

Turbidity as Cover:
Do Prey Use Turbid Habitats as Refuges from Predation?

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Abstract

Turbidity has generally been viewed as having detrimental effects on fish; yet, many turbid habitats in the world are also abundant with fish. This phenomenon is often explained as fish enjoying reduced predation pressure in turbid habitats. This represents a trade-off situation where fish should select clear or turbid habitats that provide maximum net benefits. Because turbidity reduces light penetration, both predator and prey visual ranges are reduced, rendering both less efficient foragers. For this reason, I suspected that the benefits of a turbid environment would be greatest in the presence of predators and hypothesized that when predation risk is high, prey should prefer turbid water.

Laboratory experiments showed that regardless of predation risk, fathead minnows (*Pimephales promelas*) preferred feeding in a turbid habitat. The presence of a predator, yellow perch (*Perca flavescens*) or black bullhead (*Ameiurus melas*), caused minnows to reduce feeding. There was no interaction between water clarity and predation risk, water clarity and predation risk, thus, appeared to affect the minnows' habitat selection independently. The predator's effect on the prey was the same whether in turbid or clear water.

Using the prey distributions established in the lab experiment, key parameters and assumptions were identified for a computer model which simulated both prey and predator responses to turbid water and their interactions. The model predicted that prey would always prefer the turbid habitat when one was available. Predators generally used both clear and turbid habitats. Only when its foraging efficiency was reduced significantly did the predator show strong avoidance of turbid water. As the number of predators increased, predators used both clear and turbid habitat more evenly. Turbid

environments seem to provide important habitats for small and juvenile fish. It may benefit small fish by reducing predator efficiency or reduce prey energy expenditure.

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Chapter 1

General Introduction

Introduction:

Turbidity is a common feature of most aquatic ecosystems. Many fish spend at least part of their life in turbid environments (Boehlert and Morgan 1985, Bruton 1985, Gregory 1993, Benfield and Minello 1996, Abrahams and Kattenfeld 1997). Turbidity varies both temporally and spatially (Abrahams and Kattenfeld 1997). It can cover a huge area and persist for a long period; or it can be very localized and temporary. Many factors can generate turbidity. River runoff, flood, rain, snow and wind blown dust bring both inorganic and organic material into water; wind generated wave action, movements of boats and animals, benthic foraging of fish like carp (*Cyprinus carpio*), and even large debris cause resuspension of sediment (Hilton and Philips 1982, Bruton 1985, UK CEED 1999, 2000, Parkos et al. 2003, Scheffer et al. 2003).

Turbidity creates environmental variation that can be differentially exploited by aquatic organisms, affecting both their distribution and habitat selection. Scheffer et al. (1994) observed that turbid and clear waters existed with a very sharp transition separating the two states in two Dutch lakes (Lake Wolderwijd and Lake Veluwemeer). This phenomenon should create two distinct habitats adjacent to each other; each with its own set of costs and benefits. As the same phenomenon can be found in varieties of locations, such as the mouths and sharp bends of rivers, confluences, estuaries and locations with upwellings or thermoclines, organisms should choose which habitat to occupy based on trade-offs.

Impacts of Turbidity on Fish:

Bruton (1985) stated that turbidity is a measure of both the suspensoid (solids or particles suspended in a liquid) load as well as the properties of the suspensoids and the

liquid, which cause light to be scattered and absorbed. Suspensoids can be either organic (e.g. phytoplankton) or inorganic (e.g. silt). Based on these observations, turbidity can affect aquatic organisms in two ways: the direct effects of particles on organisms and indirect effects of the particles changing the environments surrounding the organisms.

It is generally accepted that high turbidity has detrimental effects on fish, both physiologically and behaviorally (Bruton 1985, Newcombe and MacDonald 1991, Hecht and van der Lingen 1992, Gregory 1993, Rowe and Dean 1998, Johnson and Hines 1999, Bonner and Wilde 2002). Bruton (1985) summarized the suspensoids' major effects on fish as: 1) reduction in light penetration and photosynthesis resulting in reduction of food and plant biomass; 2) reduced visibility of pelagic food; 3) reduction of benthic food by smothering; 4) clogging of gillrakers and gill filaments; and, 5) reduction of aerial predation risk. Resuspended sediments are also capable of deoxygenating aerated water by the sediment's affinity for oxygen (Bruton 1985) or bacterial decomposition of organic suspensoids (Cole et al. 1999). Other papers listed additional negative effects, including: 1) reduction of growth rate; 2) lowered resistance to disease; 3) reduced efficiency at prey capture; 4) interference with the development of eggs and larvae; and, 5) interference with natural movements and migrations of fish (Newcombe and MacDonald 1991, Hecht and van der Linen 1992, Johnson and Hines 1999). Ardjosoediro and Ramnarine (2002) demonstrated that the growth rate and survivorship of double hybrid Jamaica red tilapia, (*Oreochromis aureus* x *O. niloticus*) x (*O. mossambicus* x *O. hornorum*), were negatively correlated with turbidity. Their study found that at elevated turbidity levels, fish had clogged gills and depressed appetites.

Influence of Turbidity on Habitat Selection:

Despite many negative effects, many of the world's most productive aquatic ecosystems contain turbid waters (Abrahams and Kattenfeld 1997), e.g. estuaries (Bruton 1985, Cyrus and Blaber 1987a). Some fish not only tolerate turbid habitats, they actively seek them out and thrive in them (Gradall and Swenson 1982, Cyrus and Blaber 1987a, Gregory 1993, Gregory and Northcote 1993). Cyrus and Blaber (1987a) concluded from a field experiment that turbidity was the single most important factor determining the distributions of juveniles of the common marine species in an African estuarine system, Lake St. Lucia. The distributions were created when different species preferred different ranges of turbidities. Their follow-up lab experiment further supported differential preferences of turbidity by different species (Cyrus and Blaber 1987b).

Fish, like any animal, base their decisions on trade-offs between costs and benefits of each action taken. The action which leads to the greatest net benefit should be taken to maximize the animal's fitness (Ydenberg and Dill 1986, Dill 1987, Abrahams and Dill 1989, Lima and Dill 1990). Despite the many costs associated with turbidity, one major benefit exists: lessening the chance of being eaten.

Many species of fish have well-developed eyes; and vision seems to be the major sensory input for these species (Bruton 1985, Gregory 1993, Gregory and Northcote 1993, Abrahams and Kattenfeld 1997). In murkier waters, visually hunting fish can only sample a smaller volume of water, reducing their foraging efficiency. Non-visual predators with special adaptations (e.g. catfish) should not be impeded though, in fact, turbidity may actually help them approach their prey undetected (Roderiguez and Lewis 1997).

Because suspensoids in turbid water scatter and absorb light, light travels much shorter distances in turbid water than in clear water before it is dissipated. Therefore, the visual ranges of fish will be shortened in a turbid environment. This has profound impacts on visually hunting fish. As visual range decreases, the search volume for a foraging fish also decreases; therefore less food can be seen (Benfield and Minello 1996, Aksnes and Utne 1997, Beauchamp et al. 1999). But, prey, however, experience the same penalty. Because their visual range is decreased as well, they also detect predators at a much-reduced distance, making them particularly vulnerable to predators with morphological or behavioral adaptations to turbid environment (Roderiguez and Lewis 1997). Therefore, whether turbidity is more advantageous for predators or prey needs to be investigated. Like a shooter aiming for a target, a visual predator usually requires precise information to successfully strike a prey; but a prey can often successfully escape without perfect information (just needing to upset the predator's aim), so it's not unreasonable to suspect that turbidity acts as a refuge from visual piscivores. Comparative physiological and morphological studies have found that species inhabiting predominately clear-water habitats have better developed or larger eyes, retina, optic lobes, and vision-related neural structures compared to species inhabiting turbid environments (Huber and Rylander 1992, Cambray 1994, Huber et al. 1997), further affirming that vision is of limited use in turbid water.

Several authors have suggested the idea of "turbidity as cover" (Gregory 1993, Aksnes and Utne 1997, Allouche 2002). Many species of fish are visual predators, using vision to locate their prey. As their visual range decreases with turbidity, fewer prey can be seen and, therefore, are accessible to the predators. Bruton (1985) also suggested that

turbidity reduces a predator's reactive distance (the maximum distance at which the fish reacts to prey) giving fast-moving prey, such as another fish, time to escape. Thus, for prey, selecting a turbid habitat can be seen as a compromise of paying the penalties of reduced foraging and breathing efficiency in exchange for a lower risk of being eaten.

