to which behavioral modification by the prey affects the population and community ecology is not known, but it is assumed to be large. If any environmental variables mediated the magnitude of the prey's behavioral response to the presence of predators, then we may obtain a greater insight into the role of predators in ecosystems. Essentially, if the behaviorally mediated indirect effects of predation are reduced, then the other effects of predators (the direct consumptive, indirect consumptive, and indirect effects that arise from

either physiological or morphological modification by the prey) will be relatively more important in determining the effect of predators on the prey populations and community.

Turbidity is the property of a liquid which causes light to be scattered and/or absorbed rather than transmitted (Kirk, 1983). It is both a measure of the amount of suspended sediment and the optical properties of the sediment and liquid (Bruton, 1985). Blaber and Blaber (1980) define any water with >10 Nepholmetric Turbidity Units (NTU's) as turbid. In aquatic communities, high turbidity has five major effects: reduced primary productivity as a result of a decrease in light penetration; reduced benthic food availability, due to smothering; damage to gill rakers and filaments of fish and invertebrates; reduced risk of aerial predation; and reduced visual detection of pelagic food items (Bruton, 1985). By reducing the visual detection of pelagic food items, turbidity decreases the detection abilities of the prey and may mediate the behaviorally generated indirect effects of predation because it may function to decrease the anti-predator responses of the prey..

In clear water, detection varies positively with both light intensity and the size of the object being viewed (Dill, 1974). In fish, predators are often much larger than their prey, and the fish prey can usually detect the predator first (Cerri, 1983). Visually dependent prey in clear water may benefit over predators through a detection advantage.

Turbidity reduces the importance of size and movement on the ability of one individual to detect another (Crowl, 1989). Crowl (1989) found that the carapace length and movement of crayfish (*Procambrus acutus*) showed a positive, linear relationship to the reactive distance of largemouth bass (*Micropterus salmoides*) in clear water. In turbid water, the importance of carapace size and movement of the crayfish on reactive distance was significantly diminished (Crowl, 1989). Crowl (1989) did not report the behavior of the crayfish, and it was unknown if the crayfish reacted toward the predator. However, with respect to the fish, the size and velocity of the object being viewed in turbid water is less important in detection, and prey may lose some, if not all, of their detection advantage.

An encounter between predator and prey occurs when one individual moves into the detection radius of the other (Lima and Dill, 1990). In clear water, prey do not immediately flee when they encounter a predator, but rather balance the costs of remaining or fleeing to the benefits of remaining or fleeing (Ydenberg and Dill, 1986). Predators will often move closer to the prey before attacking, and it is thought that this allows the predator to identify preferential prey items (Crowl, 1989). Once the prey is within the reactive distance, the predator will strike at the prey. Prey continuously assess the level of predation risk as the predator approaches and then make decisions on when to flee (Ydenberg and Dill, 1986).

In turbid water, predator and prey will probably detect one another at

distances close to, or within, the reactive distance. Prey will flee immediately because of the close distance and high risk of predation (Ydenberg and Dill, 1986) while predators will strike at the prey (Crowl, 1989). In turbid water, predators lose the strike specificity seen in clear water and will often strike at any detectable object. Crowl (1989) found that largemouth bass conditioned to feed on crayfish would strike at a rock (approximately crayfish-shaped) 38 out of 40 trials in turbid water. This response was never observed in clear water. In turbid water, the distances involved in the predator-prey encounter are near or within the reactive distances of both predator and prey, and both will be selected to react to any detectable object (Fig. 1.1).

In clear water, prey species assess the costs (energetic and opportunity costs) and the benefits (reduced risk of predation) of anti-predator behavior, and initiate these behaviors to decrease the probability of being consumed by a predator. Prey species will often decrease movement (Azevedo-Ramos et al., 1992; Eklov and Hamrin, 1989), or remain within refuges (Cerri and Fraser, 1983; Christensen and Persson, 1993; Gilliam and Fraser, 1987; Winkelman and Aho, 1993) to avoid predation. In turbid water, planktivorous fish, often predated by larger fish, increase foraging activity (Gregory and Northcote, 1993; Miner and Stein, 1993; Boehlert and Morgan, 1985; Gradall and Swenson, 1982), indicating that the costs and benefits involved in using anti-predator behavior may have changed. In turbid water, prey behavioral modification seems to be a result of not initiating anti-predator behavior, either because there
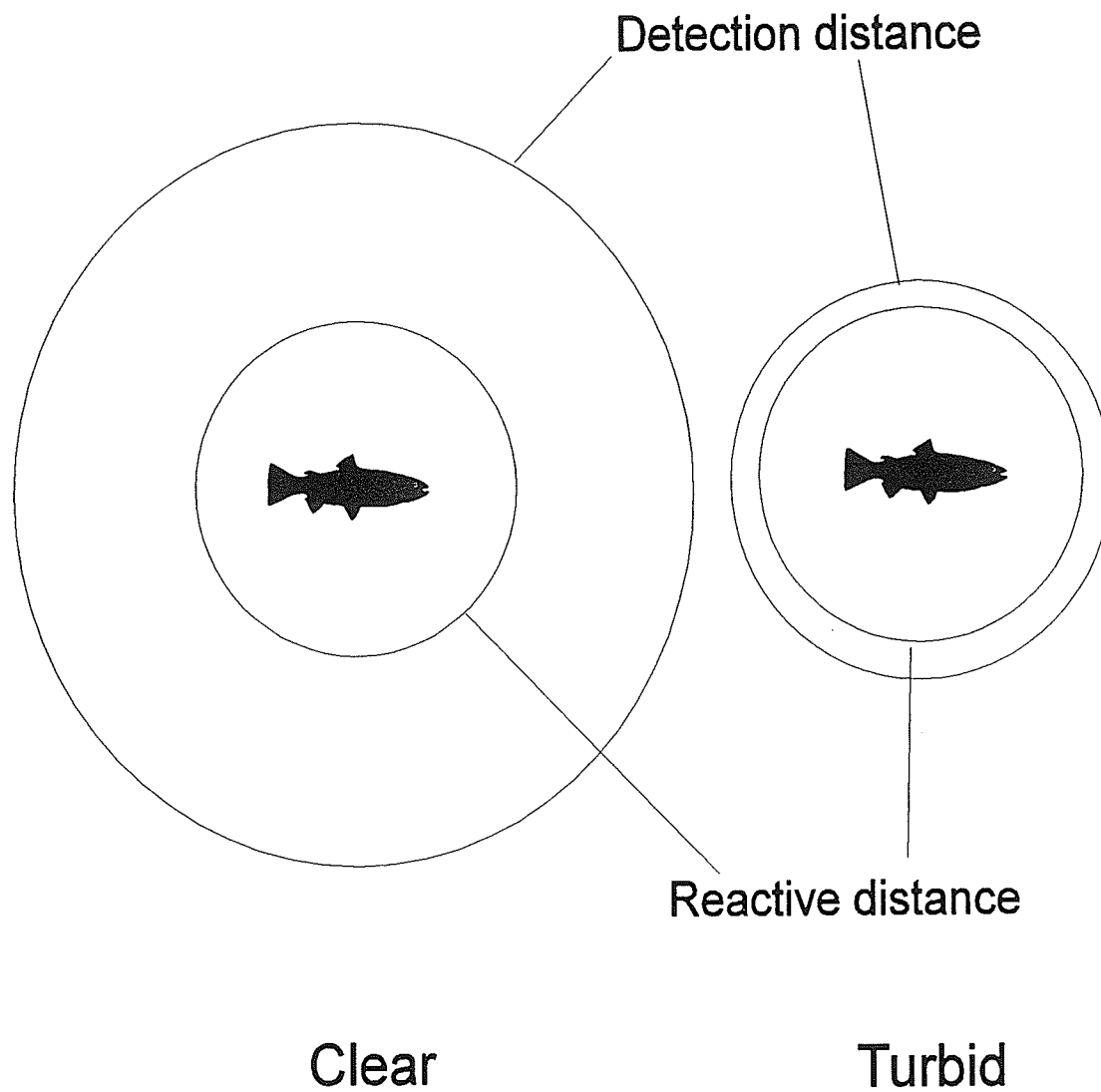
Fig. 1.1 The effect of turbidity on the detection distance (distance at which an individual first detects either a predator or prey) and the reactive distance (distance at which an individual reacts to either a predator or prey).

is a reduced risk of predation in turbid habitats or because anti-predator behavior has a reduced benefit in turbid water habitats. When prey decrease their use of anti-predator behavior, the indirect effects resulting from behavioral modification by the prey are decreased.

The purpose of this thesis is to determine if: 1) turbidity reduces the behaviorally mediated indirect effects of predation and if so, by what mechanism, and 2) turbidity can mediate the effect of predation risk on the habitat choice decisions of fathead minnows (*Pimephales promelas*) within the field.

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Chapter 2

The Effect of Water Turbidity

on the Behavioral Response of Fathead Minnows to

Piscivorous Yellow Perch

INTRODUCTION

Prey can respond to the presence of predators by using anti-predator behavior to decrease their risk of consumption (Abrahams and Dill, 1989; Lima and Dill, 1990). The presence of a predator can cause prey to shift habitats (Abrahams and Dill, 1989; Fraser and Cerri, 1982; Gilliam and Fraser, 1987; Jedrezejewski and Jedrezejewska, 1990; Mittelbach, 1981; Power, 1987; Stein and Magnuson, 1976) or initiate other anti-predator behaviors (Christensen and Persson, 1993; Johannes, 1993; Kramer et al., 1983; Savino and Stein, 1989; Stein and Magnuson, 1976; Williams and Moore, 1982). By altering prey habitat selection, predators can change prey population dynamics (Fraser and Gilliam, 1992; Tonn and Paszkowski, 1992), and affect community structure (Dill, 1987; Johannes, 1993; Marti et al., 1993).

Behavioral modification by the prey in response to predation risk affects the individual, the prey population and the community. If the prey's use of anti-predator behavior decreases, then the other effects that predators exert on prey should become significantly more important: the direct effects, the indirect effects that arise from consumption, and the indirect effects that arise through long-term modification by the prey (physiological and morphological). By reducing or removing one component of the predator-prey interaction, in this case the behaviorally mediated indirect effects of predation, it is possible to determine its magnitude.

Turbidity may decrease the strength of the behavioral response of prey to the presence of predators. Gregory (1993) observed that juvenile chinook salmon (*Oncorhynchus tshawytscha*) showed a reduced response to the presence of two predator models (a dogfish and glaucous-winged gull) in turbid water (22.7 NTU +/- 2.6 SD). Presented in clear water, the predator models caused the juvenile salmon to move into deeper areas of the test aquarium. In turbid water, the salmon were more evenly distributed throughout the tank and were not significantly affected by the fish model. The bird model did elicit a response, but the duration was approximately seven times shorter in turbid than in clear water. These data suggest that the behavioral component of the indirect effects of predation is reduced in turbid water.

Two possible mechanisms exist, both of which may explain the reduced response of prey to predation risk in turbid water. The first mechanism will be referred to as the "Turbidity as Cover" (TAC) hypothesis. Blaber and Blaber (1980) suggested that turbidity provides cover for the prey to quickly escape predation. As turbidity increases, the distance to cover or escape decreases. In turbid water, prey would be better able to avoid predators and thus the costs associated with the presence of a predator would decrease (Fig. 2.1). The TAC hypothesis predicts that prey show a reduced response to the presence of predators because they benefit from a reduced risk of predation.

Another hypothesis may explain the mechanism by which turbidity reduces the behavioral response of prey to predators. The "Turbidity Reduces
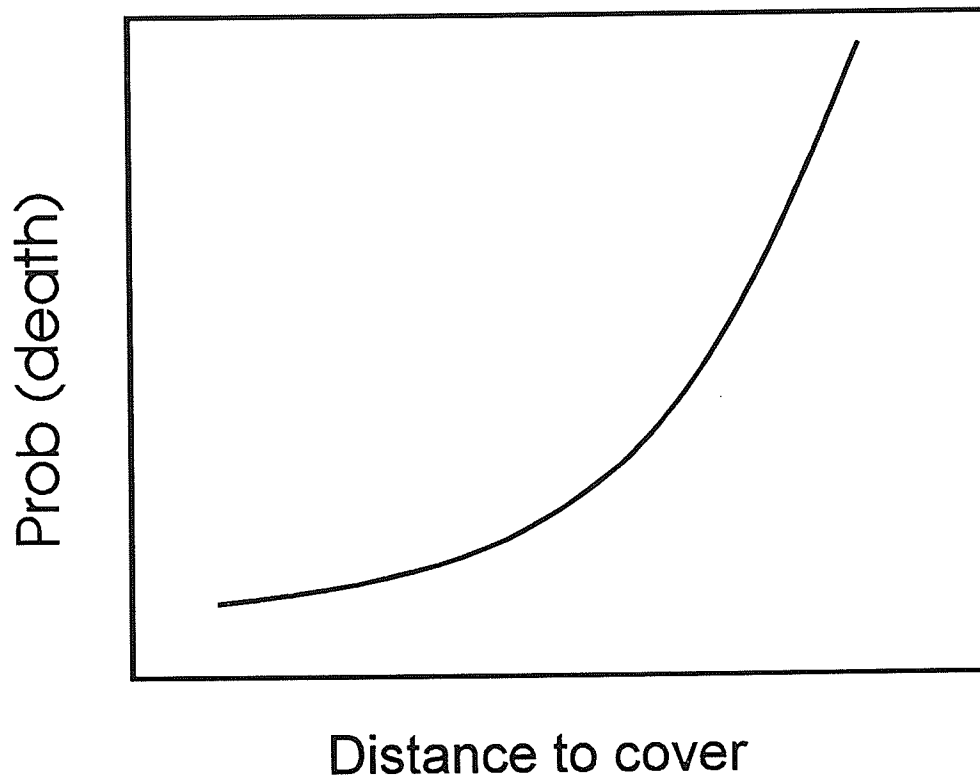
Fig. 2.1 The effect of distance to cover or escape on the probability of a prey
being consumed by a predator. The response may be linear or non-
linear.

Effectiveness" (TRE) hypothesis, developed in conjunction with M.V.Abrahams, proposes that the prey do not respond to the presence of predators in turbid water because the effectiveness of anti-predator behavior is reduced in turbid water (Fig. 2.2). The energetic cost of performing these behaviors does not change between clear and turbid habitats. However, the benefits obtained from performing anti-predator behavior may decrease in turbid water because of the close distances involved in the encounter. This reduction in benefits associated with performing anti-predator behavior leads to a lower optimum level of time spent performing these behaviors (See Fig. 2.2). Increased vigilance in clear water habitats decreases the risk of predation. In turbid water, increased vigilance may have a much reduced benefit because the distance between predator and prey will be small.

The purpose of this chapter is to determine if the response of fathead minnows to the presence of a piscivorous yellow perch is affected by water turbidity, and if so, by what mechanism, the TAC or TRE hypotheses. These questions will be assessed in two controlled laboratory experiments.

In the first experiment, I investigated the hypothesis that turbidity will reduce or remove the behaviorally mediated indirect effects of predation. Specifically, the presence of a predator in clear water should elicit a much stronger anti-predator response from the prey than the same predator in turbid water. To test this hypothesis, I used the distribution of foraging prey species, in this case fathead minnows, to determine the effect of water clarity on the
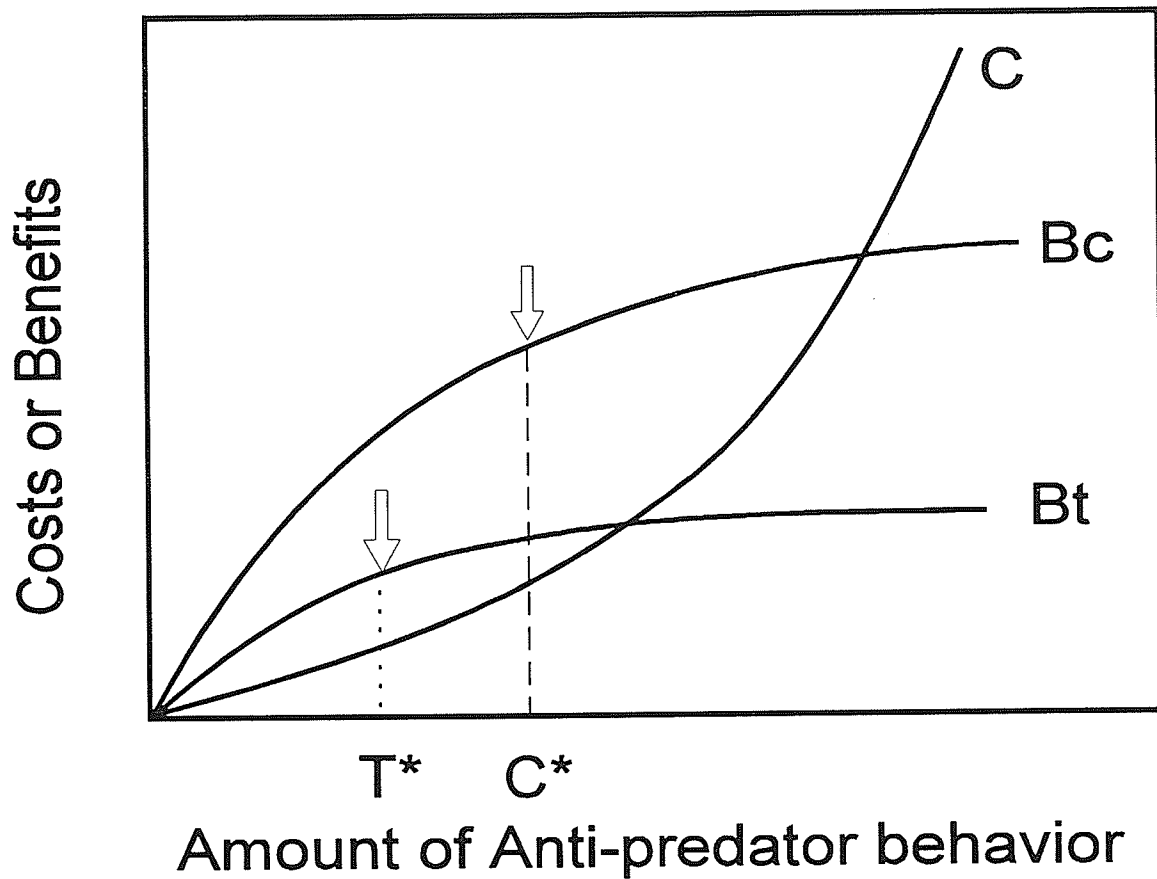
Fig. 2.2 The costs and benefits of performing anti-predator behavior in clear and turbid water. Bc and Bt are the benefits obtained in clear and turbid water, respectively, while C is the cost (both energetic and opportunity costs) of performing anti-predator behavior. C* is the theoretical optimum level of anti-predator behavior in clear water, while T* is the optimum in turbid water. The optima were determined by the maximum difference between the cost and benefit curves.

strength of the response to risk of predation. In clear water, the presence of a predator should cause a smaller proportion of the fathead minnows to feed within a dangerous habitat. In turbid water, a reduced response should be observed through a more equal distribution of foraging minnows.