Hecht and van der Lingen (1992), in an experiment with silverside (*Atherina breviceps*), a planktivore that preys on *Daphnia*, found that the feeding rate of a visual predator was reduced at higher turbidity due to a decreased reactive distance for the fish. In the field survey component of the same study, a pelagic piscivore, skipjack (*Elops machnata*), ate fewer fish in turbid habitats than their conspecifics in clear habitats, suggesting a possible shift in feeding preference away from fish. Bluegills (*Lepomis macrochirus*) showed reduced feeding rates on *D. pulex* with increasing turbidity (Gardner 1981). Gulf killifish (*Fundulus grandis*) consumed significantly fewer daggerblade grass shrimp (*Palaemonetes pugio*) in tanks containing turbid water compared to clear-water treatments (Benfield and Minello 1996). Rowe and Dean (1998) also found that juveniles of two out of the six New Zealand freshwater fish species tested, banded kokopu (*Galaxias fasciatus*) and inanga (*G. maculatus*), had significantly reduced feeding rates in turbid water. These are only a few of the examples supporting the hypothesis that turbidity reduces the efficiency of predators, therefore, lowering the risk for prey. Yet, because in most studies cited above, the prey tested were not fish, how turbidity affects piscivory needs to be investigated further.

There are also indirect ways for turbidity to increase a fish's fitness. Because a fish is less likely to be detected and attacked by its predators in a turbid habitat, it can afford to reduce its antipredator behaviors. Antipredator behaviors can be costly in two

ways: energy expended for those activities and/or lost opportunities for performing other important activities, such as foraging and selecting mates. For example, antipredator behaviors, such as vigilance or alertness, distract a fish from concentrating on foraging, therefore, reducing the rate of energy intake (Ydenberg and Dill 1986, Dill 1987, Abrahams and Dill 1989, Lima and Dill, 1990, Abrahams and Kattenfeld 1997). Abrahams and Kattenfeld (1997) showed that fathead minnows (*Pimephales promelas*) were more willing to forage in dangerous habitats that contained a predator, yellow perch (*Perca flavescenes*), in turbid water than in clear water. This reduced the competition for food among minnows, increasing their individual energy intake and potentially their fitness. Gregory (1993) exposed juvenile chinook salmon (*Oncorhynchus tshawytscha*) to models of fish and bird predators. In the absence of either predator model, juvenile chinooks preferred deeper water when it was clear. In turbid water, they distributed randomly within an experimental arena. Exposure to the predator models caused chinooks to express a startle response, a distinct, rapid movement into deeper water. Compared to the fish in clear water, fewer juvenile chinooks dove down into deeper water and remained there for shorter durations before leaving in turbid water. Gradall and Swenson (1982) found that Creek chub (*Semotilus atromaculatus*) and brook trout (*Salvelinus fontinalis*) were both more active and used less overhead cover in moderately turbid water.

In some cases, however, moderate turbidity does not obviously provide greater safety for prey. Several studies have shown that some fish actually increase their feeding rates in moderately turbid water before the rates decrease under high turbidity. Gregory and Northcote (1993) found that juvenile chinook salmon had the highest feeding rates

for surface (*Drosophila*) and benthic (*Tubifex*) prey at intermediate turbidity levels (35 - 150 NTU; Nephelometric Turbidity Units). They attributed this to fish foraging more actively because of reduced predation risk in a turbid environment. Boehlert and Morgan (1985) showed that larval Pacific herring (*Clupea harengus pallasii*) had the highest feeding rate on rotifers (*Brachionus plicatilis*) at intermediate turbidity levels (suspended sediments 500 mg/l – 1000 mg/l). Miner and Stein (1993) showed that in high-light treatments (> 460 lx), larval bluegill's consumption of crustacean zooplankton increased with turbidity (max. 31 NTU); whereas in low-light treatments (100 - 300 lx), the consumption decreased with turbidity (max. 64 NTU). The authors of both studies suggested that the increasing feeding rates might be due to increasing prey contrast provided by suspended sediments; but this should only affect transparent planktonic prey. Larger juvenile walleye (*Sander vitreus*) with more developed retina ate greater weights and numbers of fathead minnows in turbid than in clear water, revealing a predator's adaptation against turbidity (Vandenbyllaardt et al. 1991). Still other studies have shown that predator feeding rates eventually decreased at higher levels.

Several other studies found that turbidity neither increased nor decreased the risk of predation. Abrahams and Kattenfeld (1997) found that although prey reduced their antipredator behaviors, the absolute mortality rates were similar in turbid and clear waters. Gregory and Levings (1996) did not observe a significant difference between the predation rates of juvenile salmonids (chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), and cutthroat trout (*O. clarkia clarkia*)) preyed upon by adult cutthroat trout, whether in turbid or clear water. Both adult smelt (*Retropinna retropinna*) and inanga (*Galaxias maculatus*) ate as many *Daphnia* in

turbid treatments as in clear treatments (Rowe et al. 2002). Two of the six fish species collected from Canadian River, peppered chub (*Macrhybopsis tetranema*) and flathead chub (*Platygobio gracilis*), had the same prey consumption rates in both clear and turbid waters (Bonner and Wilde 2002). Vandenbyllaardt et al. (1991) found that smaller walleye fed on fathead minnows at the same rates in both clear and turbid trials. These species may be more adapted to turbid environments. They may possess other senses besides vision for detecting and attacking prey, such as chemical (olfaction) and mechanical senses (lateral line). Predators can also show behavioral modifications in attack strategies (limnetic vs. ambush), or prey preference (Hecht and van der Lingen 1992).

Localized turbidity creates more heterogeneity in the environment. This can help increase biodiversity. More successful species which primarily rely on vision may be constrained by turbidity, leaving refuges for inferior competitors and prey. Therefore, turbidity impacts fish assemblages and community structures. The decline of the razorback sucker (*Xyrauchen texanus*), an endangered native species of Colorado, has been linked to decreasing turbidity and introduction of nonnative species (Johnson and Hines 1999). Human engineering projects, like dams and reservoirs, often reduce the frequency and intensity of floods and lower flow speeds; consequently, suspended sediment loads have decreased as well (Johnson and Hines 1999). This allows nonnative species previously not adapted to this particular environment to move in; and also removes cover or refuges for the native competitors or prey (Meffe 1984, Johnson and Hines 1999). Human induced changes usually happen in quick succession; more often than not, the native species fail to adapt to these changes. Young razorback suckers

actually preferred clear over turbid waters in lab experiments. But in lab experiments, razorback larvae were also shown to be extremely vulnerable to both native, Colorado squawfish (*Ptychocheilus lucius*), and nonnative, green sunfish (*Lepomis cyanellus*), predators. Both predators were extremely effective in clear water. Colorado squawfish consumed 90% and green sunfish consumed 99.6% of razorback sucker larvae present in the trials. Young razorback suckers failed to adopt antipredator strategies against visual predators in clear water. It seemed that increased predation in clear water was the main cause of the collapse of the razorback sucker population in the clear water reservoirs and altered tributaries below the dams, e.g. Lake Mohave (Johnson and Hines 1999). Bonner and Wilde (2002) suggested that decreased turbidity was a possible cause of the reduced distribution and abundance of fish, which historically occupied the more turbid main channels. They found that species living in the previously turbid sections fed better in turbid treatments than the fish from less turbid sections. These turbid species had morphological adaptations, such as barbells (tactile sensor), olfactory lamellae (chemical sensor), and electric sensors, to facilitate non-visual foraging (Rodriguez and Lewis 1997, Bonner and Wilde 2002). Yet as the river turbidity decreased, the advantages provided by those adaptations disappeared; and they faced competitions from clear water species, which may have led to their displacement.

After reviewing the literature, the role of turbidity in mediating predator-prey interaction is mixed. This project tested the hypothesis that fathead minnows base their choice of feeding sites on the optimal trade-offs between the cost (reduced visual foraging efficiency) and benefit (reduced predation risk) of turbidity. When predation risk

is low, prey should prefer clear water habitat. When predation risk is high, more prey should be willing to stay in the turbid water habitat with a predator than in a clear habitat with a predator (Fig. 1.1).

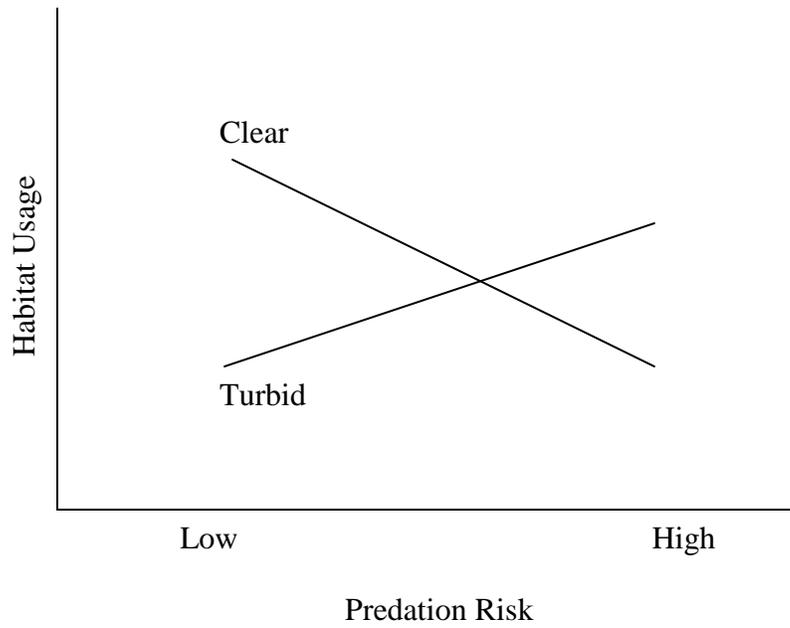


Fig. 1.1: Prediction of habitat use by prey under the influence of predation risk and turbidity. When predation risk is low, turbid water should be avoided. When predation risk is high, turbid water should be preferred.

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Chapter 2

Effects of Turbidity and Predator on Fathead Minnow Habitat Selection

Introduction:

The Ideal Free Distribution Theory (IFD) (Fretwell and Lucas 1970) predicts that when individuals have perfect information about the resource quality and location and are free to move, individuals should be distributed in accordance with the distribution of the resource (Abrahams 1986, Dill 1987, Grand 2000). Each individual then should obtain equal amount of the resource (Dill 1987). If we can identify and manipulate factors affecting the profitability of each habitat, the deviation from the IFD should represent the effects of the manipulated factors (Abrahams and Dill 1989 & 1998).

This concept is the core of several studies on the effects of predators, prey defense, and environmental factors on habitat selection. Utne and Bacchi (1997) found that both visual and chemical presence of cod (*Gadus morhua*) caused spotted gobbies (*Gobtusculus flavescens*) to reduce foraging in the affected feeding site. Grand (2000) used deviations from the IFD to measure the willingness of threespine sticklebacks (*Gasterosteus aculeatus*) of different morphology to forage in the vicinity of a predator. Abrahams and Dill (1989) first developed the technique of using deviations from the IFD plus manipulation of food ratios between patches to determine the equivalence of the risk of predation to guppies (*Poecilia reticulata*). Using the same principle and method, Grand and Dill (1997) determined the energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*). In this project, I used a modified measurement to determine deviations from the IFD. Instead of simply using numbers of fish present in each patch, the feeding activity (number of fish actively feeding) in each patch was used. This should provide a more accurate measurement because inactive fish (nonfeeders) were excluded. Nonfeeders may be satisfied fish which may not base their habitat

selection on resource level or simply fish in transit between habitats. Deviations from feeding rates predicted by the IFD were used to determine the prey's response to a predator and turbidity.

Predators can both directly and indirectly impact a prey's fitness. Predators may directly injure or kill the prey, or indirectly cause the prey to make decisions that do not maximize their energy intake (Ydenberg and Dill 1986, Persson 1993, Abrahams and Kattenfeld 1997). To avoid being detected or attacked, prey may employ antipredator behavior (e.g. schooling/grouping (Semeniuk and Dill 2004) and use of refuge (Steele 1998, Lehtiniemi et al. 2005)) or antipredator morphology (e.g. spines, size, and deepening of body (Pettersson and Bronmark 1997, Pettersson et al. 2000, Sillet and Foster 2000, Vamosi 2002)); both strategies can be energetically costly.

Studies have suggested that profitable habitats are often dangerous as well; while refuges or safer locations are often poorer foraging sites. For example, for juvenile coho salmon, gaining access to cover may mean staying in an area of slower current, suffering a lower foraging rate on in-stream drift (Grand and Dill 1997). Roach (*Rutilus rutilus*) preferred to feed on zooplankton in open water, but when they were restricted to vegetation by predators, roach suffered reduced growth rate (Persson 1993). Turbidity can be viewed in the same context. It provides cover by reducing visual abilities of predators; but as prey's visual abilities are also affected, it may also reduce their foraging efficiency. Of course, for non-visual predators or predators that are able to utilize different sensory modes, turbidity should not impede their attack, but could increase their success rate by making them harder to detect by prey (for details, see Chapter 1).

Therefore, the effectiveness of any antipredator strategy should depend on both the predator and the environment.

Many piscivores, avian or aquatic, are gape-limited (Sillett and Foster 2000, Magnhagen and Heibo 2001, Reimchen and Nosil 2002). Therefore, if an individual can reach a certain size refuge, its chance of becoming someone else's meal is greatly reduced. Crucian carp (*Carassius carassius*) develop into a deeper body shape after being exposed to chemical cues from predators. This deeper body reduces the efficiency of gape-limited predators (Pettersson and Bronmark 1997). Deeper bodied individuals may be invulnerable to smaller predators. Pettersson et al. (2000) demonstrated that individuals with a deeper body expressed less fright response when exposed to chemical cues. However, while being large decreases vulnerability, it also increases the chance of visual detection. This may suggest a dome-shaped vulnerability curve (Manderson et al. 2000) (Fig. 2.1). Smaller individuals, though vulnerable, may be more willing to take risks to obtain extra food (Grand 2000) as they are less resistant to starvation (Krause et al. 2000). Turbidity may provide cover to smaller individuals, reducing their vulnerabilities while foraging; it may allow small fish to increase feeding activities and venture out to profitable locations. That said, turbid habitats may also be less profitable due to reduced food availability and reduced detectability (for details, see Chapter 1). Therefore, whether turbidity is beneficial and who ultimately benefits from it (predators or prey) remains to be investigated. Abrahams and Kattenfeld (1997) found that smaller fathead minnows (*Pimephales promelas*) were preferred by yellow perch in clear water; but the mortality pattern was random in turbid water. Radke and Gaupisch (2005) also showed that turbidity eliminated size-selectivity using Eurasian perch (*Perca fluviatilis*)

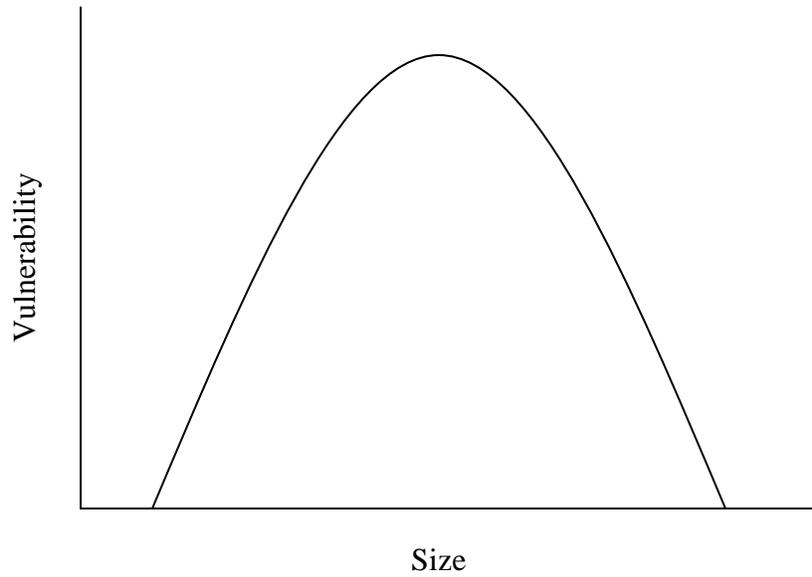


Fig. 2.1: Dome-shaped vulnerability curve. When a prey is too small, it may be hard to detect or be ignored by a predator. When a prey is too large, it may reach a size refuge and become invulnerable to predation. The highest vulnerability should fall between the two size extremes.

preying on fathead minnow. These examples seem to support the hypothesis that turbidity is more beneficial to smaller individuals.