The second experiment investigated the effect of water clarity on the predation mortality of fathead minnows and the occurrence of size-selective predation. The TAC hypothesis predicts that the predation mortality of the fathead minnows in turbid water should be significantly lower than their mortality in clear water because the prey benefit from a reduced distance to cover and reduced encounter rates with predators (Werner and Anholt, 1993).

In clear water, size-selective predation occurs by yellow perch on fathead minnows (Paszkowski and Tonn, 1994). The TAC hypothesis predicts that this size-selective predation should still occur in turbid water because the larger, faster prey will still be better able to avoid predation in turbid water. The TRE hypothesis predicts that size-selective predation should not occur in turbid water. In turbid water, the size of the fathead minnow should be less important because the effectiveness of anti-predator behaviors are reduced. Predator-prey encounters should become more random as the different sizes of prey do not benefit from reduced distance to cover and predators reduce their attack specificity (Crowl, 1989). Therefore, the TRE hypothesis predicts the predator's diet should be made up of a more even size distribution of prey in turbid water systems.

METHODS

Collection and Storage

Minnow traps were used to capture the fathead minnows while the yellow perch were collected using a beach seine. All fish were transported to the Winnipeg campus in aerated containers. The fathead minnows used in the first experiment were collected from May to August, 1993, at the University of Manitoba Field Station, Delta Marsh, Manitoba. One additional group of minnows was obtained from a local Winnipeg lake, east of Markham road, in September 1993. Two predatory yellow perch (Fork Length of predator 1A = 114, Fork Length of predator 1B = 121 mm) were collected from Lake Manitoba in May and June, 1993.

All fathead minnows used in Experiment 2 were collected from May to September 1994, at the University of Manitoba Field Station, Delta Marsh. Two yellow perch were collected from Lake Manitoba in May and June of 1993 (Wet weight / Fork length predator 2A = 73.40 g / 193 mm, predator 2B = 40.48 g / 157 mm).

The fathead minnows were held within the University of Manitoba Animal Holding Facilities in 200 L fibreglass flow-through tanks, at 12°C with a light regime of 12 L/ 12 D. The fathead minnows in these holding facilities were fed a mixture of frozen brine shrimp (*Artemia salina*) and commercial flake food. Prior to the experiment, fathead minnows were moved into the laboratory and placed in 30 L glass aquaria with 18°C water temperature, a 12 L/12 D photoperiod

and were fed brine shrimp exclusively. The predators were held in 80 L glass aquaria within the laboratory and were fed live fathead minnows and brook sticklebacks (*Culaea inconstans*) approximately once a week.

Experiment 1: The Effect of Turbidity on the Behavioral Response of Fathead Minnows to the Presence of a Piscivorous Yellow Perch.

Using the Ideal Free Distribution, IFD, (Fretwell and Lucas, 1970), it is possible to measure the relative effect of both water clarity and predation risk on the distribution of a prey species. The IFD predicts that if all individuals have perfect information and are equal competitors, they will all receive an equal share of the resource, independent of the distribution of that resource. If food enters the habitat at a constant rate, then the spatial distribution of the fathead minnows will match the spatial distribution of their food. Deviation away from the predicted distribution can be used to measure the influence of other variables, in this case predation risk (Abrahams and Dill, 1989, Tyler and Gilliam, 1995).

The dimensions of the test aquarium were 76 cm by 76 cm by 30 cm (L x W x H) with a constant water depth of 20 cm (Fig. 2.3). The aquarium was divided into two habitats by a mesh divider that allowed for the passage of minnows but restricted the predator to one half of the aquarium. Between trials the perch predator was separated from the fathead minnows by a clear Plexi-glass divider. An overhead camera was used to record the experimental trials. Two fluorescent lights, diffused by a sheet of white Plexi-glass, were placed
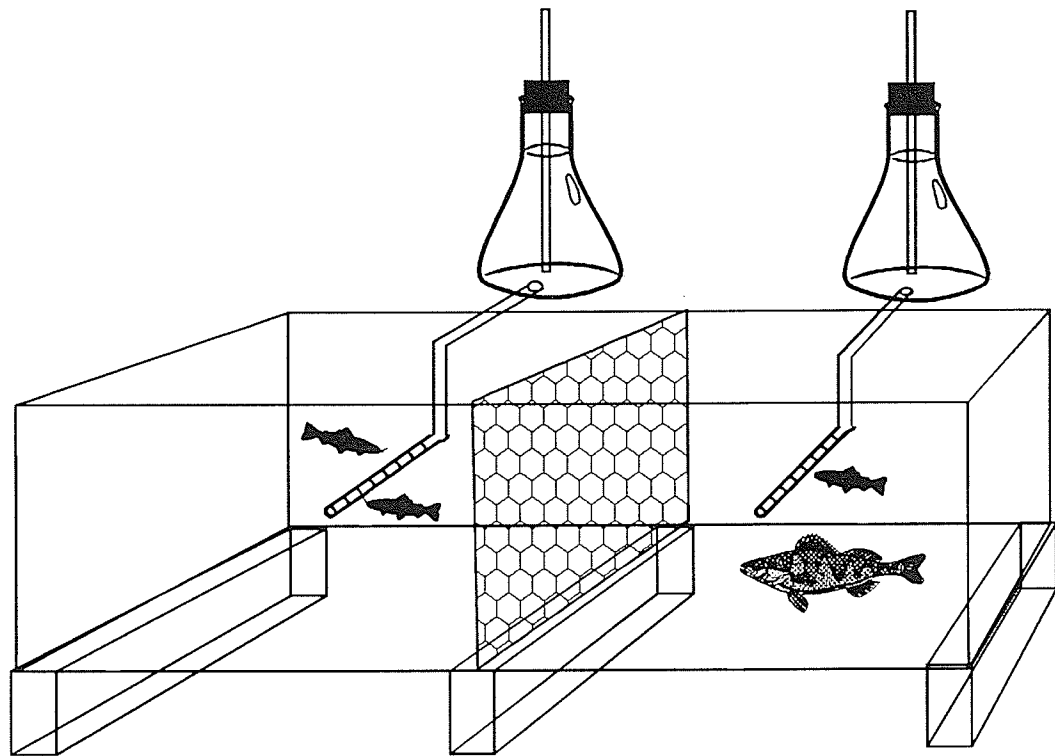
Fig. 2.3 Experiment 1 was conducted in a 170 L aquarium, divided into two habitats by a mesh partition. The partition restricted the predator to one half of the aquarium. Two identical automated feeders were used to deliver brine shrimp (*Artemia salina*) to each habitat. Two fluorescent lights were placed under the tank to allow for observation in turbid treatments. Observations were made using an overhead camera.

beneath the aquarium and used during both clear and turbid feeding trials. Since an overhead camera was used to record all observations, the fluorescent lights and white Plexi-glass increased the visibility of the fathead minnows in turbid conditions by providing a light colored background.

Due to the absence of aquarium gravel in this system, bacterial nitrogen cycling could not be maintained. To remove the metabolic nitrogenous by-products, four Hagen corner filters, containing an ammonia-absorbing Nitra-Zorb (TM) filter, were placed in the aquarium. Once every five days, 15 ml of Ammo-lock (TM) was also added to the water to detoxify ammonia. The entire volume of aquarium water was changed between turbid and clear water treatments.

Prior to the experiment, the fathead minnows were fed 0.5 g of frozen brine shrimp by automated feeders (see Abrahams, 1989 for details) in three different proportions (Left side of aquarium : Right side of aquarium = 2:1, 1:1, 1:2) in the two aquarium habitats. For two days, the fathead minnows were fed a specific proportion of food three times a day (at 900, 1200 and 1500 hours) for a total of six feeding trials per food distribution. The duration of each feeding trial was twenty minutes and during that time, the number of fathead minnows foraging at each feeder was counted every thirty seconds. Fathead minnows were considered to be actively foraging when they swam near or under the feeder bar during the two seconds prior to and after the thirty second mark. The average values from the six feeding trials were used to describe the spatial distribution of fish for each food distribution.

Two water conditions were tested, clear (< 1 Nephelometric Turbidity Unit, NTU) and turbid (Mean = 13.21 +/- 0.95 NTU). These turbidity levels were selected because they were the highest levels of turbidity that did not significantly impede observation of the fish. Turbidity was produced by adding bentonite to the aquarium water. The Hagen corner filters functioned to keep the bentonite suspended. At the beginning of the turbid water trials, approximately 4.5 g of bentonite was added to 1.8 L of aquarium water. This concentrated solution was mixed and then poured into the aquarium. Overnight, the filters removed some of the suspended sediment. So, every morning another I added concentrated solution, produced by adding approximately 2 g of bentonite to 1.8 L of aquarium water. Before every experimental trial, a water sample was taken and the turbidity of that sample was measured for each feeding trial. Turbidity was measured using a Hach model 2100A turbidimeter.

The experiment used a two-factor design where water clarity (clear and turbid) and the presence or absence of a predator were manipulated experimentally. First, water clarity was randomized. In order to minimize disturbance of the fish, all predator treatments (predator on the right side, no predator, and predator on the left side) were randomized and completed in one clarity level before proceeding with the second. The fathead minnows were exposed to each predator treatment during the feeding trials, three times a day (at 900, 1200 and 1500 hrs) for two days.

Six groups of sixteen similarly sized fathead minnows (mean fork length = 48.49 +/- 0.84 mm, mean weight = 1.1917 +/- 0.0628 g) were used in the experiment. Equal amounts of brine shrimp (0.5 g per feeding trial) were delivered to each habitat by automated feeders three times a day (at 900, 1200 and 1500 hours) (see Abrahams, 1989 for details).

During each feeding trial, the positions of the actively feeding fathead minnows were recorded every thirty seconds for twenty minutes. Fathead minnows were considered to be actively feeding if they had swam near or under the feeder bar within 2 seconds immediately before or after the thirty second mark. The average values from the six feeding trials were used to describe the spatial distribution of fish.

After each group of fathead minnows completed all experimental treatments, the minnows were anesthetized using 2-phenoxyethanol (1 ml diluted in 1800 ml of water) . The fork length and wet weight of each individual was then measured (Table 2.1).

The expected distribution for each group was determined by the proportion of fathead minnows feeding in either habitat during the control treatment (predator absent) in both clear and turbid water. Deviations away from the expected distribution were calculated by subtracting the proportion of fish in each habitat in the presence of a predator from the proportion of fathead minnows feeding in each habitat during the control. This calculation controlled for any side biases.

Table 2.1 The mean fork length and wet weight of each group of fathead minnows used in the predator treatments.

	Fork Length (mm)		Wet Weight (g)	
Group	Mean	Std. Error	Mean	Std. Error
1	42.47	6.57	0.79	0.39
2	53.12	4.86	1.36	0.33
3	50.60	6.35	1.40	0.60
5	49.32	3.55	1.17	0.27
6	47.23	5.48	1.12	0.35

Data Analysis

All proportional data were arcsine squareroot transformed prior to the statistical analysis to ensure homogeneity of variance. T-tests were used to determine if the presence of the predator affected the distribution of the foraging fathead minnows. These t-tests compared the proportion of fathead minnows feeding in the control and predator treatments in both clear and turbid water.

Experiment 2: The Effect of Turbidity on the Predation Mortality of Fathead Minnows by Predatory Yellow Perch

Three days before an experimental trial, thirty-two fathead minnows were moved into an aquarium, identical to the experimental tanks (76 X 30 X 30 cm,L,W,H), within the laboratory. For two days prior to the experiment, the fathead minnows were fed only brine shrimp through automated feeders (see Abrahams, 1989 for details).

Two water conditions were tested in this experiment, clear (<1 Nephelometric Turbidity Unit, NTU) and turbid (Mean = 11.01 +/- 0.34 (SE) NTU). The turbidity levels in this experiment were selected to match approximately the levels in the first experiment. Turbidity was produced by adding approximately 8.0 grams of bentonite to 1.8 liters of water. This mixture was stirred and then added to the turbid water experimental tank on the first morning of the experiment. Turbidity was measured using a Hach model 2100A turbidimeter (TM). Each test aquarium was equipped with Hagen (TM) corner

filters in order to keep the water well circulated. Pebbles (approximately 1 cm in diameter) were used as the substratum on the aquarium bottom to minimize the amount of bentonite filtered from the water. However, some siltation did occur and, as a result, a bentonite/water mixture was added to the aquarium every morning. This bentonite/water mixture was produced by adding 0.4 g of bentonite to 1.8 liters of water.

Two habitats existed within both tanks: a large dangerous habitat (yellow perch predator present) (56 X 30 X 30 cm L,W,H) and a small predator-free area (20 X 30 X 30 cm L,W,H). A mesh partition, which allowed for the free movement of fathead minnows but restricted the predator, was used to create the two habitats (Fig. 2.4). During the entire experiment, one tank was the turbid water tank and the other always remained clear. For each experimental group of fathead minnows, the predators were placed randomly within either the clear or turbid tank and were considered to be an experimentally manipulated variable. Each predator was used in five turbid and five clear water treatments.

On the afternoon preceding the experiment, the thirty-two fathead minnows were anesthetized using a diluted concentration of 2-phenoxyethanol (1 ml in 1800 ml of distilled water). The fork length and wet weight of the fathead minnows was then measured, and the minnows were separated randomly into two groups. On the following morning, one group was placed within the clear water tank and the other in the turbid water tank. For three days, the fathead minnows were kept within the experimental tanks and were fed 0.5 g of
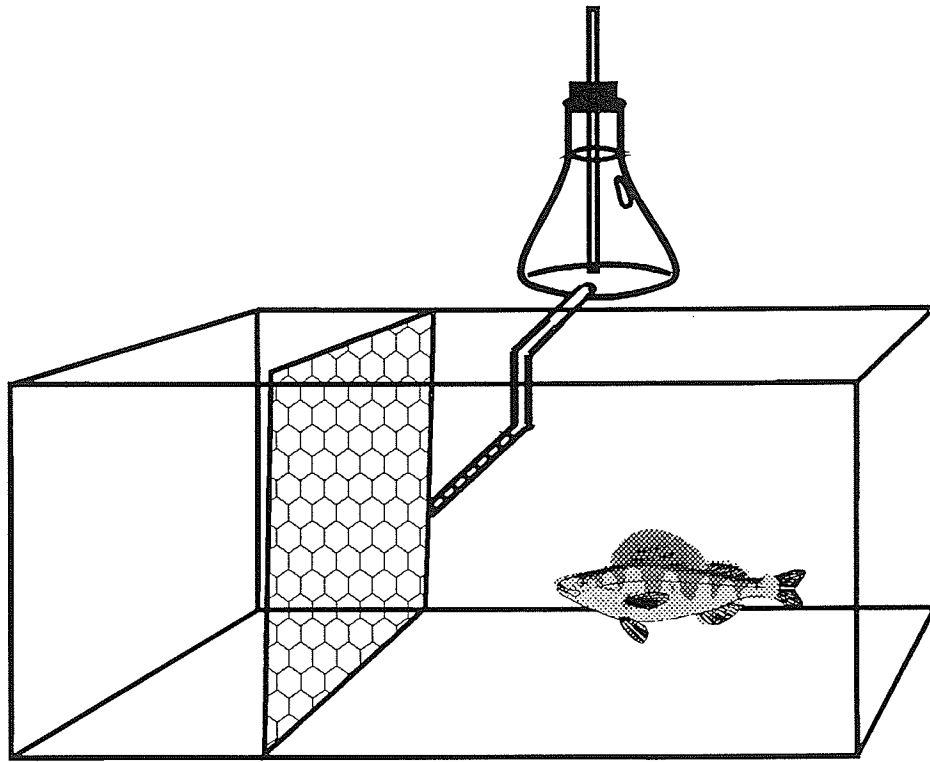
Fig. 2.4 Experiment 2 was conducted in two 80 L aquaria. Two habitats in each tank were created using a mesh divider which restricted the predator to the larger proportion of the aquarium. Food was delivered to the fathead minnows by an automated feeder and a food delivery bar (placed approximately 5 cm into the dangerous habitat). One aquarium was used for the clear water trials (< 1 NTU) while the second was used for the turbid treatments (11.01 NTU, SE = 0.34).

frozen brine shrimp by automated feeders, three times a day (900, 1200 and 1500 hours). Prior to each feeding trial, a water sample was taken from the tanks and the current turbidity level was measured. The turbidity values for each feeding trial were averaged to estimate the turbidity level for the whole group. After three days, the remaining fathead minnows were removed and their wet weight and fork length were measured. Ten groups of thirty-two fathead minnows were used in the experiment. Groups of fathead minnows were considered independent observations for statistical analysis.