Experiments were planned with two different species of predators, yellow perch (*P. flavescens*) and black bullhead (*Ameiurus melas*). These two species are assumed to use two different strategies of predation. Yellow perch is assumed to be a visual predator because it has no specialized external sensory apparatus other than relatively large eyes. Yellow perch have often been used in experiments involving visual foraging (Paszkowski and Tonn 1994, Abrahams and Kattenfeld 1997, Granqvist and Mattila 2004). Black bullhead, with 4 pairs of prominent barbells around its mouth, relies on chemical cues (Sherman and Moore 2001, Valentincic 2005). Therefore, turbidity should reduce predation efficiency of perch but should not have an impact on bullheads. In the laboratory experiments minnows were expected to recognize these two very different predators and adjust their habitat selection accordingly. Three predictions were tested: 1) without predator, turbidity will be avoided because it represents an adverse environment (reduced visual foraging efficiency) compared to clear water; 2) with yellow perch, turbidity reduces predation risk, allowing more minnows to feed in the presence of a predator; 3) for the trials with black bullhead, prediction 2) should not be true; and there should not be more minnows feeding in turbid water in the presence of a bullhead. The effect of prey size difference was also tested as the sizes of minnows varied greatly between 2004 and 2005. The prediction was that, with yellow perch as the predator, smaller individuals' feeding should be suppressed compared to larger individuals' in clear water. But in turbid water, smaller individuals should utilize the resource in the same fashion as their larger conspecifics.

Methods:

Animals:

The fish used in this experiment were fathead minnows and their predators, yellow perch and black bullhead. Both perch and minnows were collected from the University of Manitoba field station at Delta Marsh (98°23'W, 50°11'N) on the southern tip of Lake Manitoba. Perch were collected in September 2000. Minnows were collected in September of 2003 and September of 2004. The minnows collected in 2003 were used in 2004; the ones collected in 2004 were used in 2005. Both species were held in 70L glass aquaria in the University of Manitoba Animal Holding facility with a 12h-light (7 am – 7 pm), 12h-dark photoperiod. The aquaria were kept aerated with a flow-through system at room temperature (~ 17°C). Minnows were fed alternately with smaller Martin Classic Sinking Fish Feed No. 3 trout pellet and frozen brine shrimp (*Artemia salina*). Perch were fed alternately with larger Martin Classic Sinking Fish Feed No. 5 trout pellet and frozen brine shrimp. Bullheads were collected at Pembina River (at Highway 31, Manitoba; 98°20'W, 49°05'N) in September of 2001 and held in a 70L aquarium filtered by an AquaPlus 300 filter system in the fish lab of the Department of Zoology at room temperature (~ 20°C). The bullheads were fed approximately once a day ad lib with trout pellets and frozen brine shrimp. Exposure to "daylight" was sporadic, but on average 8 hours a day.

Apparatus:

To create a system that allows free movement of minnows between two habitats with different levels of turbidity (~ 0 and ~ 20 NTU) while maintaining a stable turbidity gradient, an aquarium was divided into three chambers by inserting two pieces of

Plexiglas to create a small chamber in the middle of the tank (Fig. 2.2, 2.3). Before both pieces of Plexiglas were inserted, two 4cm diameter holes were cut in each piece. Two vinyl tubes, 8cm long and 3.8cm in diameter created two tunnels through the center chamber. Six small holes of 0.64cm in diameter were drilled on the sides of each vinyl tube to allow freshwater to enter the tunnels and flow into the two side chambers.

Dechlorinated water flowed into the center chamber, generating water currents outwards from the center chamber into both side chambers, preventing mixing of water between the two side chambers yet permitting fathead minnows to move freely between the two locations. One hole was cut at both ends of the tank to release excess water.

Bentonite solution was created by mixing 200g of bentonite (Aldrich Cat. # 285234) into each of two containers holding 83L of dechlorinated freshwater. Air was constantly bubbled into both containers via air stones to keep bentonite in suspension. The solution was also stirred periodically (~ 3 times a day) with a wooden stick. When required by the trial condition, Bentonite solution was continuously pumped into either one of the two side chambers to create a turbid habitat by two Masterflex L/S Pump Heads (Model 7013) driven by the same motor. Two Tygon tubes leading out of the pumps were clamped on the front and back walls at the middle of the side chamber selected to be turbid. A pump speed setting of 4 was the most ideal for maintaining the desired turbidity levels (~ 0 NTU vs. ~ 20 NTU) but adjustment of pump speed was occasionally performed as required. These turbidity levels were selected because they provided the maximum contrast between them while still allowing adequate observation into the turbid side. Furthermore, Cyrus and Blaber (1987b) reported that water with a value > 10 NTU is often considered as turbid. Fluctuations in turbidity were common

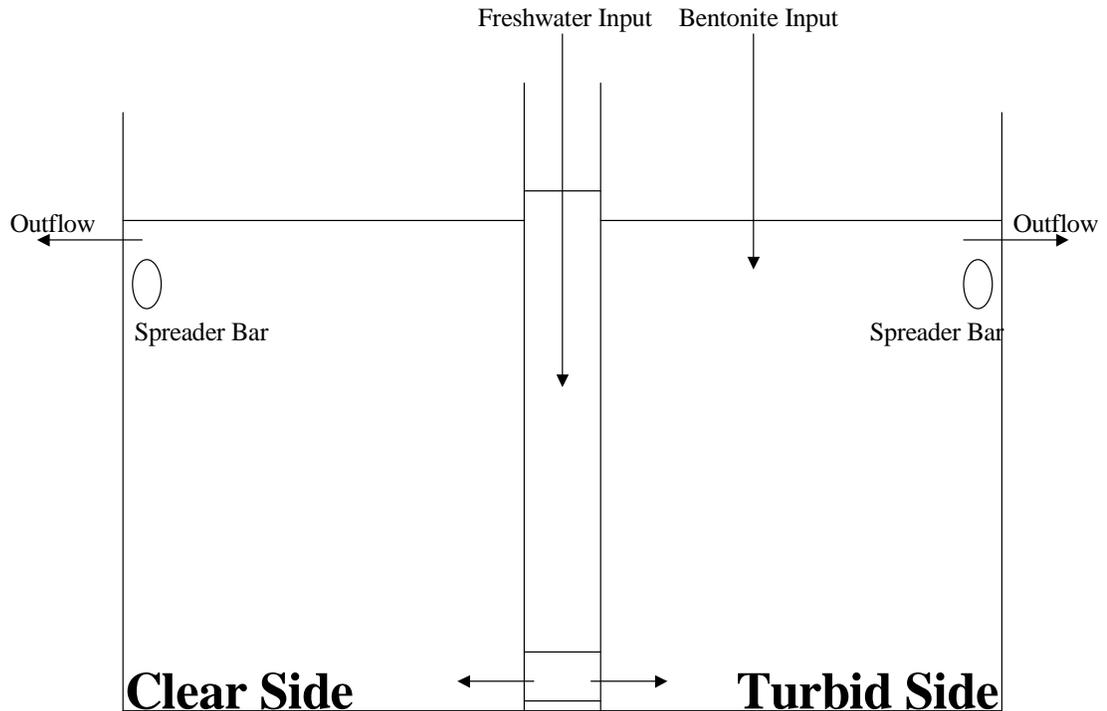


Fig. 2.2: Schematic diagram of the testing tank. The test tank was modified from a 122cm x 32cm x 46cm glass aquarium. This tank was divided into three chambers. Dechlorinated water was added to the small chamber in the middle of the tank. Two tunnels (3.8cm in diameter, 8cm in length) with six holes 0.64cm in diameter drilled into the tunnel walls connected the two large side chambers. This created positive pressure between the two sides of the apparatus, preventing diffusion of bentonite while allowing free movement of fish between the two large side chambers. Two outflows of 1cm in diameter, one at the each end and 35cm from the bottom, drain off water. When a turbid side was generated, the outflow of the clear side was shut off.

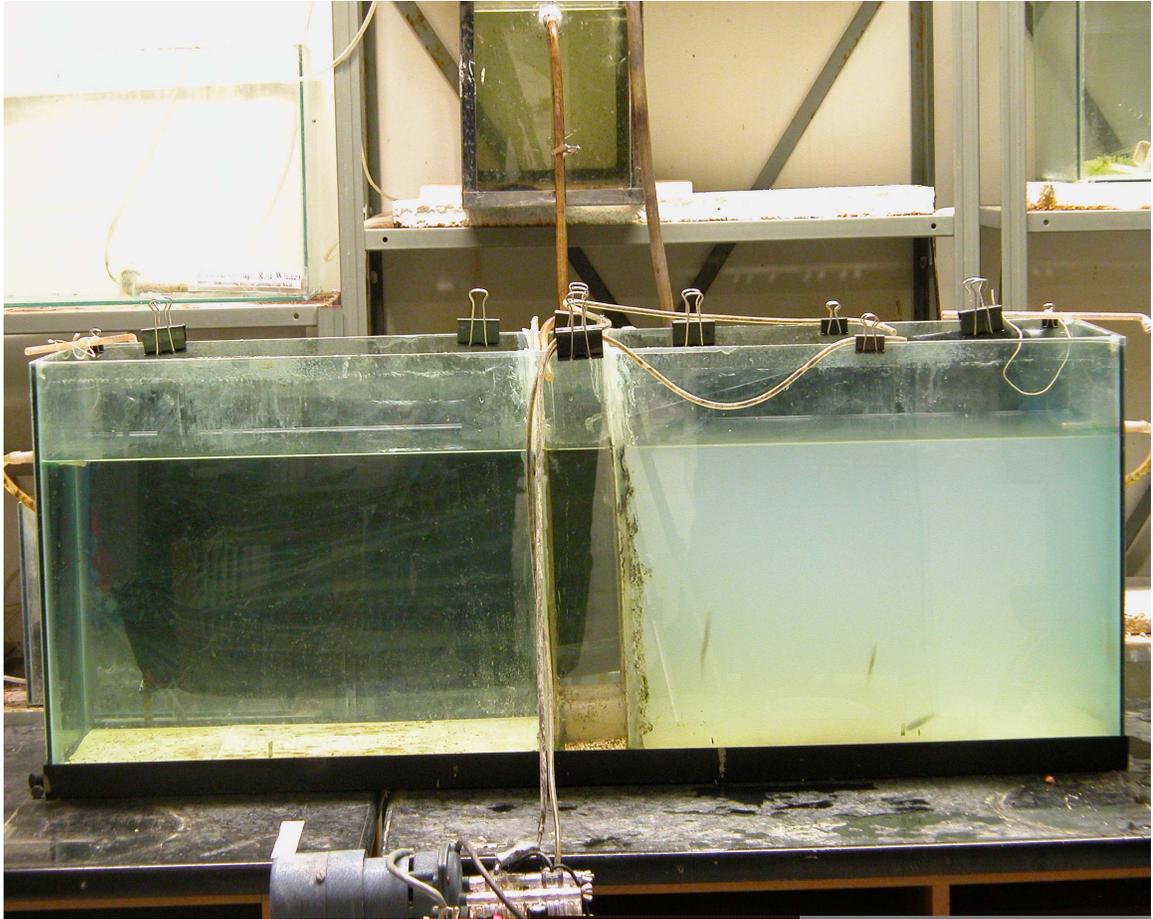


Fig. 2.3: Photograph of the apparatus at work. Removing the side panels revealed its ability to hold differential turbidity levels side by side.

but could be controlled by fine adjusting the clamps on the freshwater input and outflows. Turbidity was regularly monitored and adjusted prior to and between trials. Acceptable ranges for these experiments were < 3 NTU for clear and $18 \sim 25$ NTU for turbid.

This apparatus was capable of generating and holding the desired turbidity gradient of ~ 0 NTU and ~ 20 NTU (Fig. 2.3, Table 2.1). This was made possible by continuous freshwater flow into the center chamber, thus creating enough positive pressure from the center chamber into the two side chambers to prevent dispersal of fine bentonite between the two chambers. Furthermore, by shutting off outflow from the clear side, the direction of freshwater flow carried bentonite away from the clear side.

An automated feeder was placed at each end of the tank with a spreader bar submerged in the water across the end of the tank (Fig. 2.4) to provide a continuous feed of brine shrimp for up to 30 min (for details, see Abrahams 1989). A Sony digital camera (DCR-TRV120) was set at each end of the tank (Fig. 2.4) to record feeding activities. For the trials conducted in 2004, signals from both cameras were recorded onto one single Hi-8 tape via a Videonics MX-1 Digital Video Mixer providing a time synchronized view of fish behaviors at both ends of the apparatus. In 2005, the recording system was upgraded to a Pioneer DVD recorder (DVR-310). Three sides (front, back, and bottom) inside each side chamber were lined with non-reflective white plastic sheets to minimize disturbances to fish, remove glare and reflections from glass walls, and improve contrast between fish and their background. Images were recorded with negative imaging effect (light colors show up in black and dark colors show up in white) to increase contrast between fish and their background. This was particularly helpful when analyzing data from the turbid side.

Table 2.1: Summary of average turbidity levels for both before and after trials of different treatments in control and treatment chambers. Turbidity was measured in Nephelometric Units (NTU). C = Clear, T = Turbid, N = No Predator, P = Yellow Perch, B = Black Bullhead.

n	Treatment	Control Side (Before)	SE	Treatment Side (Before)	SE	Control Side (After)	SE	Treatment Side (After)	SE
10	C-CN	0.55	0.04	0.55	0.04	0.56	0.04	0.56	0.04
10	C-CP	0.64	0.06	0.64	0.06	0.64	0.06	0.64	0.06
6	C-CB	0.67	0.11	0.62	0.09	0.67	0.11	0.64	0.09
10	C-TN	0.81	0.09	20.40	0.30	0.90	0.08	20.45	0.38
10	C-TP	0.84	0.09	19.98	0.29	0.93	0.10	20.28	0.43
6	C-TB	1.00	0.21	20.21	0.47	1.05	0.20	20.17	0.52

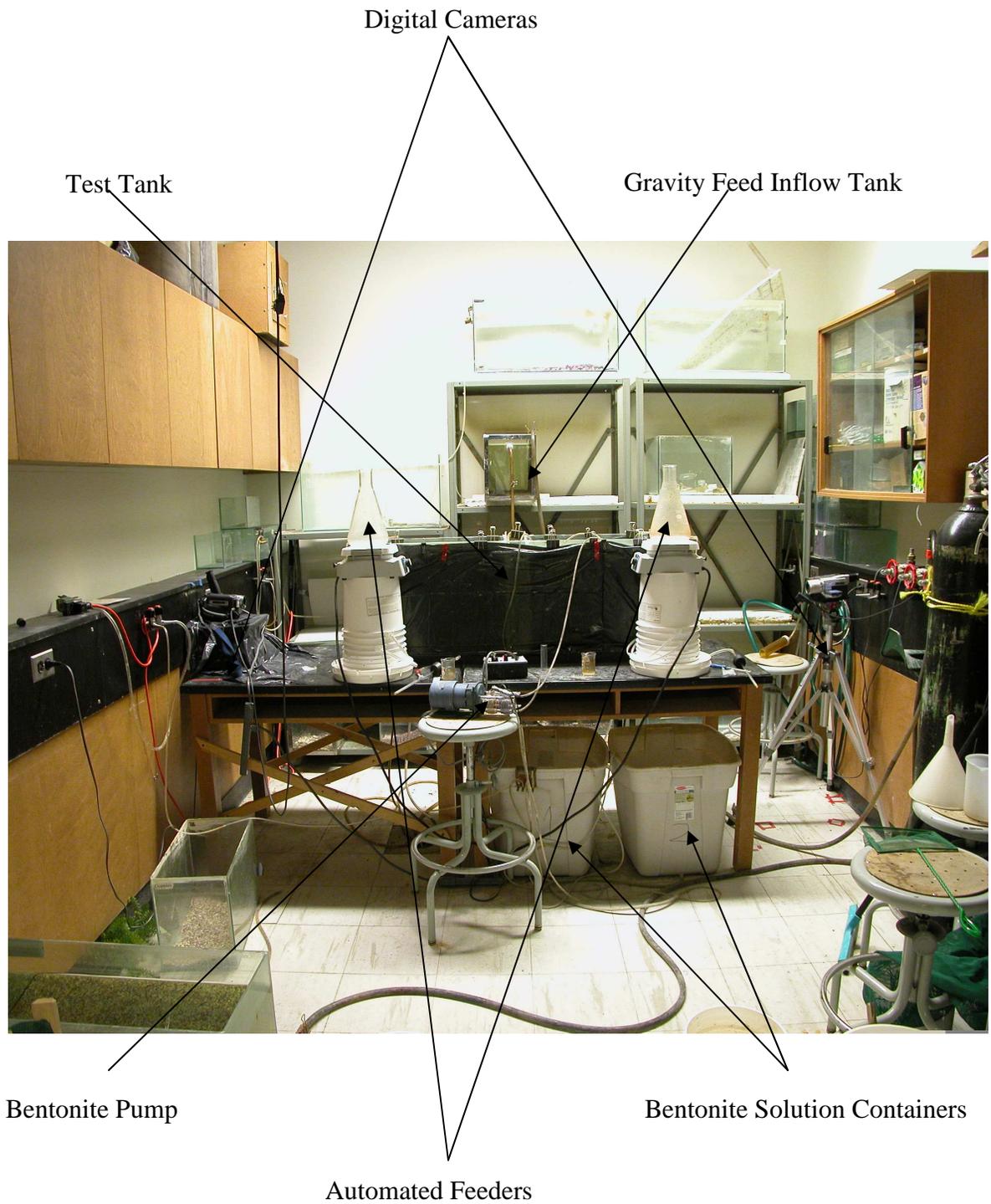


Fig. 2.4: Photograph of the test tank and peripheral equipment setup.