Data Analysis

All of the mortality data were standardized to control for the different levels of feeding by the two yellow perch predators. The number of fathead minnows each perch consumed within a single group was divided by the total number of fathead minnows that the predator consumed in all ten groups (five clear and five turbid water treatments per predator). Thus, in analysis, the proportion of fathead minnows consumed per group was used to determine if there were differences in mortality rate as a result of the water clarity. All proportional data were arcsine squareroot transformed prior to analysis. A t-test was used to determine if there were any significant differences in the mean mortality of fathead minnows between the clear and turbid treatments.

To determine if size-selective predation occurred in the clear or turbid water, the fathead minnows were grouped into twelve size classes based on

their length (< 40mm, 40.00 to 41.99mm, 42.00 to 43.99 mm, ..., 58.00 to 59.99 mm and > 60 mm). A frequency distribution of the size classes was determined in both clear and turbid water, prior to and after the experiment. Ivlev's electivity index (Krebs, 1989) was used to determine if size-selective predation by the perch could be detected. Ivlev's electivity index is:

$$E_i = (r_i - n_i)/(r_i + n_i) \qquad (2.1)$$

where r_i is the percentage of size class i in the diet and n_i is the percentage of size class i in the environment. Ivlev's electivity index ranges from the values -1 (highly avoided) to + 1 (highly preferred).

To test statistically for the presence of size-selective predation, t-tests were used to compare the mean fork length of the fathead minnows, in both clear and turbid water, prior to and after the trials.

Although the turbidity levels did not vary greatly between groups of fathead minnows, a regression analysis was performed to determine if the small changes in the mean turbidity values per group had any affect on the group mortality of the fathead minnows. The mortality rates used in the regression were those produced by converting actual mortality to proportion of total mortality.

RESULTS

Experiment 1

The relative abundance of food within two habitats had a significant effect on the distribution of the foraging fathead minnows (Fig. 2.5). Since each food

distribution was delivered for two days, only the second day's distribution of fathead minnows was used in the analysis. This was done because the distribution on the first day could have been affected by prior information (i.e. the previous day's food distribution). The distribution of brine shrimp during the feeding trial had a significant effect on the distribution of the foraging fathead minnows (slope = 0.539, t-test to determine if the slope is significantly different from zero produced a t = 3.193 and a p value of 0.0057). The fathead minnows were sensitive to changes in relative resource abundance and attempted to match the distribution of their food resource. These results are consistent with predictions made by the IFD and optimal habitat choice models.

One group of fathead minnows (group 4) was excluded from predation risk / water clarity analysis because the predator (Perch 1A) became inactive. By remaining inactive and not stalking the prey, the perch no longer imposed any risk of predation on the fathead minnows. A new predator (Perch 1B) was used for the remainder of the experiment.

In clear water, the presence of the predator caused a significant reduction in the proportion of fathead minnows feeding within the dangerous habitat (one-tailed t-test, t_4 = 3.17, p = 0.004) (Fig. 2.6). This effect was not observed in turbid water (one-tailed t- test, t_4= 1.24, p = 0.14). One tailed t-tests were used because the hypothesis predicted that the effect of the predator would be less in turbid water than in clear, not that the effect would be different.
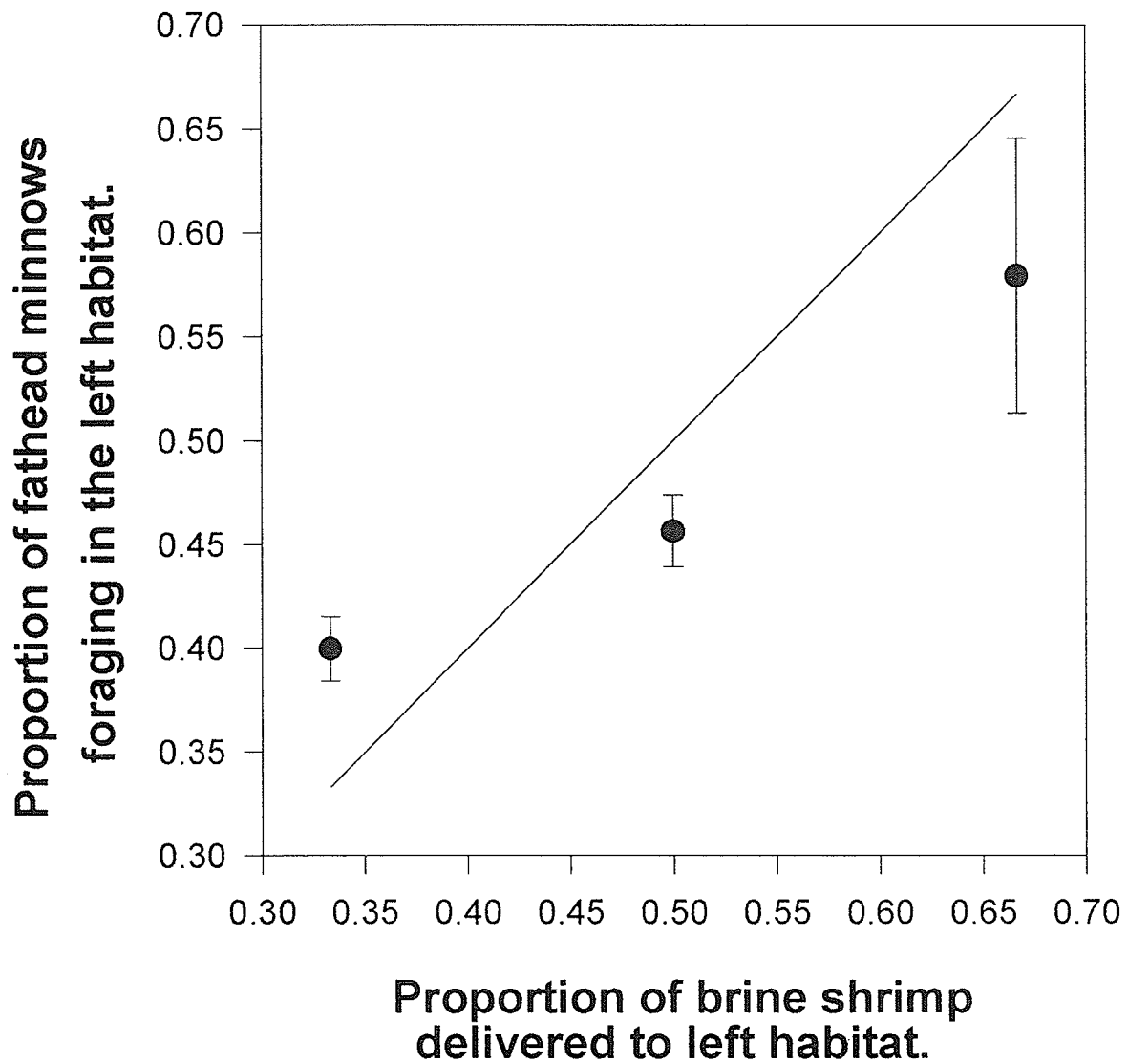
Fig. 2.5 The effect of food distribution on the habitat choice of fathead minnows. The straight line is the expected distribution if the distribution of fish matched exactly the distribution of the food. Error bars represent 1 standard error, n = 6.
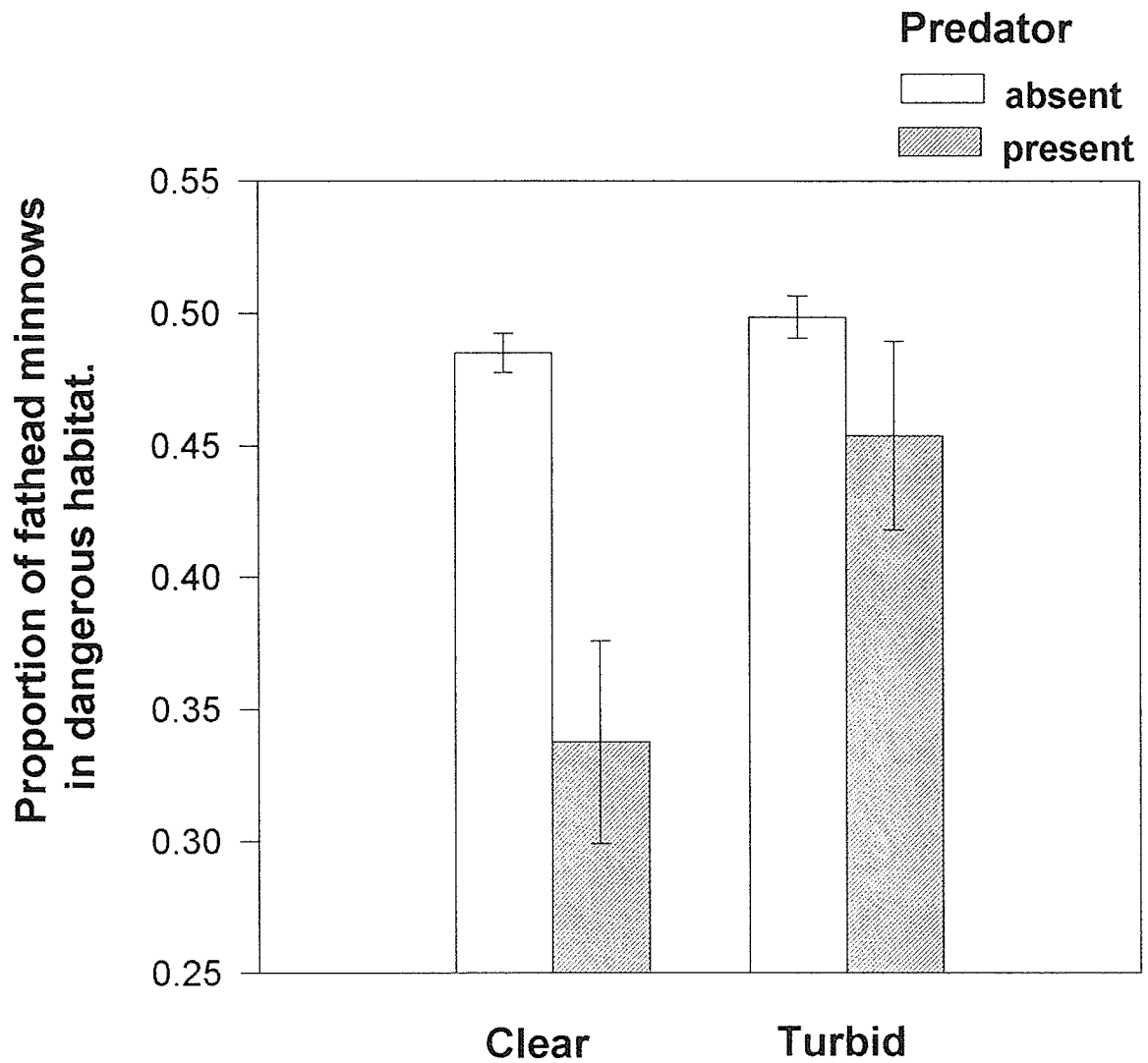
Fig. 2.6 Mean proportion of fathead minnows feeding in the dangerous habitat
for each experimental treatment (clear, predator ; clear, no predator ;
turbid, predator ; turbid, no predator). Error bars represent 1 standard
error, n = 5.

To compare the strength of the response to the predator in both clear and turbid water, I used the size of the deviations away from the expected distribution of fathead minnows. These deviations were calculated by subtracting the distribution of the fathead minnows in the presence of the predator from the control distribution (predator absent), and thus, could be positive or negative deviations. The presence of the predator in clear water caused a significantly larger deviation away from the expected distribution than its presence in turbid water (Fig. 2.7) (one-tailed t-test, t_4 = 2.41, p = 0.037). The fathead minnows showed a significantly reduced response to the presence of the predator in turbid water.

The size of the fathead minnows had no effect on their response to the presence of the predator in clear water. Linear regression using either fork length or wet weight to predict the deviation away from the expected distribution in the clear-predator treatments showed that neither variable had any measurable effect ($F_{1,3}$ = 0.16 , p = 0.716 , r^2 = 0.05062 and $F_{1,3}$ = 0.01, p = 0.921 , r^2 = 0.00378, respectively). In turbid water, neither fork length nor wet weight had any significant effect on the deviation away from the expected caused by the presence of the predator ($F_{1,3}$ = , p 0.141 = 0.732, r^2= 0.04493 and $F_{1,3}$ = 0.007 , p = 0.939 , and r square = 0.00231, respectively).
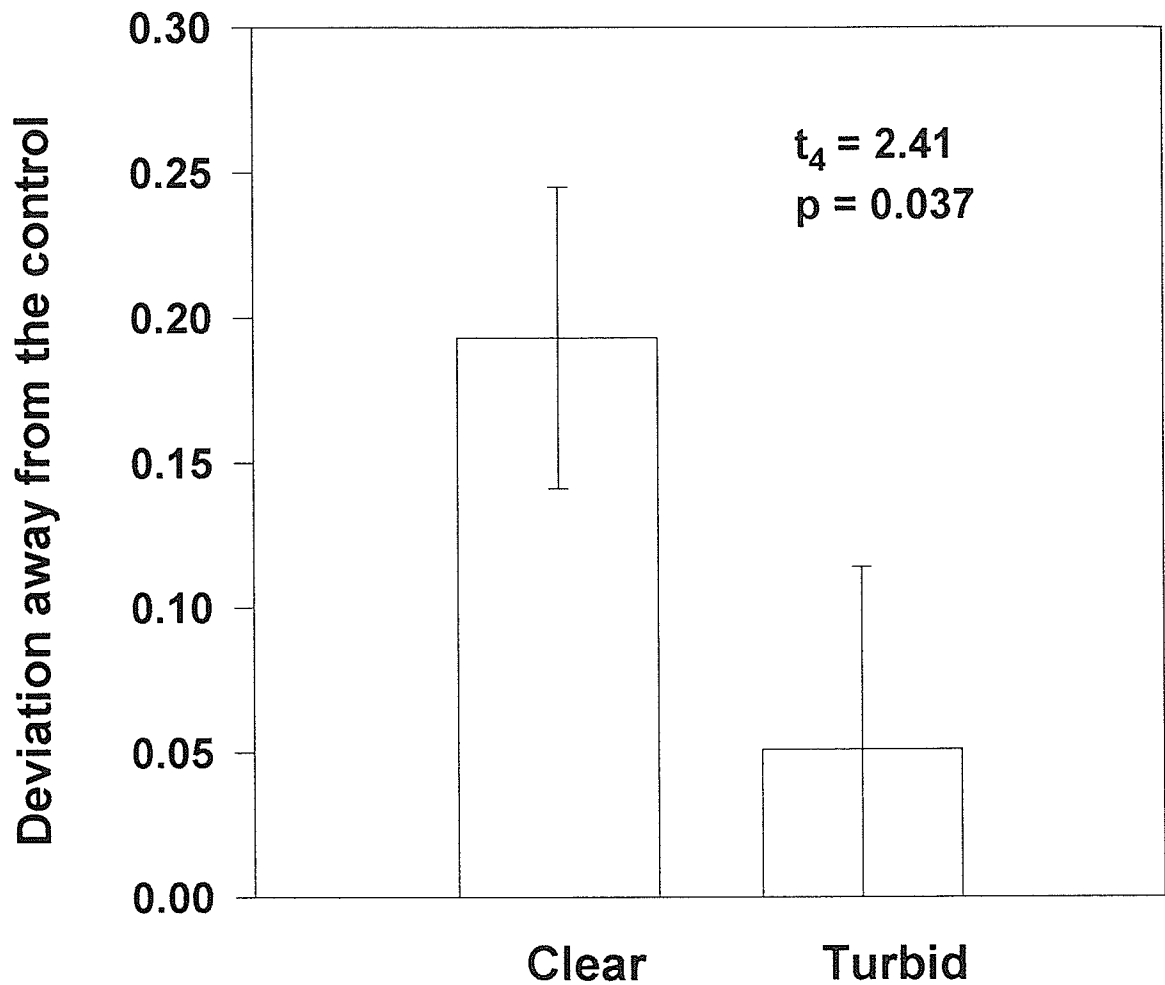
Fig. 2.7 The effect of water clarity on the habitat use of foraging fathead
minnows. Deviation away from the control is the difference between the
distribution of fathead minnows in the presence of the predator and their
distribution in the absence of the predator. Positive deviations indicate
avoidance, while a negative deviation would indicate preference. Error
bars represent 1 standard error, n = 5.

Experiment 2

Water clarity did not have a significant effect on the proportion of fathead minnows consumed (two-tailed t-test, t_{18} = 0.787 , p = 0.442)(Fig. 2.8). In the clear water treatments, the yellow perch predators consumed an average proportion of 0.102 (SE = 0.003, n = 10) fathead minnows per three days of exposure to the predator, while in the turbid water a proportion of 0.098 (SE = 0.006) fathead minnows per three days of exposure to the predator were consumed. The regression of proportional mortality per group and varying turbidity levels was not significant (p = 0.668). Small changes in the mean turbidity per group had no effect on the mortality of the fathead minnows within the turbid tank.

In clear water, the perch predators tended to feed upon the smaller fathead minnows (Fig. 2.9). The Ivlev's electivity index suggests that fathead minnows less than 50 mm in length are most at risk to predation by the yellow perch. In turbid water, the data do not indicate any pattern of preference. The Ivlev's electivity index values are much closer to zero (no preference or avoidance) and no patterns are readily discernible. Therefore, it appears that size-selective predation occurs in clear water, but not in turbid water. However, in two size classes (58.00-59.99mm in clear water and 48.00-49.99 mm in turbid water) more fathead minnows were present after the trial than before indicating that some of the fathead minnows had grown during the experiment. This growth is highly unlikely because the experiment only lasted for three days, and
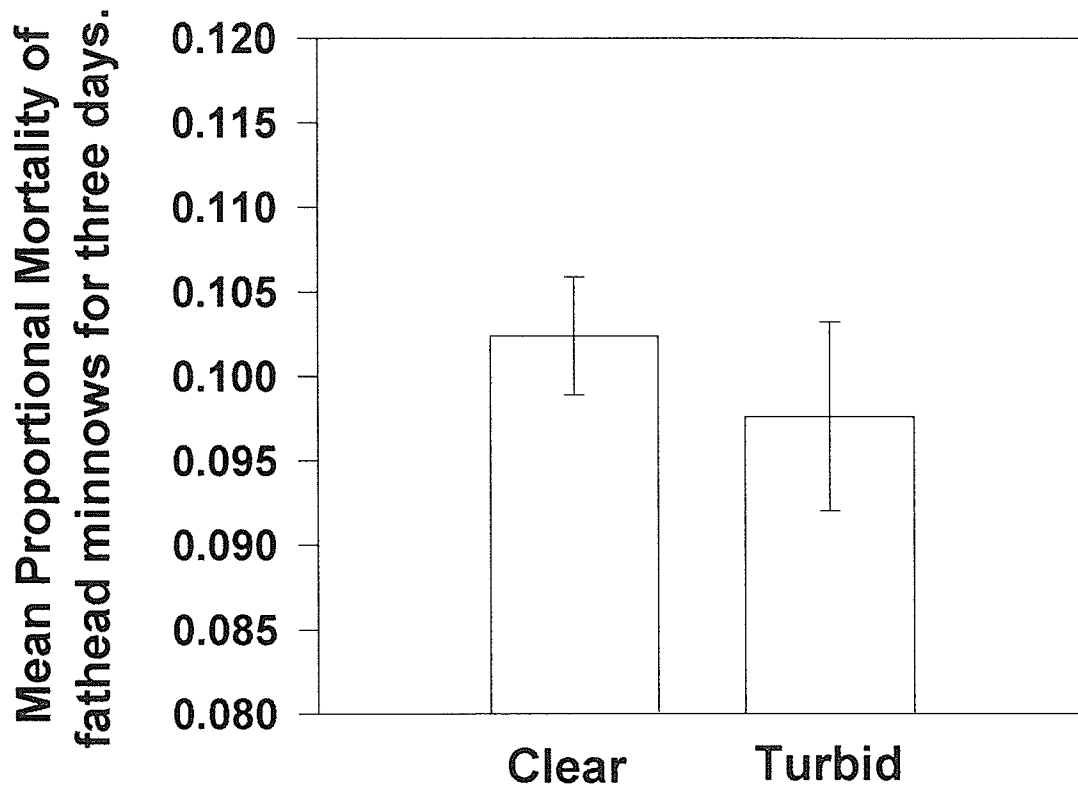
Fig. 2.8 The mean mortality rate of fathead minnows predated by piscivorous perch for three days. The mean proportional mortality for three days is calculated by dividing the number of fathead minnows consumed in a group by the total number of fathead minnows consumed by a predator. This controlled for different levels of feeding between the two predators, as it standardized which proportion of the fathead minnows the predators consumed came from a particular group and treatment. Error bars represent 1 standard error, n =10.
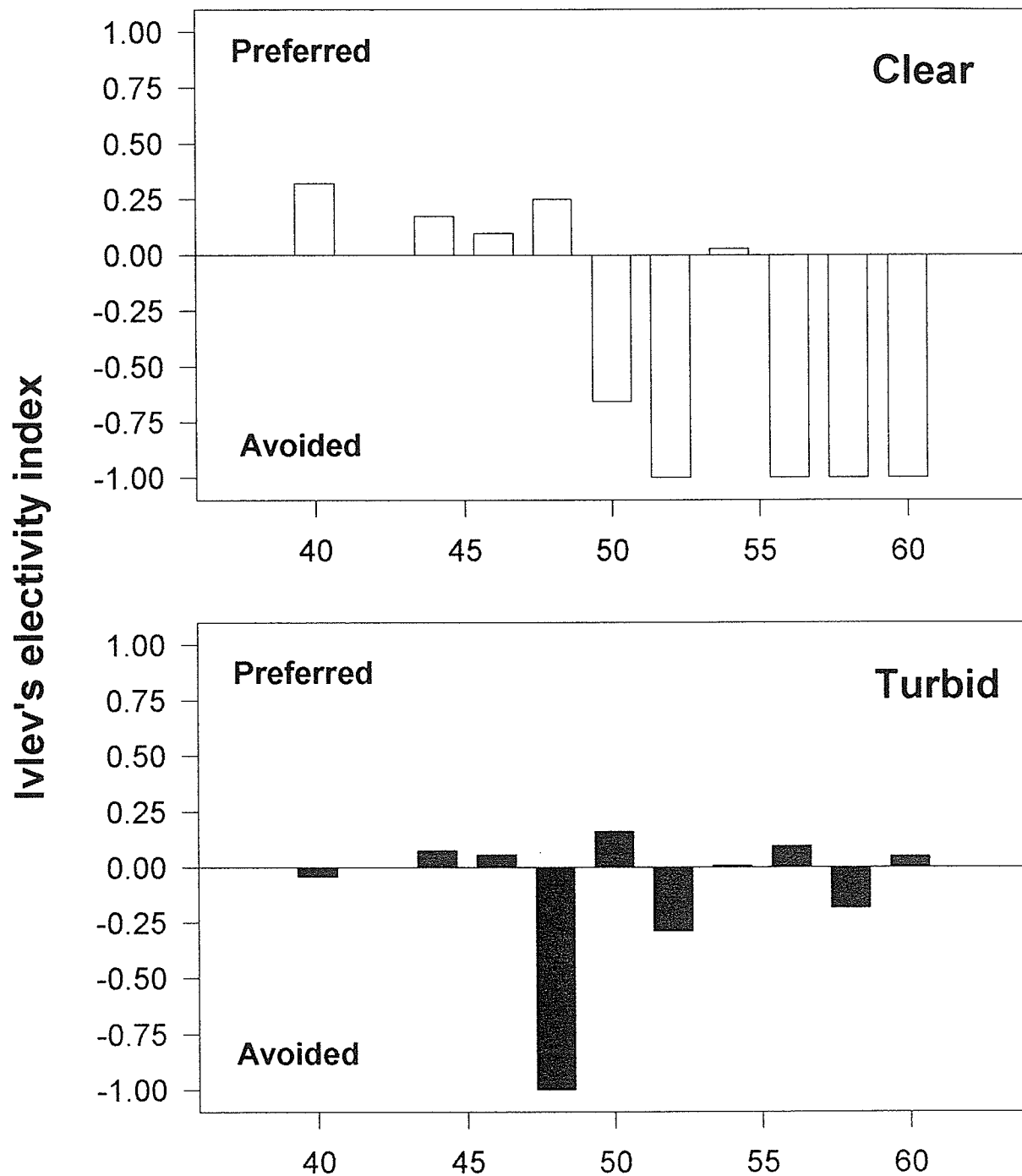
Fig. 2.9 Ivlev's electivity index values for the various size classes of fathead minnows. Ivelv's electivity index indicates which sizes of prey are preferentially consumed or avoided. Positive values indicate a preference for a particular size class, while negative values indicate avoidance. Ivlev's electivity index ranges between +1 and -1. The frequency distribution was calculated using 320 fathead minnows.

it is probably a result of measurement error. Although this could affect the size preference analysis, it is likely that the small changes in length were not significant enough to bias the results since only three fathead minnows out of three hundred twenty showed this apparent increase in size.

Changes in size-selective predation should also be evident by changes in the mean group size of the fathead minnows before and after the experiment (Fig. 2.10). Prior to the experiment, the mean group fork length of the fathead minnows in the clear water (49.87 mm, SE = 0.37, n = 160) and turbid water (50.37 mm, SE = 0.52, n = 160) treatments did not vary significantly (two-tailed t-test, t_{18}= -0.791 , p = 0.439). After the experiment, the mean fork length of the remaining fathead minnows from clear (51.58 mm, SE = 0.39) and turbid (50.49 mm, SE 0.34) water did vary significantly (two-tailed t-test, t_{18} = 2.12, p = 0.048). This shift in mean size indicates that in clear water, smaller fathead minnows were selectively preyed upon. In turbid water, this preference did not exist.

DISCUSSION

In Experiment 1, a larger proportion of the fathead minnows remained within a refuge to avoid the predator in clear water. The fathead minnows responded to the level of predation risk by altering their habitat use. In turbid water, the deviations away from the distribution expected by the IFD were less than in clear water, indicating that the behaviourally mediated indirect effects of
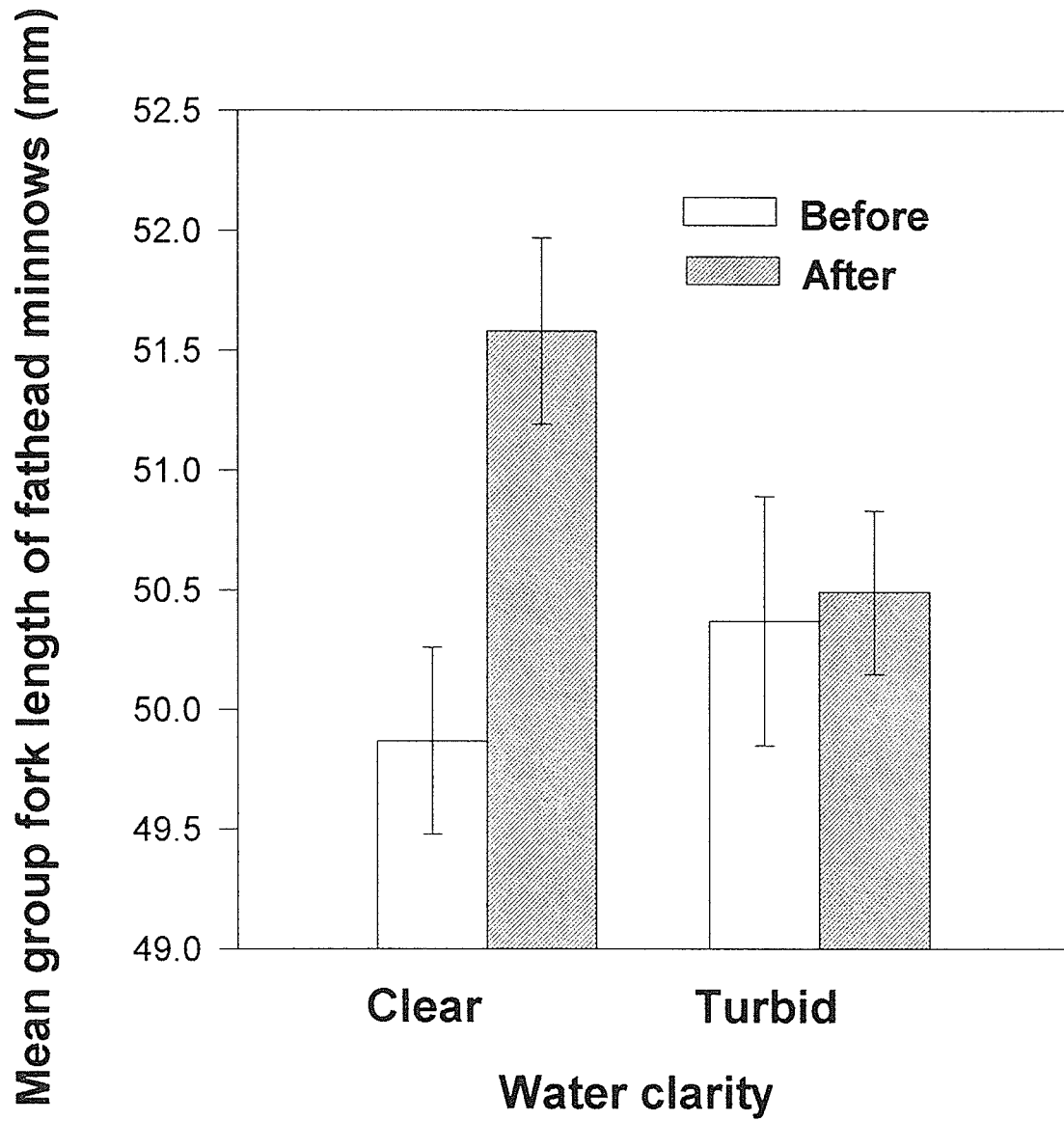
Fig. 2.10 The effect of water clarity on the mean size of fathead minnows before and after the treatments. Significant differences indicate that certain sizes of prey are preferentially consumed. Error bars represent 1 standard error, n = 10.

predation had been reduced. The results support the hypothesis that predation risk has a reduced effect on prey behavior in turbid water habitats.

Gradall and Swenson (1982) investigated the effect of turbidity on brook trout, *Salvelinus fontinalis*, and creek chub, *Semotilus atromaculatus*, activity levels. In moderately turbid water (mean 7.1 Formazin Turbidity Units, FTU; 1 FTU approximately = 1 NTU) activity levels increased. In clear water (2.3 FTU), creek chubs and brook trout used overhead cover and spent much of their time in association with the bottom, a typical anti-predator responses. The creek chubs and brook trout decreased their use of overhead cover, increased activity, and reduced their association with the substratum in turbid water. Gradall and Swenson (1982) believed that this increased activity and reduced use of cover occurred because turbidity functioned to isolate individuals from one another. However, these data are consistent with the results of this experiment and support the hypothesis that prey reduce their use of anti-predator behavior in turbid water.

Gregory and Northcote (1993) also examined the effect of turbidity on the foraging rate of juvenile chinook salmon. In turbid waters, juvenile chinook salmon had increased foraging rates for benthic, planktonic, and surface prey. In clear water, the juvenile salmon tend to remain stationary and in deeper water to avoid predation (Gregory, 1993). However, in turbid water, the distribution of the juvenile chinook is more even throughout the water column, indicating that the clear water response to avoid predation is not used in turbid water. As in

Experiment 1, the planktivorous fish reduced their use of anti-predator behavior, which resulted in an increase in activity level and foraging rate.

Boehlert and Morgan (1985) found that turbidity (500 mg · L $^{-1}$ to 1000 mg· L $^{-1}$ of estuarine suspended sediment and volcanic ash) enhanced the foraging rate of larval pacific herring (*Clupea harengus pallasi*). They proposed that increased visual contrast of the prey or increased scattering of light, illuminating the prey from all directions, were responsible for the increase in feeding. However, their results are consistent with the hypothesis that prey show a reduced response to predators in turbid water. Turbidity may reduce the amount of time the larval herring performed anti-predator behaviour and, as a result, increased the amount of time available for other activities, such as feeding.

By reducing the response of planktivorous fish to piscivorous fish predators, turbidity may increase foraging rates, primarily through an increase in activity. At high levels of turbidity (> 150 NTU), the suspended sediment impairs vision significantly and leads to reductions in feeding rate (Gregory and Northcote, 1993).