Experimental protocol:

Trials took place between May and September of both 2004 (4 replicates) and 2005 (6 replicates). Two weeks prior to the start of the experiments, the predators were moved from the animal holding facilities and kept in a holding tank (76cm x 32cm x 42cm) at room temperature (~ 20⁰C) in the lab for the duration of the experiment. The photoperiod in the lab was also 12h light (7 am – 7 pm), 12h dark. Fish were anesthetized with clove oil and their lengths (fork length for yellow perch; full length for black bullhead) and wet weights were recorded before the start of the first trial (Table 2.2). The predators were fed No. 5 trout pellets ad lib while in the holding tank. Ten days prior to the beginning of the 1st trial, 16 minnows were moved from the animal holding facility into a holding/training tank (51cm x 27cm x 31cm) where they received food exclusively from two automated feeders twice a day for 7 days. The total daily amount fed to the minnows was 10% of approximated total wet weight of a group of 16 fish. This diet kept the fish at a relatively constant size during each trial. Three days prior to the 1st trial, 10 fish were randomly selected from the 16 minnows in the holding tank. These 10 fish were also anesthetized with clove oil and their fork lengths and wet weights recorded (Table 2.3). They were then moved into the test apparatus to allow for acclimation. Training with automated feeders continued in the test tank until the start of trials with a daily ration of 10% of the fish's total wet weight. The same maintenance diet was used throughout all of the trials in one replicate. The 6 minnows left in the holding tank were used if replacement fish were required because of mortality. Any minnow not used in trials was retained to facilitate the next group's training with automated feeders. Additional fish were added to bring the total number of minnows in the holding/training

Table 2.2: Fork length and wet weight of predators used in the experiment.

Predator	Year used	Fork Length (cm)	Wet Weight (g)
Yellow Perch #1	2004	21.40	113.60
Yellow Perch #2	2005	22.00	106.20
Black Bullhead	2005	22.50	145.78

Table 2.3: Average fork length and wet weight for each group (n = 10) of fathead minnows used.

Year Used	Group	Fork Length (cm)		Wet Weight (g)	
		Mean	Standard error	Mean	Standard error
2004	1	6.90	0.25	3.55	0.39
	2	6.48	0.25	3.70	0.57
	3	6.35	0.29	2.96	0.38
	4	7.25	0.25	5.41	0.64
2005	5	4.82	0.17	1.19	0.18
	6	4.91	0.21	1.14	0.23
	7	4.72	0.20	1.02	0.24
	8	4.80	0.18	1.35	0.24
	9	5.20	0.12	1.79	0.11
	10	5.40	0.11	1.90	0.14

tank up to 16 again.

For 2004, yellow perch was used as the predator with four groups of minnows exposed to 4 different treatments. In 2005, trials with a second type of predator, black bullhead, were added to the original scheme. Six replicates were carried out. Each treatment consisted of one chamber with just clear water (control chamber) and another chamber in which the condition is the product of two manipulated factors (treatment chamber). This type of experiment is of a two factor repeated measures design. The two within group factors were: water clarity (turbid or clear) and risk of predation (yellow perch, black bullhead, or no predator) (Fig. 2.5). The appropriate statistical analysis for this experiment is a multiple factor repeated measures ANOVA (Zar 1996).

Each treatment was run for two days with two feeding trials (0830 and 1500, 1/4 daily maintenance diet per feeder) per day to allow sufficient time lag between trials and ample time for image analysis. The order of treatments was randomly assigned. To eliminate any potential side effect, the positions of the clear chamber and manipulated chamber were reversed between the 1st day and the 2nd day of each treatment. For the treatment that had clear water and no predator in both chambers, the side chamber with open outflow was used for data analysis to ensure consistency with turbid trials.

When required by the experiment, turning on the bentonite pump at midnight (0000) on the test date would produce a turbid chamber. Test runs of the apparatus had shown that this would allow enough time to reach the desired turbidity level (~ 20 NTU) for the turbid side before the 1st feeding trial began at 0830. The turbidity only fluctuated slightly once the desired level was reached and could be easily regulated by fine adjustment of the inflow, outflow, and/or bentonite pump (Table 2.3). Once the day's

	Clear	Turbid
No Predator	Treatment 1	Treatment 2
Yellow Perch Predator	Treatment 3	Treatment 4
Black Bullhead Predator	Treatment 5	Treatment 6

Fig. 2.5: Six treatments, each with two factors to manipulate, to be tested by this two-way factorial design with water clarity (turbid or clear) and risk of predation (no predator, yellow perch, or black bullhead) as the two main effects.

trials were concluded, the pump was shut off if the turbid side was to become clear for the next day. Test runs indicated that bentonite would be removed from the apparatus after being drained off for 6 - 8 hours and the turbid side would be returned to a clear state. The perch or bullhead predator was placed in the appropriate chamber in the afternoon (1600) prior to predator trials. Depending on the requirement of the next day's trials, it would be either moved over to the other side chamber or back to the holding tank after the completion of the day's two trials (also at 1600). The number of minnows was counted at the end of each day and mortalities were replaced. After each replicate was completed, the surviving minnows were moved to another holding tank (76cm x 32cm x 42cm) in the lab, so these fish would not be used repeatedly.

Once a trial began, two cameras recorded the minnows' feeding activities continuously for 20 minutes. Then, the numbers of fish feeding in each side were counted every 30 s. A fish was considered to be feeding if it was swimming in the close vicinity (< 10cm; a line was marked on the bottom of the tank 10cm from the glass wall facing the camera) of a feeder bar and oriented toward the feeder bar or seen intercepting food or picking up food from the bottom within a 2 s period before and after each 30 s interval. Before and after each feeding trial, turbidities in both chambers were measured using a Hach Laboratory Turbidimeter Model 2100A. Any trial with turbidity levels outside acceptable ranges (< 3 NTU for clear and 18 ~ 25 NTU for turbid) was discarded and repeated the next day at the same time.

From each recording, the proportions of feeding fish in each side were determined. Only the data from the treatment chamber were used in further analysis (number of feeding fish in the treatment chamber / total number of feeding fish in the treatment and

the control chamber). The proportions from the 4 feeding trials were averaged into one single value for each treatment within one replicate. Therefore each replicate contributed one single observation for each experimental treatment. Over the two years, ten replicates were carried out. The data from these replicates were then subjected to statistical analysis to test if the two factors (water clarity and risk of predation) and their interactions affected fathead minnow's habitat use. At the end of the experiment, overall mortality rates were calculated by dividing the total number of minnows killed by a predator (2 perch and 1 bullhead) in clear or turbid trials by the total number of minnows (including replacement) exposed to that predator in clear or turbid trials.

Statistical Analysis:

Data in percentages were arcsin transformed prior to analysis. All repeated measures ANOVAs were done using StatView 5.0.1; while one-tailed t-tests were performed to compare the average sizes from 2004 groups and 2005 groups using JMP IN 5.1.

Results:

Both water clarity and predation risk significantly affected fathead minnows' choice of feeding site; so did the interaction of predation risk x size. Size and the interactions of water clarity x size, water clarity x predation risk, and water clarity x predation risk x size were not found to have significant impacts on minnows (Table 2.4). Minnows preferred to feed in the turbid habitat regardless of the presence or absence of yellow perch (Fig. 2.6). Presence of yellow perch, however, suppressed feeding of minnows in both clear and turbid water (Fig. 2.6). Only data from the yellow perch predator treatments of 2004 and 2005 were used in this analysis.