In Experiment 1, the reduced response of fathead minnows to the presence of a predator in turbid water was not simply a result of them not detecting the predator. The dimensions of the experimental tank were 76 X 76 X 30 cm and a mesh divider divided the aquarium into two habitats. The predator was kept within the tank during the predator treatments, even between feeding

trials, to minimize disturbance in the tank and stress on the predator. To keep the predator away from the fathead minnows between feeding trials, a clear Plexiglass sheet was placed within the tank, in the dangerous half of the tank. This allowed the fathead minnows to investigate both habitats without risking consumption between the feeding trials. I observed numerous encounters between predator and prey during the feeding trials as the predator would often hunt in the area near the feeder bar where the minnows were actively foraging. Many chases occurred, both in clear and in turbid water. Therefore, the fathead minnows were able to detect the presence of the predator, but they did not respond to its presence as strongly in turbid water as they did in clear water.

Fathead minnows and other species belonging to the Superorder Ostariophysi are able to detect predators through both vision and olfaction (Chivers and Smith, 1994; Mathis and Smith, 1993a). Through an alarm pheromone (Schreckstoff) released from epidermal cells when the skin of fathead minnows is mechanically damaged (e.g., while being consumed), the fathead minnows are able to identify areas of increased predation risk and label dangerous predators (Mathis and Smith, 1993b). The predator was fed approximately one fathead minnow per week within its own holding tank. The alarm substance released by the fish functioned to label the perch as a predator. In addition, an average of 1.1 (SE = 0.33) fathead minnows were consumed by the predator per group of experimental fathead minnows. This consumption further labeled the predator and increased the ability of the fathead minnows to

identify the risky habitat. Therefore, the reduced response of the fathead minnows was not simply a result of them not detecting the predator, but rather because turbidity either provides cover for the prey to escape, or reduces the effectiveness of anti-predator behavior.

Water clarity had no significant effect on the total mortality of fathead minnows. In turbid water, the predators consumed the same proportion of fathead minnows as they did in clear water. Similar results were found by Vandenbyllaardt et al. (1991) where small juvenile walleye (less than 75 mm fork length) consumed the same prey weight of fathead minnows in turbid water, up to 100 NTU, as they did in clear water. These walleye had not yet developed a tapetum lucidum which enhances vision at low light levels and in turbid water (Vandenbyllaardt et al., 1991). Therefore, visually dependent piscivorous predators, which do not have any special detection adaptations, can consume the same quantity of prey in both clear and turbid water. These data do not support the TAC hypothesis because the prey did not benefit from a reduced distance to cover in turbid water. The TRE hypothesis does not make any predictions about the predation mortality in both clear and turbid water, as mortality rates will be primarily determined by the predator and prey species involved and their life history characteristics.

The size of the experimental apparatus may have contributed to the results I obtained. Since the tank volume was only 80 L, the encounter rate between predator and prey was high. In a natural habitat, it is likely that the

encounter rates would be significantly lower and thus the mortality may be decreased as well. Even though the encounter rate within the aquaria was artificially high, this would have served to exaggerate any escape benefits obtained by the prey and would have biased the results in favour of the TAC. Since the results suggest that turbidity does not provide the prey with cover into which they can escape, the TAC hypothesis is rejected on the basis of these data.

Abrahams (in prep.) found that fathead minnows employ rapid swimming speed and erratic direction changes to avoid consumption by a predator. However, the maximum velocity attainable by fathead minnows is positively correlated with body size. Fathead minnows attain maximal velocity in an average of 0.22 seconds (Abrahams, in prep.), and larger minnows have a higher acceleration, and are better able to avoid predation. In clear water, Paszkowski and Tonn (1994) found that yellow perch predators (> 190 mm total length) consumed significantly more small than large fathead minnows in mixed size populations of minnows. It is possible that when compared with the smaller minnows (< 50 mm fork length), the larger individuals were better at escaping predation and thus required a higher energetic cost to capture. Therefore, the yellow perch consumed greater proportions of smaller fathead minnows.

In clear water, the yellow perch predators consumed greater numbers of small fathead minnows, a result that was not observed in turbid water. In turbid water, a more random size distribution of consumed individuals was found

suggesting that the prey did not detect an attack until close range. The TAC hypothesis predicts that turbidity provides cover for prey to escape predation. As turbidity increases, detection radii decrease and, therefore, the distance to cover would decrease as well. Since larger fathead minnows swim faster, they should be able to cover this distance much more quickly than smaller individuals and be better able to avoid predation. A greater proportion of the large fathead minnows were preyed upon in turbid water, indicating that the TAC hypothesis does not explain the interaction between predator and prey in turbid water systems.

The TRE hypothesis predicts that size-selective predation should not occur in turbid water systems, if all individuals in the population are susceptible to predation. The size of the prey should not alter the effectiveness of anti-predator behaviors, such as refuge use and vigilance. Therefore, a more random distribution should exist in the size of prey consumed by predators in turbid water systems. However, size-selective predation could still occur if size refuges to predation exist. In this case, the selective predation is not a result of the escape abilities of the prey or preferences by the predator, but rather the physical size of the prey.

From my results, the TAC hypothesis does not explain the preference of juvenile marine fish for turbid water habitats. Blaber and Blaber (1980) found that juvenile fish distributions were positively correlated with turbidity in Indo-Pacific estuaries. They attributed this correlation to the TAC hypothesis and

believed that turbidity reduced predation pressure. However, these turbid water zones were also shallow and only a few large fish predators, which prefer deeper water, were caught in these areas (Blaber and Blaber, 1980). Therefore, the turbid water areas may be relatively free of predation pressure due to the absence of large predators, such as sharks, carangids and sciaenids, not because turbidity provides cover for prey to escape.

In the Indo-Pacific estuaries, few avian predators were observed feeding in the turbid water habitats, while numerous birds fed in clear water areas (Blaber and Blaber, 1980). Avian predation may also be reduced in turbid water areas because of a decrease in the ability to detect fish prey. The dark background of the deeper water and substratum may make it increasingly difficult for prey to be detected and caught. Further, the avian predators may be easier for the prey to detect because of the light background. Gregory (1993) found that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) showed a greater anti-predator response to the presence of an avian predator model than a fish predator model in turbid water indicating that the bird predator may be more easily detected.

Swenson (1978) found a positive correlation between high turbidities and zooplankton densities in surface waters (in Blaber and Blaber, 1980). Although Blaber and Blaber (1980) did not measure zooplankton densities, they believed that the increased availability of food for the juvenile fish was important. It is not surprising that these turbid habitats are the preferred foraging habitats of the

juvenile fish, not because turbidity provides cover for prey to escape, but rather because these areas have few predators and high food densities.

The TRE hypothesis predicts that prey have a reduced response to the presence of predators because the effectiveness, and thus the benefits, of anti-predator behavior decrease in turbid water. Although the TRE hypothesis does not make any predictions about the mortality levels in clear or turbid water, as they will be a result of the predator and prey species and their life history characteristics, it does predict that size-selective predation should not occur in turbid water systems (as long as no size refuge to predation exists). Larger prey should not benefit over smaller individuals because of the close distances involved in the predator/prey encounter.

Turbidity reduces the effectiveness of anti-predator behavior because of the close distances involved in the predator-prey encounter. As a result, prey decrease their use of anti-predator behavior in turbid water. This can lead to an increase in activity levels and foraging rates. By reducing the response of prey to the presence of predators, turbidity reduces the behaviorally mediated indirect effects of predation. Because the behaviorally mediated indirect effects of predation can affect population dynamics (Fraser and Gilliam, 1992; Tonn et al., 1992) and community structure (Dill, 1987; Johannes, 1993; Marti et al., 1993), a reduction in these indirect effects should have far reaching consequences. In turbid water habitats, predators should primarily affect prey populations through direct consumption, the indirect effects that arise through consumption and the

indirect effects that arise through physiological or morphological modification by the prey; not by prey's use of anti-predator behavior. The presence of a predator in the habitat should no longer cause prey to extensively use refugia or initiate other anti-predator strategies. Therefore, in clear habitats we would expect prey to behaviorally respond to the presence of the predator and should observe the use of behavioral anti-predator strategies to avoid predation. In turbid water, there should be a marked decrease in the use of anti-predator behavior and the predator should exert primarily consumptive effects or indirect effects that arise through long term modification by the prey.

He and Kitchell (1990) found that the behaviourally mediated indirect effects of predation were largest in a whole lake experiment immediately after the introduction of pike predators into the system. In late May and June, many prey fish emigrated out of the lake. During this time, the biomass change due to emigration (indirect behavioral response to predation risk) was larger than the biomass change as a result of consumption by the pike (direct consumptive response to predation). He and Kitchell (1990) believed that the introduction of the pike caused a significant short-term behavioral response to the presence of the predator and that the indirect effects of predation decrease when the total fish biomass in the lake is low, as it was in July and August. However, during May and June, water clarity was at its highest at an average of 0.7 m secchi depth. At this clarity level, the fish may have been able to detect the predators at a distance where behavioral avoidance (emigration) was effective. Later in

the summer, during July and August, the direct effects of predation (consumption) were larger than the behavioral mediated indirect effects (emigration). In July and August, the secchi depths ranged between 0.4 m and 0.2 m indicating that the lake was markedly more turbid than in the spring. In the more turbid water, there may have been a reduced anti-predator response to the presence of the predator and, thus, predation risk. Therefore, He and Kitchell's (1990) whole lake experiment produced results which are also consistent with my hypotheses, that in turbid water systems, the direct effects of predation are significantly more important than the indirect effects which result from behavioral decisions by the prey.

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Chapter 3
The Effect of Predation Risk,
Food Resource Abundance,
and Turbidity on the Natural Distribution
of Fathead Minnows

INTRODUCTION

Animals should select habitats which provide the greatest net rate of energy intake (Hugie and Dill, 1994; MacArthur and Pianka, 1966; Pyke et al., 1977). When these areas are also the most dangerous, prey must make decisions that balance the conflicting demands of access to food and access to safety (Cerri and Fraser, 1983; Gilliam and Fraser, 1987; Lima and Dill, 1990). By selecting or avoiding specific habitats, animals can balance both their energetic intake, as well as their risk of being killed by predators (Lima and Dill, 1990).

In laboratory experiments, the distribution of foraging fathead minnows (*Pimephales promelas*) was affected strongly by the distribution of food (Chapter 2). When a predator was present, the distribution of fathead minnows changed in response to predation risk. The presence of the predator caused the fathead minnows to employ anti-predator behavior and shift habitats; a larger proportion of the fish foraged within a refuge (Chapter 2, Experiment 1). Within small-scale controlled experiments, both food availability and predation risk were important in determining the habitat choice of fathead minnows in clear water. Turbidity decreased the response of fathead minnows to predation risk (Chapter 2). By decreasing both the detection abilities of both predator and prey, and the effectiveness of anti-predator behavior, turbidity reduced the behaviorally mediated indirect effects of predation. In turbid water, fathead minnows should show decreased use of anti-predator behavior.

To examine the effect of predators and food on the large-scale habitat choice of fathead minnows in the field, minnow traps were used to estimate the relative abundance of fathead minnows in different habitats. By using minnow catch per unit effort, it was possible to estimate the relative abundance of fathead minnows in various channel habitats at Delta Marsh, Manitoba. Minnow

traps placed in two transects (1, 8 and 15 meters from shore) were used to measure the large-scale responses of fathead minnows to predation risk and relative food abundance. Laboratory results and foraging models predict that the fathead minnows should be most abundant in areas with either high food, or low predation risk. However, the habitat selection of the fathead minnows should be based on the balancing of the need for food and the need for safety.

To determine the effect of local predation risk on the small-scale behavioral response of the fathead minnows, predator exclosures (artificial refuges), used to create predator-free areas, were also placed in two transects from the shore to the open water. By using minnow traps, both inside and outside the exclosure, the relative abundance of fish caught within the exclosure can be used to determine if prey are responding to local predation risk by selecting less risky habitats. Further, by monitoring environmental parameters simultaneously, it may be possible to quantify their effect on the response of fathead minnows to predation risk. Based on my laboratory experiments, I predict that a greater number of fathead minnows should be caught within the exclosures, especially in those areas with higher predator densities. Within the laboratory, fathead minnows were able to assess the level of predation risk and responded to it by selecting a less risky habitat. In a natural channel, when presented with a refuge to predation, the fathead minnows should assess the differences in the local levels of predation risk and select the area free of piscivorous predators.

Environmental parameters may mediate the behavioral response of the fathead minnows to predation risk. When turbidity levels increase, fathead minnows should show a reduced response to the predators (i.e. decreased use of the exclosures) due a decrease in the effectiveness, and thus, benefits of anti-predator behavior. Other environmental variables, such as aquatic plant density

and other water quality parameters, may also play mediating roles on the effect of food and predators on the distribution of fathead minnows. Dense macrophytes provide the habitat with physical structure and cover. However, the fathead minnows may either remain near cover or avoid it, because aquatic macrophytes can act as cover for escape or cover to harbour ambush predators (Lima and Dill, 1990). Since some fish are sensitive to specific environmental parameters (e.g., low dissolved oxygen levels), natural refuges to predation may occur because the predators may avoid areas of extreme values of a certain parameter.

Study Site

The study site was the Blind Channel, a former bed of the Assiniboine River, in Delta Marsh (50° 11' N: 98° 23' W), Manitoba. The marsh is located on the southern shore of Lake Manitoba, and the Blind Channel is connected to the lake via a man-made cut and Cram Creek. The connection to Lake Manitoba causes the water within Blind Channel to be chemically similar to the lake water (pH 8.0 - 8.5, brackish >= 1500 mg / L T.D.S.) and to be influenced by seiches on the lake that can cause the water level to fluctuate by 15 cm or more (Suthers and Gee, 1976). The Blind Channel is a winding channel bordered primarily by cattail (*Typha* sp.) and some bullrush (*Scirpus* sp.), with a maximum depth of approximately one meter. The two transects were located near the north end of the Blind Channel (Fig. 3.1).

In the Blind Channel, two main habitat types exist, the open water and the vegetated periphery formed by stands of cattail. Stations 1 and 4, the inshore stations, were within the peripheral habitat while stations 3 and 6, the offshore stations, occurred in the open water habitat. The open water habitat was the deepest area, mean depth 72.0 cm (SE = 1.3, n =16), and received the most wind and wave action. The peripheral habitat was sheltered, shallow with a
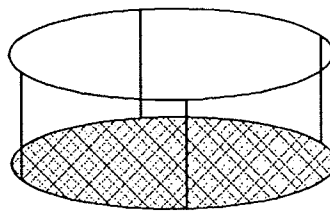
A)
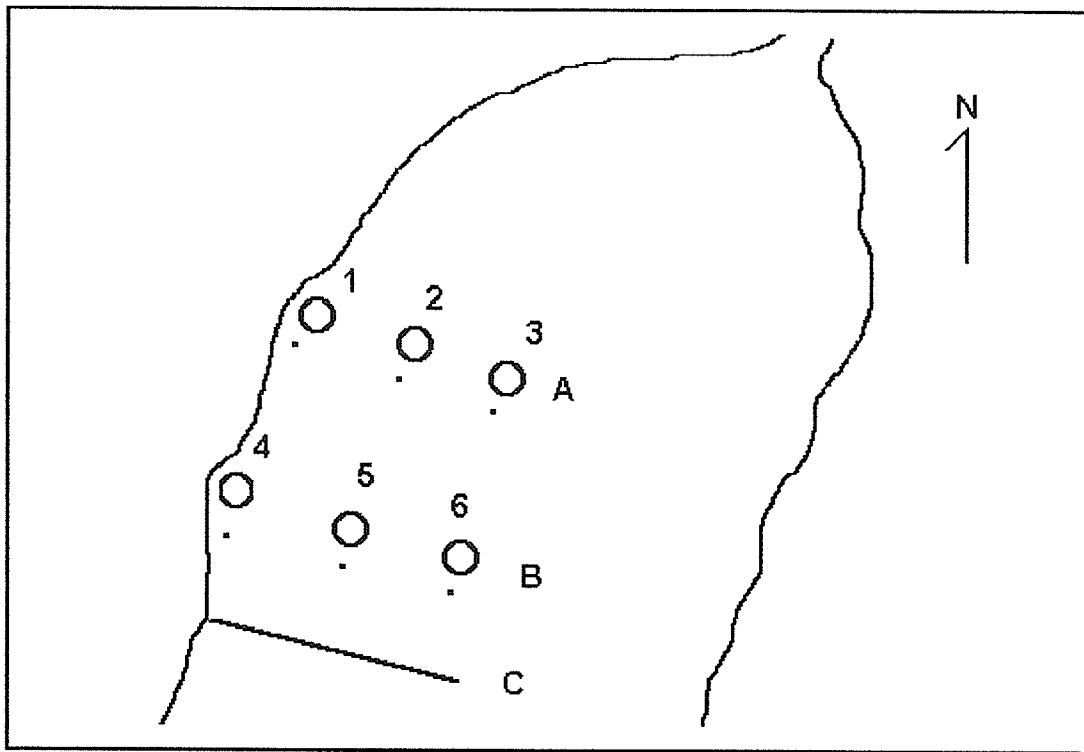
B)

Fig. 3.1 a) Map of the Blind Channel at Delta Marsh. Each transect (A and B) comprised three stations, inshore, midshore and offshore, placed at increasing distance to shore (1, 8, and 15 m, respectively). The numbers represent the station number of each exclosure. Transect C was used to estimate the distribution of predation risk within the channel. b) The predator exclosures placed at each station had a diameter of 1.83m and a height of 1.22 m. Netting was stretched over an ABS pipe frame. The netting (stretch mesh size 4 cm) allowed for the movement of fathead minnows and other small fish, but kept all fish predators out. Another mesh was draped over the top to exclude avian predators.

mean depth of 53.4 cm (SE = 1.4, n=16) and densely vegetated. The midshore stations, 2 and 5, represent a transition between the two different habitats with intermediate characteristics of both (mean depth 62.7 cm, SE = 1.4, n=16).