Table 2.4: Summary of repeated measures ANOVA on percentages of feeding fathead minnows using the treatment chamber. Data from both 2004 (n = 4 groups of fish) and 2005 (n = 6 groups of fish) are included. Each replicate had 10 minnows. Data were arcsine transformed prior to analysis. Factors: Size (size of the prey: large and small), Water Clarity (clear and turbid), and Predation Risk (absence and presence of a yellow perch).

Factors	DF	F	p	Power
Size	1	4.704	0.0619	0.472
Water Clarity	1	60.714	<0.0001	1.000
Water Clarity * Size	1	0.331	0.5808	0.079
Predation Risk	1	173.225	<0.0001	1.000
Predation Risk * Size	1	7.498	0.0255	0.673
Water Clarity * Predation Risk	1	3.462	0.0998	0.364
Water Clarity * Predation Risk * Size	1	1.531	0.2510	0.187

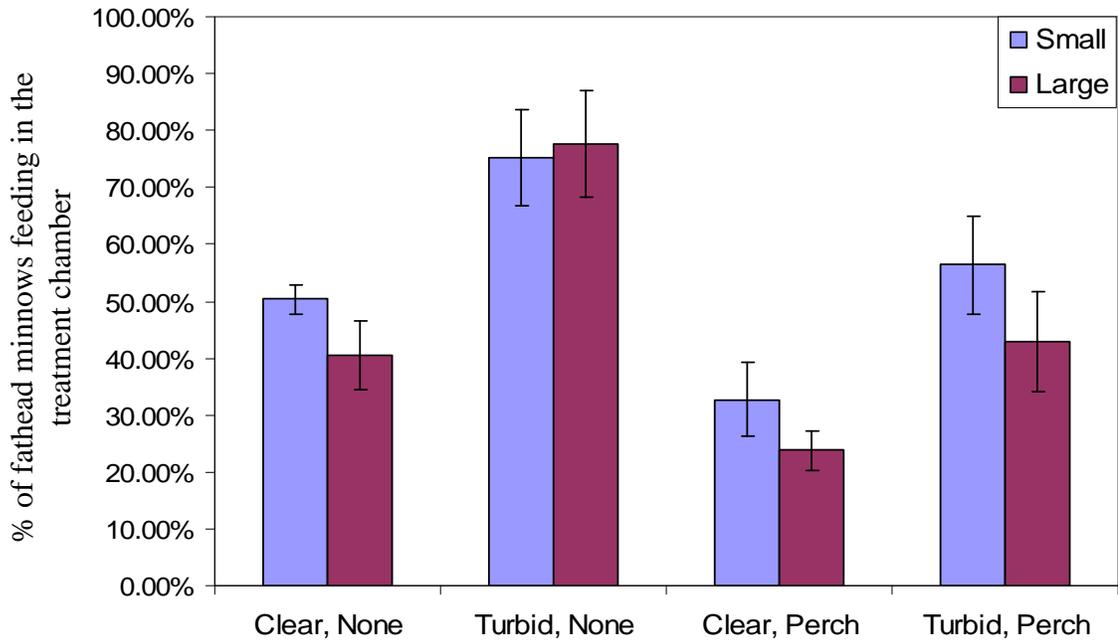


Fig. 2.6: Mean percentages of fathead minnows feeding in the treatment chamber. Only the yellow perch predator treatments are shown here. Large = larger minnows used in 2004 (n = 4 groups of fish); Small = smaller ones used in 2005 (n = 6 groups of fish). Each replicate had 10 minnows. Clear = clear water; Turbid = turbid water; None = no predator; Perch = yellow perch. Error bars represent 95% confidence interval.

Fathead minnows used in 2004 (designated as large) ($n = 4$ groups of fish; mean \pm standard error = 6.74 \pm 0.14cm; 3.90 \pm 0.28g) were significantly larger than the ones used in 2005 (designated as small) ($n = 6$ groups of fish; 4.98 \pm 0.07cm; 1.40 \pm 0.09g) (fork tail length: one-tailed t-test, $t_{0.05, 8} = 8.345$, $p < 0.0001$; wet weight: one-tailed t-test, $t_{0.05, 8} = 5.498$, $p = 0.0003$). Therefore, size class of minnows was a valid between group factor for the repeated measures ANOVA (Table 2.4) in addition to the within group factors of water clarity and predation risk.

Analysis of the complete set of data from 2005 (Table 2.5) showed that both water clarity and predation risk significantly affected minnows' choice of feeding site. The interaction of water clarity \times predation risk, however, did not. Again, minnows preferred to feed in turbid water (Fig. 2.7). Increasing predation risk decreased feeding (Fig. 2.7). Minnows, however, did not react differently to yellow perch and black bullhead (post hoc Tukey/Kramer test: yellow perch vs. black bullhead, mean difference = 3.771 $<$ critical difference = 8.058, $\alpha = 0.05$). The 2005 data were analyzed by a two factor (water clarity and predation risk) repeated measures ANOVA (Table 2.5) with 3 levels of predation risk, no predator, perch, and bullhead. Overall mortalities of fathead minnows are presented in Table 2.6.

Discussion:

Fathead minnows preferred to feed in the turbid habitat (~ 20 NTU) regardless of the predation risk. This is contrary to the original expectation of turbidity being avoided when no predator was present. Turbidity has generally been described as having negative effects on fish (Bruton 1985, Newcombe and MacDonald 1991), therefore, it is logical to

Table 2.5: Summary of repeated measures ANOVA on percentages of feeding fathead minnows using the treatment chamber. Only data from 2005 are included (n = 6 groups of fish). Each replicate had 10 minnows. Data were arcsine transformed prior to analysis. Factors: Water Clarity (clear and turbid), and Predation Risk (no predator, presence of a yellow perch, and presence of a black bullhead).

Factors	DF	F	p	Power
Water Clarity	1	139.909	<0.0001	1.000
Predation Risk	2	12.408	0.0020	0.978
Water Clarity * Predation Risk	2	3.376	0.0758	0.496

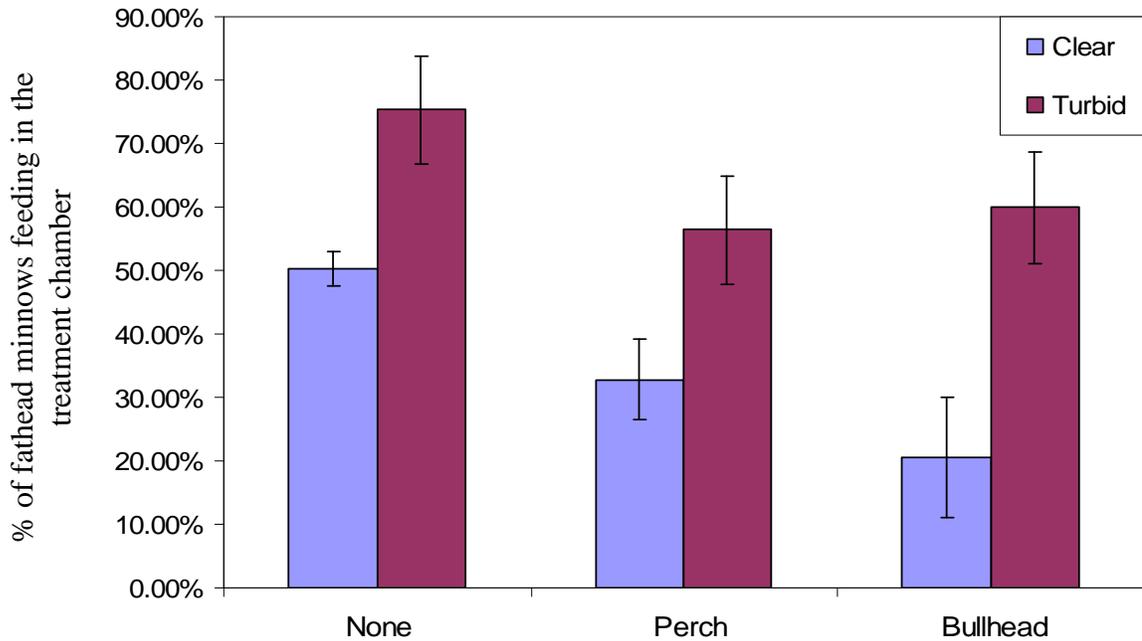


Fig. 2.7: Mean percentages of fathead minnows feeding in the treatment chamber. Both yellow perch and black bullhead predator treatments are shown here. Only minnows used in 2005 ($n = 6$ groups of fish) were included in the analysis. Each replicate had 10 minnows. Clear = clear water; Turbid = turbid water; None = no predator; Perch = yellow perch; Bullhead = black bullhead. Error bars represent 95% confidence interval.