METHODS

Six predator exclosures, 1.83 m diameter by 1.22 m deep, were arranged in two transects in the Blind Channel near the University of Manitoba field station at Delta Marsh, Manitoba. The predator exclosures, made with flexible ABS pipe (Fig. 3.1), were placed in the marsh during early May to allow for the natural growth of aquatic macrophytes into the exclosures. Netting (stretch mesh size of 4 cm), which allowed for the movement of minnows (and other small prey species) in and out of the exclosure but kept predatory fish out, was stretched over the ABS frame. The bottom of each predator exclosure was made with a finer mesh (stretch mesh size 1 cm), while the top was covered with black netting (stretch mesh size of 9 cm) to keep the exclosures free of avian predators. Therefore, the predator exclosures acted as prey refuges by creating an area free of large piscian and avian predators.

In each transect, one exclosure was placed at the periphery of the channel, one in mid-water, and another in the open water habitat (5 meter distance between exclosures). Two meters adjacent and parallel to each predator exclosure, metal posts, two meters long, were pushed into the substrate to allow for the attachment of minnow traps. The metal post and the exclosure were considered to be one trapping station. Field sampling was conducted between July 1, 1994 and July 21, 1994, however only data obtained between July 1 and July 16,1994 were analyzed as total catches of fish were very low after that date (i.e. the total number of fathead minnows caught per day was less than eight fish and ranged from 0 to 7).

Four unbaited minnow traps (height, 42 cm; diameter, 22.5 cm; mesh, 6 mm) were used at each trapping station (except the inshore stations 1 and 4, where it was too shallow to have a surface and bottom trap), two within the exclosure and two adjacent to the exclosure mounted on the metal posts. One trap of each pair was positioned at the surface, while the other was located on the bottom. At stations 1 and 4, the inshore stations, the trap was placed in the middle of the water column, approximately 15 cm from the surface and bottom. Traps were set at 10:00 am and collected at 6:00 p.m. By trapping during the day, it would be possible to determine the effect of varying turbidity levels on the distribution of fathead minnows. All fish caught in each trap were identified to species, counted and released. To correct for the differences in trapping effort between the inshore station (2 traps, 1 within the exclosure and 1 outside) and the midshore and offshore stations (4 traps, 2 within the exclosure and 2 outside) and to convert to catch per unit effort, the daily fish catches in the midshore and offshore catches were divided by two.

Water quality parameters, such as water temperature, conductivity and turbidity were measured twice daily, once when the traps were set (1000 hours) and also midway through the trapping time(1400 hours). By measuring the parameters at 1000 and 1400 hours, both measurements could be used to estimate the daily mean values of the water variables while disturbance in the trap area would be minimised. All measurements and collections were taken at each station, adjacent to the predator exclosure. Water temperature was measured at the surface and bottom of the water column using an electronic thermometer and a temperature probe. Water samples, collected in BOD bottles, were taken from a water depth of approximately 30 cm. The conductivity of these samples was measured within the laboratory using an electronic multimeter. Dissolved Oxygen (DO) was also measured in these samples, but

problems with the equipment led to inaccurate and unreliable values. Turbidity was measured in the lab using a Hach model 2100A turbidimeter. Water samples were collected in sampling tubes using the same technique as the conductivity samples.

The amount of photosynthetically active radiation (PAR) [in the air] per day, hours of direct sunlight per day, wind direction and speed were also measured. These measurements were taken during the entire day from the University of Manitoba at Delta Marsh Weather station. Using a meter stick, the water depth at each sampling station was measured at six locations adjacent to the exclosure at 1000 and 1400 hours.

Aquatic macrophytes were sampled on July 5 using 50 X 50 cm quadrats in the area between the two transects, and on July 20 immediately adjacent to the transects because this is a period of maximum macrophyte growth (Hann, pers.comm.). The first transect allowed for an estimation of plant abundance at the beginning of the sampling period, while the second gave a more accurate estimation of the plant abundance in the transect areas. All plants within the quadrats were removed, separated by species, bagged and taken back to the field station where they were dried in ovens at $90^{\circ}C$ for three days. Plant dry weight was used to estimate the amount of cover available for both predator and prey. To estimate cover and correct for differences in mean water depth, the mean dry weight of the plants per quadrat were transformed by dividing the volume of the quadrat (50 X 50 X water depth cm) by the dry weight. Since 50g (dry weight) of plant material provides different amounts of cover if the average water depth along the transect is 35 cm or 75 cm, the transformation was performed to better estimate the local cover.

Fathead minnows are omnivorous and will consume anything from micro-crustaceans to insect pupae and larvae, rotifers, protozoans, algae, detritus, and

plant matter (Becker, 1983; Litvak and Hansell, 1990; Price et al., 1991). In this field experiment, only the distribution of the zooplankton was used to estimate the food distribution. Through stomach content analysis, Abrahams and Dick (unpublished) found that zooplankton was the preferred food of the fathead minnows at Delta Marsh, and thus zooplankton distribution was used to estimate the food distribution. Furthermore, where the diet of fathead minnows was made up of a large proportion of plant material, algae, and detritus, the fathead minnows were primarily observed feeding near the substratum (Becker, 1983). Previous sampling in the Blind Channel at Delta Marsh by Suthers (1984) showed that the fathead minnows were most abundant near the surface in the open water habitat. Since the fathead minnows in the Blind Channel were associated with the water surface, rather than the substratum, the zooplankton abundance was used to estimate the food availability in the different habitats.

Zooplankton was sampled twice (1430 hours, July 4 and 1430 hours, July 12) by placing a large black PVC tube (4 cm diameter, length 50 cm, volume = 628 cm^3) vertically through the water column three times at each trapping station. In areas where the water depth was shallower than 50cm, the actual depth was noted and used to correct for the volume of water sampled. Each of the three samples represented a cross-section through the water body and a rigid plankton filter (100 micrometer mesh size) was used to remove the zooplankton from the sample. The zooplankton sample was then washed with distilled water and preserved in a 35% ethanol solution. This sample procedure was used to estimate the spatial distribution of food within the study area for that week.

Five 5 ml subsamples were drawn from each zooplankton sample, and the zooplankton within the sample was identified to Order (Phylum in the case of Rotifers) and enumerated using a dissecting microscope. At each trapping

station, 15 subsamples were used to estimate the relative abundance (#'s/L) of the zooplankton (3 main zooplankton samples and 5 subsamples from each main sample). To determine if the size of all organisms sampled varied between the two weeks, a random sample of rotifers, copepods and cladocerans was taken from the inshore, midshore and offshore stations on both July 4 and July 12. The size of these zooplankton was determined using a calibrated ocular micrometer. The size of the zooplankton was estimated by measuring the longest cross-section of the organism.

To estimate the spatial distribution of predation risk, baited barbless hooks (size 1, 0.36") were used to determine the areas of the transect with the greatest risk. Frozen salted emerald shiners (*Notropis* sp.) were placed on pickerel rigs and attached to a 30 g weight. These hooks were attached to metal posts using 12 lb. test fishing line. Twelve of these hooks were used and each pole was placed 1.5 meters apart in a transect from the edge of the marsh to the middle of the open water channel. During seven twenty-four hour periods, the removal rate of the bait was monitored every eight hours, and empty hooks were rebaited. It was assumed that the removal rate of the bait would correlate with the mortality rate for fathead minnows, and thus this data would provide an estimate of the spatial distribution of predation risk.

RESULTS

Using multiple regression analysis, the daily effect of all environmental variables: conductivity, hours of light, marsh water depth, PAR, precipitation, water temperature and water turbidity, on total daily fathead minnow catch was determined (For a summary of the environmental data see Table 3.1). The total daily fathead minnow catch refers to fish caught at all the stations, both inside and outside of the refuge. These data do not deal with the ability of the fathead

Table 3.1 Summary of the daily mean values of the environmental data
collected between July 1 and July 16, 1994. The hours of direct light refer
to the hours of direct sunlight and are used to estimate the intensity of the
sunlight. (cloud cover reduces the hours of direct sunlight and provides
some shading). Temperature is the mean daily water temperature
sampled at each station and averaged over the entire transect.
Conductivity is in microSiemens corrected to 25 °C.

Variable	Mean	Std.Error	n	Max.	Min.
Hours of direct light	6.6	0.68	16	9	0.3
Wind speed (knots)	7.4	0.94	16	14.2	2.9
Conductivity (uS)	2179	13	15	2240	2080
Temperature (°C)	20.9	0.35	16	22.44	16.94
Turbidity (NTU)	3.3	0.28	16	5.53	1.82
Precipitation (mm)	2.5	1.23	16	14.8	0
Dock depth (cm)	61	2.2	16	76	40
PAR (E/m^2)	1.75	0.11	16	2.21	0.51

minnows to respond to predation risk, but rather the effect of turbidity on the total numbers of fish caught. A backward polynomial regression (probability of excluding in the equation is 0.10) produced an equation using water conductivity (slope = -278.1, t = -4.581, p = 0.002), turbidity (slope = -11.1, t = -3.902, p = 0.005) and precipitation (slope = 2.7, t = 3.603, p = 0.007). These three variables explained 83.59 percent of the variation in daily fathead minnow catch. As turbidity and conductivity increased, fathead minnow catches declined; during periods of precipitation, the catches increased.

A regression of the distance to shore and the frequency of frozen bait removal produced a significant positive relation ($F_{1,10}$ = 17.65, slope = 0.324, p = 0.0018) (Fig. 3.2). I assumed bait removal was correlated with predation risk, and therefore concluded that the open water habitats had the highest level of predation risk.

On July 4, the regression of the number of zooplankton/L in each habitat and the distance to shore did not produced a significant relationship (Fig. 3.3, Table 3.2). However, for all zooplankton sampled (copepods, cladocerans and rotifers), the lowest abundances always occurred within the offshore habitat. On July 12, no significant relationship existed between the abundance of zooplankton and distance to shore. Both the inshore and offshore stations had low levels of zooplankton, except in the case of rotifers. Rotifer numbers were highest in the midshore habitat, but were also relatively high in the offshore habitat. Therefore, during the two weeks of sampling, the most abundant levels of zooplankton occurred in either the inshore or midshore habitats, and only in the case of rotifers were there ever higher numbers of zooplankton in the open water habitat. The open water habitat consistently had the lowest numbers of zooplankton, and therefore, the lowest levels of food. The size of any
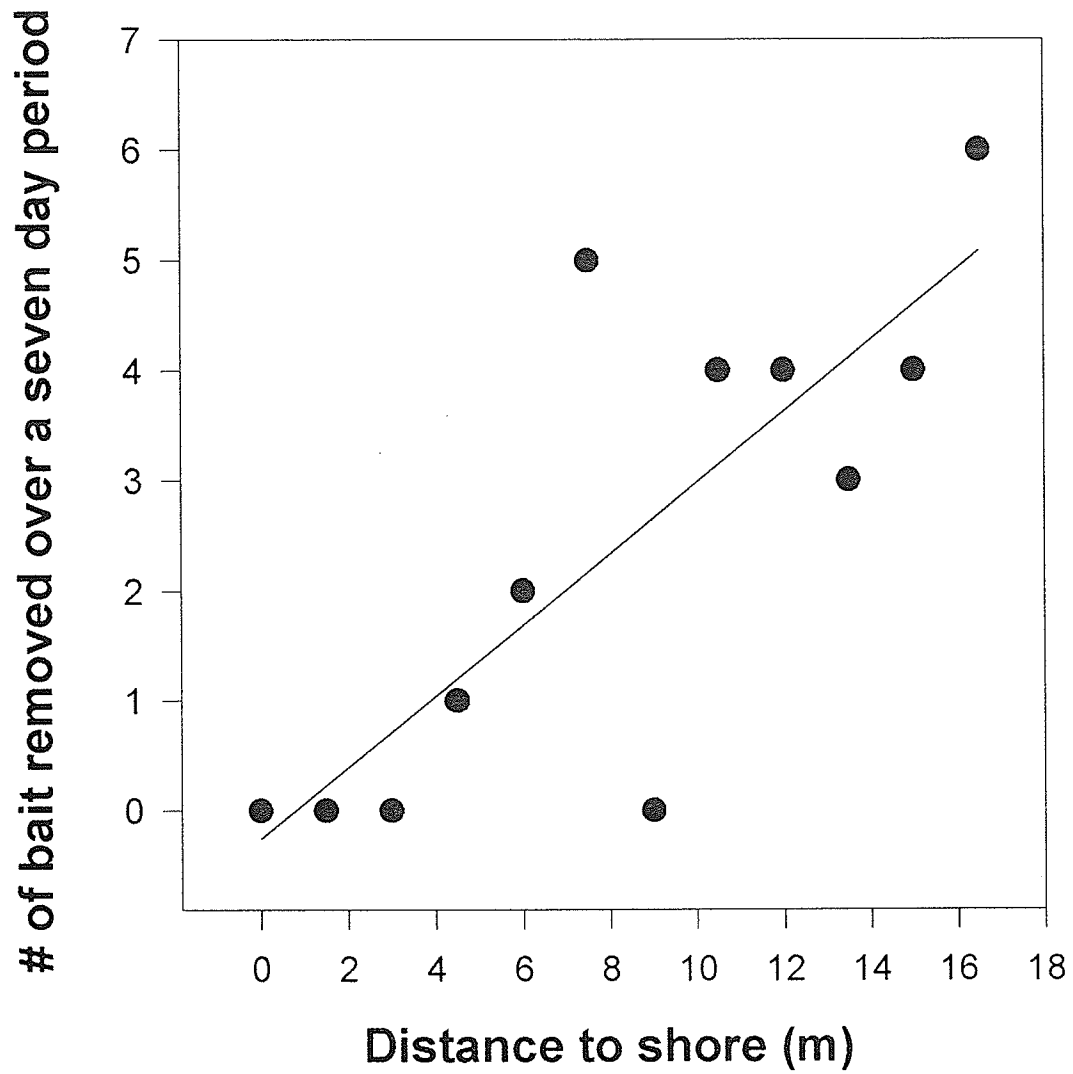
Fig. 3.2 The effect of distance to shore on the frequency of frozen bait removal from barbless hooks. If frozen bait removal is correlated with predation risk, then the open water habitats are most dangerous.
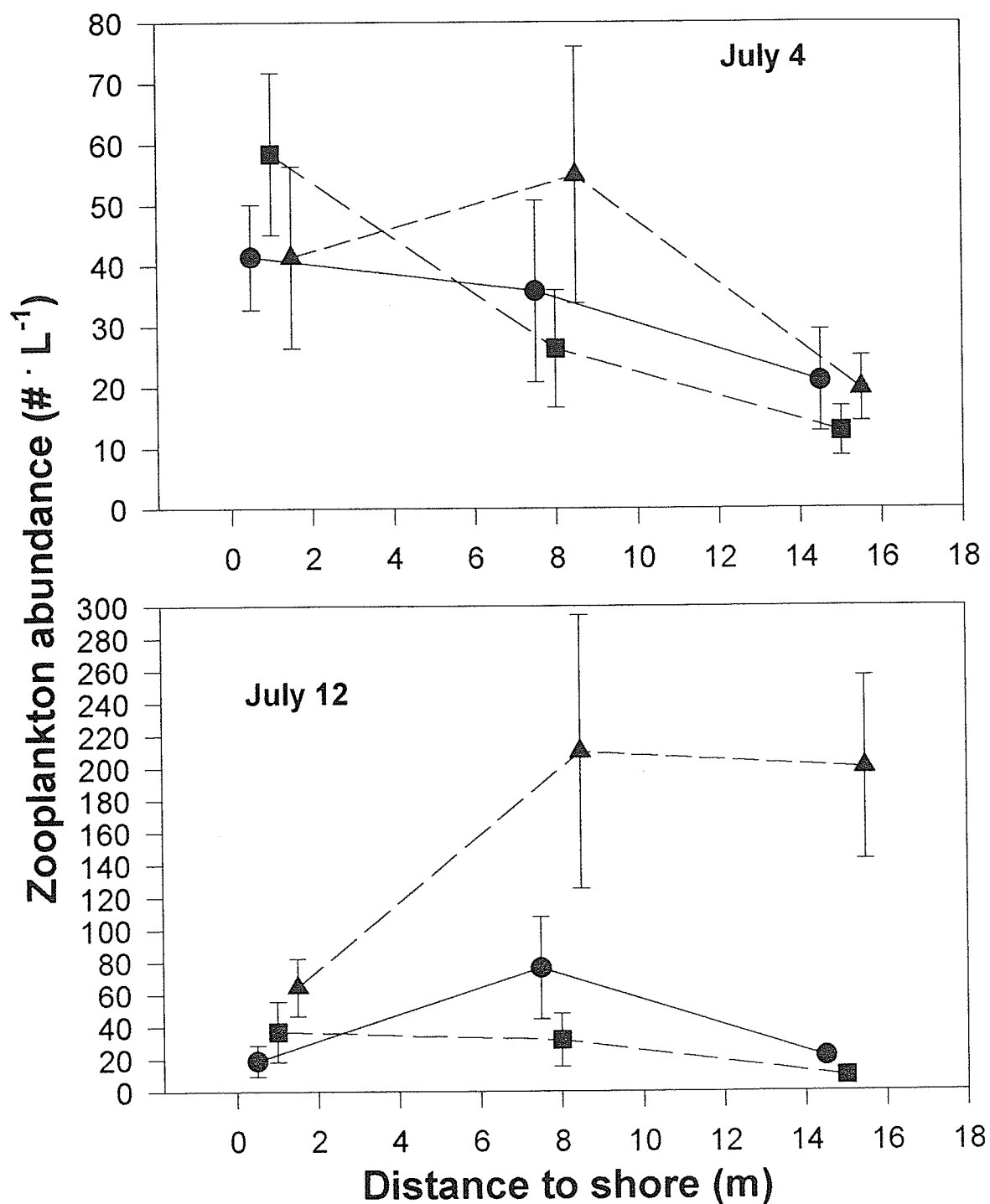
Fig. 3.3 The estimated abundance of zooplankton in the three different habitats (inshore, midshore and offshore). The solid circles represent the copepods, the solid squares represent the cladocerans and the solid triangles represent the rotifers. Sampling performed on July 4 was used to estimate abundance between July 1 and July 8, while sampling on July 12 was used to estimate between July 9 and July 16. Error bars represent 1 standard error, n = 6.

Table 3.2 The estimated abundance of zooplankton (copepods, cladocerans and rotifers) in the three different channel habitats. The distance to shore is for each of the habitats. Inshore is at 1 m from shore, midshore is at 8 m and offshore occurs at 15 m from shore.   Three zooplankton samples were taken at each position in the two exclosure transects.

July 4	Distance to shore (m)		
Zooplankton (# /L)	**1**	**8**	**15**
Copepods Mean	41.4	35.8	21.
Standard Error	8.7	15	8.4
n	6	6	6
Cladoceran Mean	58.4	26.3	12.7
Standard Error	13.3	9.7	4.1
n	6	6	6
Rotifer Mean	41.4	54.9	19.7
Standard Error	15	21	5.4
n	6	6	6

July 12	Distance to shore (m)		
Zooplankton (# /L)	**1**	**8**	**15**
Copepods Mean	19.1	76.4	21.6
Standard Error	9.6	31.7	3.1
n	6	6	6
Cladoceran Mean	37.1	31.8	9.5
Standard Error	18.8	16.2	3.4
n	6	6	6
Rotifer Mean	64.7	210.9	200
Standard Error	17.8	84.5	56.7
n	6	6	6

zooplankton taxon did not vary significantly between July 4 and July 12 (Table 3.3).

On average, the total number of fathead minnows caught daily was 28.2 (SE =4.4, n =16). During the first week the catches ranged between 62 and 9 fathead minnows per day and during the second week they ranged between 31 and 9 fathead minnows per day. After July 16, total daily minnow catches at the trapping stations were consistently below eight fathead minnows.

The mean number of fathead minnows caught $trap^{-1} \cdot day^{-1}$ within the exclosure was 1.74 (SE = 0.36, N=16) while the number caught outside the exclosure was 0.89 (SE = 0.21, N=16) (Fig. 3.4). Fathead minnows were significantly more common within the predator exclosures than outside (Wilcoxon Matched-Pairs Signed-Ranks test, Z = -1.965, p = 0.0494). However, because the distribution of predation risk differed in the marsh, a sign test was used to determine the effect of local predation risk on the use of the exclosures. The sign test was calculated by subtracting the daily catch outside the exclosures from the daily catch within the exclosures. The fathead minnows showed no preference for the refuge in the inshore stations where predation risk was low (7 positive differences out of a total of 15 differences, p = 1.0), but preferred the exclosures in the more dangerous areas, the midshore (18 positive differences out of a total of 23 differences, p = 0.01) and offshore stations (19 positive differences out of a total of 26 differences, p = 0.031). Therefore, in the more dangerous habitats, the fathead minnows increased their use of the predator exclosures.

The mean daily catches per minnow trap at the inshore, midshore and offshore stations were 1.72 (SE = 0.79, N=16), 2.48 (SE = 0.64, N=16), 3.70 (SE = 0.74, N=16) fathead minnows, respectively. There was an upward trend between mean daily minnow catches per trap and distance to shore. A

Table 3.3 Size (estimated by length in mm) of zooplankton during first and second week of sampling. July 4 was used to estimate zooplankton size between July 1 and July 8, while July 12 was used for July 9 to July 16. The t_2 value refers to the actual t value generated by a t test to compare mean sizes of zooplankton. The p value is the probability value associated with the t value for a two-tailed t-test.

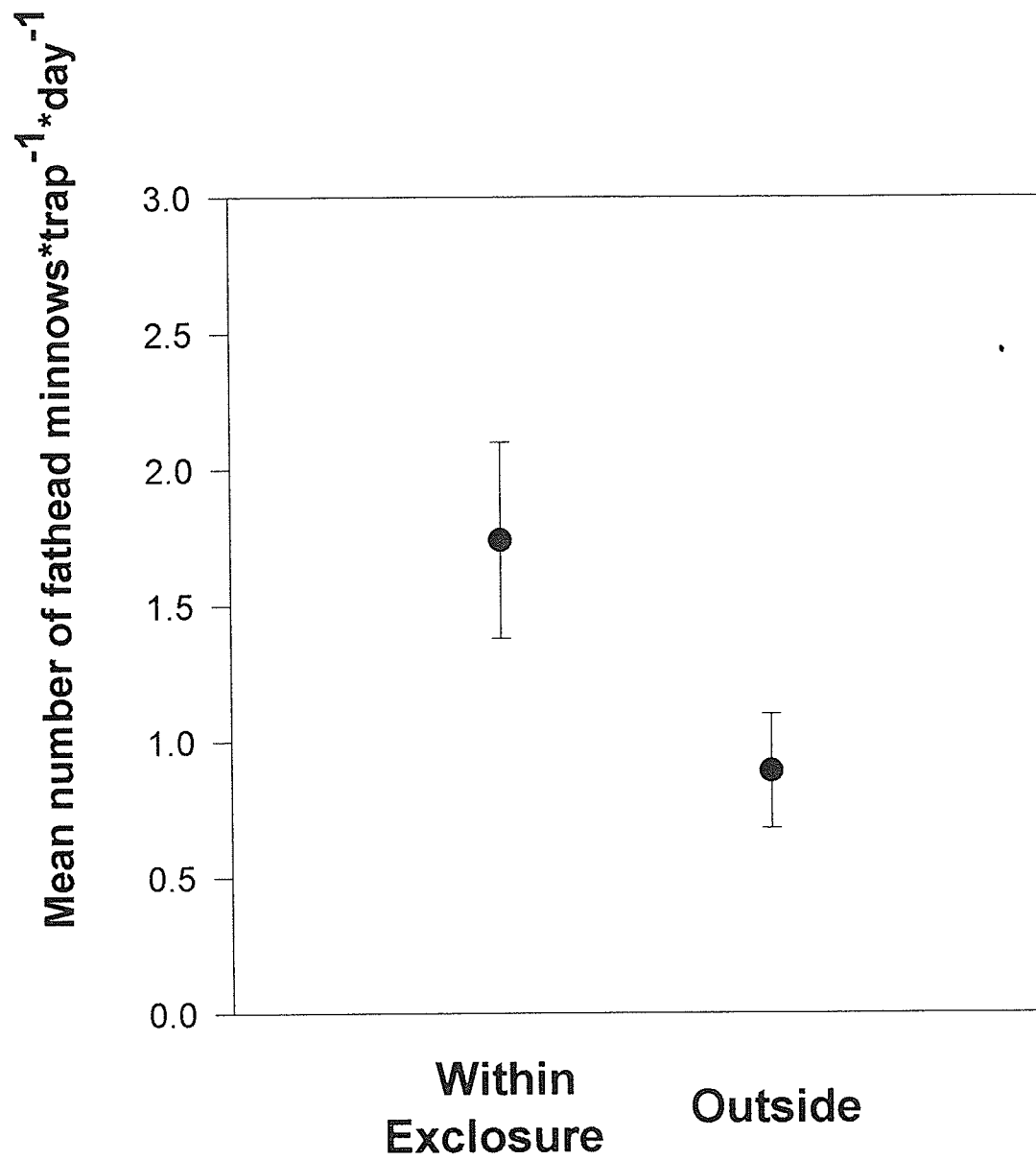|	Copepods		Cladocerans		Rotifers	
	July 4	July 12	July 4	July 12	July 4	July 12
Mean	0.87	0.81	0.72	0.79	0.26	0.24
S.E.	0.03	0.03	0.03	0.04	0.01	0.01
n	68	70	75	68	75	75
t_2 value	1.42		-1.40		1.02	
p value	0.16		0.16		0.31	

Fig. 3.4 The mean number of fathead minnows caught per trap per day
(corrected for trapping effort) both within the predator exclosures and
outside. Error bars represent 1 standard error, n = 16.

Friedman two-way ANOVA produced a Chi-square value of 8.0938, df = 2, and a p value of 0.0175 indicating that more fathead minnows were caught in the open water habitat, an area that is considered to be higher in predation risk.

Both surface and bottom minnow traps were used to determine the vertical distribution of fathead minnows the midshore and offshore stations. In the surface traps, the mean number of fathead minnows caught· trap^{-1}· day^{-1} was 2.04 (SE = 0.13) while the bottom traps caught an average of 1.05 minnows· trap^{-1}· day^{-1} (SE = 0.26). The fathead minnows significantly preferred the surface traps during the daylight hours (2 tailed paired t-test, t_{15} = 2.21, p = 0.043).

Myriophyllum sp., *Potamogeton* sp. and *Utricularia* sp. were the only aquatic macrophytes that occurred within the quadrats. No significant relationship existed between plant dry weight/volume sampled and the distance to shore for either transect (July 5 or July 20) (Fig. 3.5, Table 3.4). A regression of aquatic macrophyte cover, estimated by plant dry weight/volume of water sampled, with the total number of fathead minnows caught at each station produced a significant negative relation (r^2 = 0.68, $F_{1,4}$ = 8.61, slope = -371.28, p = 0.0426) (Fig. 3.6). Only data from the July 20th transect was used in the regression because of the closeness of the transect to the exclosures.

DISCUSSION

The intention of this experiment was to determine if turbidity played a major role in the effect of predation risk and food resource abundance on the natural distribution of fathead minnows. Unfortunately, the natural turbidity did not vary significantly during the experiment and only once reached a maximal daily mean of 5.5 Nephelometric Turbidity Units (NTU) on July 8. In the laboratory experiments, the mean level of turbidity was 13.2 NTU and 11 NTU.
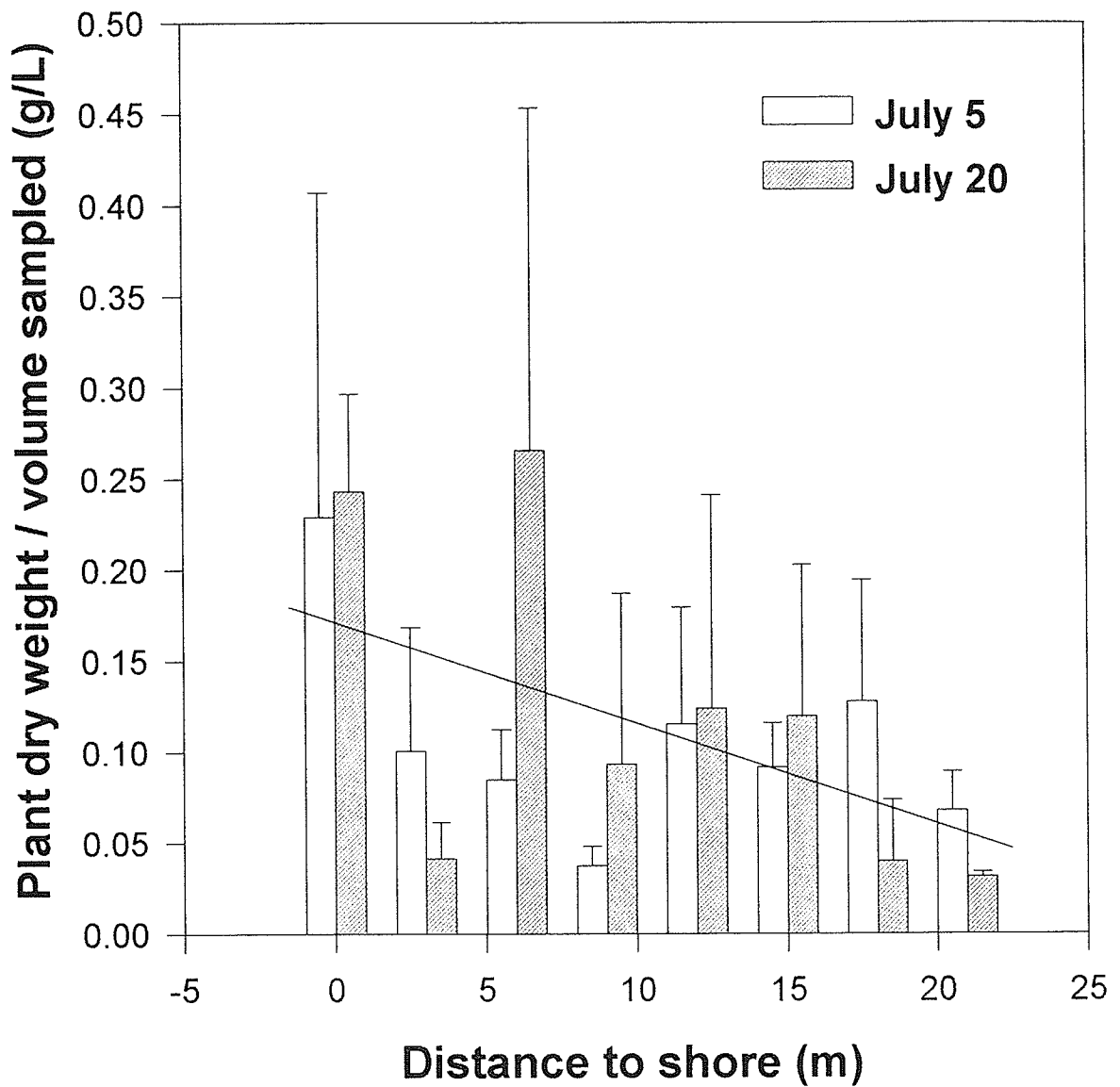
Fig. 3.5 The effect of distance to shore on the amount of aquatic macrophyte cover. The total dry weight of the macrophyte was divided by the volume of the quadrat to correct for differences in mean water depth along the transects. Three transects were performed in the area between the exclosure transects on July 5, while two transects were performed immediately adjacent to the exclosure transects on July 20. The regression line uses all of the data on the graph. The relationship is not significant. The error bars represent standard error (July 5, n = 3, and July 20, n= 2)

Table 3.4 Summary of the aquatic macrophyte data. Plant dry weight is the total dry weight for all three species with a quadrat (50 X 50 cm). Cover is estimated by dividing the plant dry weight by the volume of the sampling unit. The volume of the sampling unit is determined by multiplying the area of the quadrat by the average water depth at a particular distance. The July 5 transects were taken from the area between the exclosure transects, while July 20 transects were taken immediately adjacent to the exclosures.

July 5	Plant dry weight (g)			Cover
Distance	Mean	S.E. (n = 3)	volume (L)	g/L
0	23.1	16.32	118.3	0.20
3	11.77	7.99	115	0.10
6	11.3	3.52	135	0.08
9	5.3	1.51	142.5	0.04
12	16.37	8.64	148.3	0.11
15	14.77	4.02	160	0.09
18	19.77	9.74	160	0.12
21	11.1	3.56	163.3	0.07

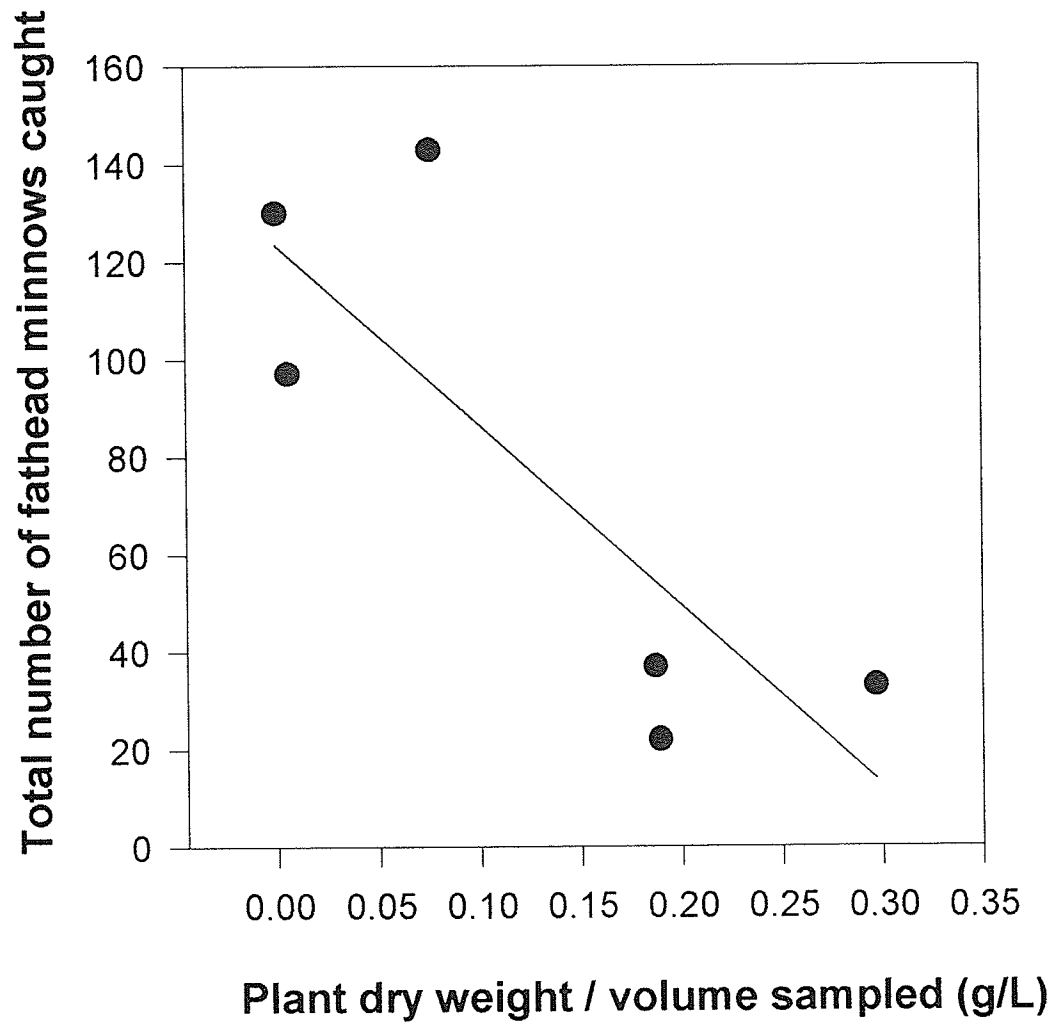| July 20	Plant dry weight (g)			Cover
Distance	Mean	S.E. (n = 2)	volume (L)	g/L
0	34.6	24.47	143.75	0.24
3	5.95	4.21	147.5	0.04
6	35.9	25.39	141.25	0.25
9	14.5	10.25	162.5	0.09
12	20.25	14.32	172.5	0.12
15	20.7	14.64	180	0.12
18	6.9	4.88	181.25	0.04
21	6	4.24	191.25	0.03

Fig. 3.6 The effect of aquatic macrophyte cover on the total number of fathead
minnows caught at each station during the entire sampling period. Only
data from the July 20 transect were used in analysis due to the close
proximity to the exclosure transects. The amount of aquatic macrophyte
cover had a significant negative effect on the total number of fathead
minnows caught. The greatest number of fathead minnows was caught in
areas where the transformed total dry weight of aquatic macrophyte per
quadrat was low. The straight line is the regression line.

(Chapter 2, Experiment 1 and 2, respectively). Any water with a value of less than 10 NTU is not considered to be turbid (Blaber and Blaber, 1980), and as a result, it was not possible to determine the effect of variable turbidity levels on the habitat choice of fathead minnows. However, even the low levels of turbidity, along with conductivity and precipitation, did have a significant effect on the total daily fathead minnow catch. Daily fathead minnow catches decreased with increased levels of conductivity and turbidity, but increased during periods of rain. It is not unreasonable to assume that movement is important in the catching success of the minnow traps, and therefore, it is possible that during periods of low to intermediate turbidity the fathead minnows responded by decreasing their movement rate.

Werner and Anholt (1993) predict that the encounter rate between predators and their prey is dependent on the movement rate and detection abilities of both individuals. Since turbidity decreases the detection abilities and the fathead minnows responded by further decreasing movement rate, the encounter rate between the predators and prey may be significantly lower during periods of higher turbidity at Delta Marsh. Decreased movement is an anti-predator response to predation risk and functions to decrease encounter rate between predator and prey and the detectability of prey (Azevedo-Ramos et al., 1992; Werner and Anholt, 1993). Therefore, at these very low turbidity values, fathead minnows may still be employing anti-predator behavior because: 1) the anti-predator behavior is effective, and 2) the periods of turbidity were quite short and the costs of decreased movement on the feeding rate may not be high. During prolonged periods of high turbidity, the costs of reduced feeding, through decreased movement, would increase and the fathead minnows would have to balance between the use of anti-predator behavior and the need to consume food.

The highest level of predation risk within the Blind Channel occurred in the open water habitat and, to a lesser degree, the mid-water habitat. No bait fish were removed within 4.5 meters of the vegetated edge. Only one predatory fish was caught in the predation risk transect, a black bullhead (*Ictalurus melas*). Through previous sampling by Kattenfeld and Abrahams, northern pike (*Esox lucius*) and yellow perch (*Perca fluviatilis*) are also known to occur within this section of the marsh. All predators caught were large enough to consume even the largest fathead minnow. For these predators, no size refuge to predation exists within the Blind Channel habitats.

The distribution of the zooplankton was measured twice, once to estimate the food levels between July 1 to July 8 and a second sample to estimate between July 9 to July 16. During the first period, the inshore stations had a larger number of zooplankton than the mid or open-water habitats. In the second week, the mid-water habitat had the highest abundance, while both the inshore and offshore stations were low. During the entire sampling period, the open-water habitat was the lowest quality habitat in terms of the food resource and had the highest level of predation risk. Despite these distributions, the fathead minnows were most abundant in the open water habitat.

The fathead minnows at Delta Marsh prefer the open water habitat, a habitat with the lowest level of food and the highest level of predation risk. This habitat choice indicates that fathead minnows do not remain within safer habitats to avoid predation in a natural channel. The inshore areas had the lowest levels of predation risk, and yet very few adult minnows were caught there. Savino and Stein (1989) found similar results where fathead minnows within outdoor pools did not exhibit significant distributional modifications in the presence of largemouth bass (*Micropterus salmoides*) and northern pike predators. In the presence of bass, bluegill sunfish moved into areas offering the most cover while

the fathead minnows did not show this distributional shift (Savino and Stein, 1989).

Dissolved oxygen (DO) may have played an important role in the distribution of the fathead minnows within the Blind Channel at Delta Marsh. Unfortunately, technical problems with the O_2 meter led to inaccurate and untrustworthy results. However, by using Suthers'(1984) data it may be possible to estimate the importance of DO to the distribution of the fathead minnows. My sampling sites were located in the same area as Suthers' site A transect and thus may allow for some comparison. The distribution of the fathead minnows during the summer of 1994 was similar to their distribution in the summer of 1982 and 1983. Suthers (1984) also found that the majority of adult fathead minnows occurred near the surface in the open water habitat. Because of the similarities between our sampling sites and results, it may be possible to use DO trends obtained by Suthers (1984) to explain the similar distributions of the fathead minnows.

Although DO does have a significant influence on the habitat choice of fish, it may not be significant factor in determining the (day only) distribution of the fathead minnows at Delta Marsh. First, fathead minnows are fairly hardy with respect to low DO levels, and were able to survive in all channel habitats, even those which may become severely hypoxic, during the day (Suthers, 1984). Second, by sampling the distribution of the fathead minnows during the day, I sampled when DO levels were at their highest in all habitats. In July, DO levels never became severely hypoxic near the top or bottom traps at sampling stations that were positioned from 2 meters offshore to the middle of the channel (Suthers, 1984). These distances correspond to my mid and open-water stations. Therefore, low DO levels may cause adult fathead minnows to avoid severely hypoxic areas close to the densely vegetated edge or inshore habitat. However,

the mid and offshore habitats were never severely hypoxic, near the bottom or top. Therefore, DO does not completely explain the preference of fathead minnows for the top 30 cm of the open water habitat as they are physically able to survive in all channel habitats during the day.

Inter- and intraspecific competition with young-of-the-year (YOY) fish may also play a role in the habitat choice of the adult fathead minnows. Extremely high densities of YOY fish were observed at both inshore stations (1 and 4) whenever the traps were set and collected (1000 and 1800 hours), as well as when the water quality parameters were measured (at 1400 hours). Most YOY fish were too small to be caught by the minnow traps and any attempts to quantify the habitat use of the YOY did not yield any dependable results. The adult fathead minnows may have avoided areas with high densities of YOY fish to decrease inter- and intra-specific competition. The distribution of the YOY fish within the Blind Channel may play a role in the distribution of the adult fathead minnows.

Although the submerged macrophyte density did not decrease significantly with distance to shore, adult fathead minnows may have avoided the areas of highest plant density by remaining at the surface in the open water habitat. Since aquatic macrophytes provide cover, for both predators and prey, the fathead minnows may have avoided areas of dense plant matter. Many organisms seek cover to avoid predation, but others view cover as both a source of attack by predators and a refuge to avoid predation (Lima and Dill, 1990). The northern pike is an ambush predator and can forage in areas of high submerged plant density using little activity. By using reduced movement, the pike decrease their energetic output and the probability of alerting other prey nearby (Savino and Stein, 1989). The black bullhead forage in areas of dense vegetation and are usually associated with the bottom (K.W.Stewart, pers.comm.). The fathead

minnows may have preferred the surface, open water habitat, to avoid areas of dense submerged vegetation because of the threat of predators, especially northern pike and black bullhead.

The predator exclosures were used to determine the local, small-scale response of fathead minnows to predation risk. When presented with the exclosures (predator refuges) within the preferred habitat (i.e. mid and open water areas), the fathead minnows were able to assess the relative levels of predation risk and showed a strong preference for the safe habitats (significantly more abundant in refuge). Therefore, on the small-scale fathead minnows were able to assess the relative level of risk of predation, and made behavioral decisions based on that information.

No environmental parameters of those measured had a significant effect on the small-scale response of fathead minnows to predation risk. A stepwise multiple regression of proportional exclosure use with all environmental variables did not produce a model equation. Unfortunately, because the turbidity within the marsh did not vary significantly during the study (i.e. always <10 NTU), it was not possible to determine the effect of turbidity on the large-scale or small-scale response of fathead minnows to the presence of predators. In areas with longer and larger fluctuations in turbidity levels, it may be possible to measure the degree to which turbidity decreases the behaviorally mediated indirect effects of predation, at the population and community level.

In conclusion, the large-scale response of fathead minnows at Delta Marsh to predators and food was that they inhabited areas of high predation risk and low food abundance, findings that are not consistent with what one would predict using foraging models and laboratory studies. Competition with YOY fish and avoidance of areas of high submerged macrophyte density and ambush predators may explain the resulting distribution of the fathead minnows. At the

small-scale, fathead minnows were able to assess local differences in predation risk and sought out areas of safety, indicating that predation risk does play a role in the habitat choice of the fathead minnows. By observing the behavior of a prey species within a natural prey assemblage, one can possibly determine what other parameters, both biotic or abiotic, and interactions are potentially significant to a prey species. Even though predation risk and energetic intake are important to the fitness of an individual, many other conflicting pressures or demands must be balanced within an entire mixed habitat.

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Chapter 4
Conclusion

The purpose of this thesis was to determine the effect of turbidity on the interaction between predator and prey. Chapter 2 examined the response of fathead minnows to the presence of the predator through two laboratory experiments. The first experiment demonstrated that fathead minnows had a greater response to the presence of piscivorous perch in clear water compared to turbid water. However, two possible mechanisms exist which can account for the reduced response.

The second experiment from Chapter 2 differentiated between Blaber and Blaber's (1980) "Turbidity as Cover" (TAC), and Kattenfeld and Abrahams' "Turbidity Reduces Effectiveness" (TRE) hypotheses. The TAC had been used since Blaber and Blaber (1980) proposed the hypothesis to predict the habitat choice of prey fish with respect to the presence of predators. It had never been tested within the laboratory and was assumed to be the mechanism by which turbidity affected habitat choice. The results from Chapter 2 supported the TRE hypothesis as it predicted the observed results. Therefore, turbidity reduces the effectiveness of anti-predator behavior in a small-scale, controlled experiment.

Since the effectiveness of anti-predator behavior is reduced in turbid water, prey must balance the costs and benefits of performing these behaviors. In turbid water, foraging fathead minnows showed a reduced response to the presence of a predator within an aquarium habitat when compared to their response in clear water. The fathead minnows reacted to the reduced effectiveness and benefits of anti-predator behavior by reducing their use of these behaviors in turbid water. Therefore, in turbid water, the behaviorally mediated indirect effects of predation are reduced.

Chapter 3 examined the effect of turbidity and other environmental variables on the large-scale (i.e. over a 16 meter transect) and small-scale habitat choice of fathead minnows. On the large-scale, fathead minnows did not

conform to predictions made through foraging models and laboratory results, which predict that prey fish should balance habitat choice between the need for food and the need for safety. Within the channel at Delta Marsh, the greatest number of fathead minnows were found in the open water habitat, the area with the highest predation risk from piscivores and the lowest numbers of zooplankton. On the small-scale (i.e. choosing between remaining inside or outside a predator exclosure), the fathead minnows were able to assess the level of local predation risk and occupied areas that were less risky. Unfortunately, because the water turbidity did not reach over the levels tested in the laboratory, it was not possible to determine if turbidity decreased the small-scale behavioral response of the fathead minnows to predation risk.

This thesis has shown that turbidity does decrease the behaviorally mediated indirect effects of predation within the laboratory. By reducing the ability of prey to avoid predators through anti-predator behavior, the direct effects, the indirect effects that arise from consumption, and the indirect effects that arise through long-term modification (physiological and morphological) by the prey should be significantly more important in turbid waters. Although it was not possible to test these predictions in a natural habitat, this study shows that an environmental parameter can mediate the behavioral response of prey to predation risk.

In a natural habitat, turbidity should allow for the determination of the magnitude of the behaviorally mediated indirect effects of predation. By comparing between similar clear and turbid water bodies, it will be possible to determine the extent to which behavioral modification by the prey affects population and community structure. In turbid water habitats, the consumptive effects (both direct and indirect) and the long term modifications (physiological and morphological) by the prey will be important in controlling prey populations.

By removing one portion of predators' effects on prey, it will be possible to quantify the relative strengths and importance of consumption by the predator, long term modification by the prey and short term behavioral changes by the prey.

The role of predators in clear and turbid water systems should be markedly different. In clear water habitats, the prey's behavioral response to risk of predation should have the largest effect on the prey population and community. The predator will affect numerous prey species in a clear water community by causing an increase in anti-predator behaviors, such as habitat shifts, refuge use and vigilance. These habitat shifts may increase competition between species because they are forced into similar refuges (Persson, 1991). Werner et al. (1983) demonstrated that the behavioral modification made by bluegill sunfish in response to predation risk changed the population dynamics and community structure. In clear water, the entire community will be affected by the behavioral modifications made in response to predation risk.

In turbid habitats, the effect of risk of predation should be much reduced. Interactions between predators and prey should be primarily effected by the predator population numbers and the encounter rates with the prey. The affects of the predator will be a result of consumption of the prey. Predators will affect all prey species because they will not primarily consume favorable prey items, as their attack specificity decreases in turbid water (Crowl, 1989). Since the behavioral modification by the prey is less effective in turbid water, morphological and physiological modification by the prey should become relatively more important. As a water body becomes turbid, communities originally dominated by soft-bodied prey may change over time and be dominated by spiny-rayed, deeper bodied fish. Because these deeper bodied fish have morphological adaptations to respond to predators, they may best co-

exist in the turbid water habitats. In Dutch turbid lakes (30 - 40 cm secchi depth), Lammens et al. (1992) found that the presence of the predatory pikeperch determined which prey species, the roach or the common bream, dominated the lake community. The roach are softer bodied slender fish while the common bream is a deep bodied spiny fish. Therefore, as the effectiveness of behavioral modification decreases, fish species which possess morphological or physiological modification to avoid predation should benefit in turbid communities. These data suggest that as eutrophication, which causes water turbidity (Hosper and Jagtman, 1990), increases in lake communities, the prey species assemblages will shift from soft bodied slender fish to deep bodied spiny fish as more lakes become turbid.

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