Table 2.6: Summary of mortality rates of fathead minnows.

Year	Predator	Prey Size Class	Water Clarity	Minnows Killed	Minnows Used	Mortality Rate (%)
2004	Perch # 1	Large	Clear	2	42	4.76
			Turbid	0	40	0.00
2005	Perch # 2	Small	Clear	2	62	3.23
			Turbid	5	65	7.69
2005	Bullhead # 1	Small	Clear	5	65	7.69
			Turbid	9	69	13.04

expect fish to avoid it. But if some fish adapt higher tolerance for turbidity, they should be able to take advantage of this void left by other fish (less competition and predation).

There are many examples of fish avoiding turbid areas (Bisson and Bilby 1982, Sigler et al. 1984, Servizi and Matens 1992, Richardson et al. 2001, Mayr 2002, Richardson and Jowett 2002, Baker 2003); but on the other hand, turbid estuaries are known to attract juveniles of many species (Blaber and Blaber 1980). Although turbidity is mostly adverse for fish, it is not imminently lethal (Chiasson 1993); the severity of its impact is a product of sediment concentration and exposure length (Newcomb and Jensen 1996). So, a fish may survive extremely high turbidity for a short duration; or moderate turbidity at length. Some species have higher tolerance for turbidity than others. Boubee et al. (1997) tested juvenile migratory stages of 6 New Zealand fish for their turbidity avoidance behavior in a lab setting. Banded kokopu was the most sensitive and showed a 50% avoidance response at 17 and 25 NTU to two different sources of suspended sediment. Koaro (*G. brevipinnis*) and inanga (*G. maculatus*) showed the same level of response to the latter source at 70 and 420 NTU respectively. Three other species, shortfinned elvers (*Anguilla australis*), longfinned elvers (*A. dieffenbachia*), and redfinned bullies (*Gobiomorphus huttoni*), showed no avoidance even at 1100 NTU. Cyrus and Blaber (1987b) also found the tolerance of turbidity varies among species. Therefore, fathead minnows' preference for turbid water shown in the lab experiment is not without precedence.

Furthermore, many juveniles of different estuarine and inshore species are attracted to turbidity in Australia (Blaber and Blaber 1980). Juveniles were observed to follow high turbidity over seasons; while adults only occur in low turbidity areas. They

attributed the juveniles' preference for turbidity to reduced predation pressure and high abundance of zooplankton associated with turbidity. Similar results were also found in marine species in southeastern Africa (Cyrus and Blaber 1987a). The benefits of turbid water for walleye larvae (*Stizostedion vitreum*) are that they feed earlier, grow longer and heavier, suffer less cannibalism, and have an overall higher survival rate (Bristow and Summerfelt 1994, Bristow et al. 1996).

Although many species suffer reduced foraging and growth rates in turbid habitats (Ardjosoediro and Ramnarine 2002, Sweka and Hartman 2001a, b), others thrive in them. Fathead minnows preferred turbid habitat even when there was no predator present. It is possible that minnows might not have suffered reduced foraging in turbid water. They may have adapted other senses or strategies for locating food because turbid water is a common feature of their habitat (e.g. Delta Marsh, see Sandilands et al. 2000). Several studies have documented an increase in feeding rates on plankton and benthic invertebrate prey at intermediate turbidities (Boehlert and Morgan 1985, Hinshaw 1985, Gregory and Northcote 1993, Miner and Stein 1993, Utne-Palm 1999, 2004, Horppila et al. 2004). This might be the result of sediment particles enhancing prey contrast from the background, thus, making transparent prey more detectible. Minnows could also be feeding more actively because turbidity reduced predation pressure. Both effects could lead to more minnows feeding in turbid water.

Because fathead minnows were not merely indifferent but preferred turbid water, they should have gained extra benefit by staying in the turbid habitat. Small fish without any armor or defensive structures should be vulnerable to predators. It may be a sound strategy for small fish to always be cautious with or without immediate danger.

It is not surprising to see that the presence of predators suppressed feeding (Fig. 2.6 and 2.7). It has been well documented that predators cause prey to reduce foraging (Lima and Dill 1990). Pike larvae (*Esox lucius*) reduced attack rate on zooplankton in clear water in the presence of predator cues (Lehtiniemi et al. 2005). Both *Lythrypnus dalli* and *Coryphopterus nicholsii* (species of temperate reef fish) responded to predators by reducing foraging rate and hiding (Steele 1998). There was no interaction between predation risk and water clarity, which would imply that the effect of a predator on fathead minnows was not different whether in clear or turbid water and minnows perceived the same level of danger from predation in both clear and turbid water. However, the borderline p values and weak powers (Table 2.4 and 2.5) make this observation less than robust. It is possible that this effect could be found with more replicates; unfortunately there were not enough fathead minnows for more trials (about 2/3 of 2005 minnows died in a parasitic outbreak during the quarantine period). My original prediction was that prey would react less strongly to a predator in turbid water.

While not quantified, I observed that in clear water, when a predator was present, the fathead minnows using the same patch usually formed a tight and structured school with most heads pointing toward the predator and stayed away from it as far as possible. The fish were distracted from feeding. When the predator swam close or made a sudden move, the school would quickly scatter and reform away from the predator. In contrast, in turbid water, minnows did not exhibit such behaviors and often seemed to be totally focused on feeding and react late to the approaching predator.

Lehtiniemi et al. (2005) reported that pike larvae hid less in vegetation in turbid water than in clear water when exposed to visual or/and chemical signals from perch

predators (*P. fluviatilis*). The authors suggested the reduction in hiding behavior was due to turbidity making predators less effective. Miner and Stein (1996) found that when turbidity was greater than 10 NTU, small bluegills greatly increased their use of open water habitat instead of vegetated areas in the presence of largemouth bass (*Micropterus salmoides*).

Radke and Gaupisch (2005) reported reduced predation success of Eurasian perch (*P. fluviatilis*) on cyprinids in phytoplankton-induced turbidity. Similarly, consumption of juvenile salmonids (*Oncorhynchus* spp.) and steelhead by smallmouth bass (*M. dolomieu*) were lower in more turbid rivers (Naughton et al. 2004). Gregory and Levings (1998) concluded that higher turbidity reduced encounter and mortality rate of age-0 Pacific salmon by fish piscivores. They also noted that in turbid water salmon were active throughout the day instead of peaking their activity at twilight. This diel activity pattern may reduce the risk of predation by avoiding the periods in which their visual predators are most effective. Predation of migrant sockeye salmon fry (*O. nerka*) by rainbow trout (*Salmo gairdneri*) was higher at lower turbidities (Ginetz and Larkin 1976). The predation of white sturgeon yolk sac larvae (*Acipenser transmontanus*) by prickly sculpins (*Cottus asper*) were tested under different turbidities (Gadomski and Parsley 2005). The highest proportion ingested (98%) was found at 20 NTU. The mortality decreased with increasing turbidity, though was not eliminated at the highest turbidity tested, 360 NTU (42%). Turbidity also decreases danger from avian predators. Increasing turbidity in fish ponds has been proposed as a solution to reduce loss to fish-eating birds for fish farms. Cezilly (1992) reported significant reduction in catches by little egrets (*Egretta garzetta*) in turbid water.

These studies all concluded that predators were impeded by turbidity; therefore, prey should react less strongly to predators. Abrahams and Kattenfeld (1997) also found that the decreases in feeding caused by predators were smaller in turbid water than clear water. They attributed this to the reduced effectiveness of antipredator behavior, as the overall mortality rates did not differ in turbid and clear water. Interestingly, the mortality results showed that, for 2005 minnows, more fish were killed in turbid water. This seems to support the reduced antipredator behavior hypothesis. Because this project primarily investigated predator-prey interaction from the prey's perspective, prey mortality was intentionally minimized by keeping the predators satiated. Mortality was highly variable among trials, making statistical analysis of the data impossible.

In this experiment, I did not find a significant interaction between water clarity and predation risk. It suggests that water clarity and predation risk might have affected fathead minnows independently. The threat of the predator might be equal whether in turbid and clear water. Cerri and Fraser (1983) did not find an interaction between patch quality and predation risk. They predicted that minnows (*Semotilus atromaculatus* and *Rhinichthys atratulus*) should take proportionally more risk when using a high food patch and proportionally less risk when using a low food patch. They termed this a "balancing" strategy. Their results showed that predation risk had the same amount of suppression regardless of the quality of the patch. Gotceitas and Colgan (1990) discussed risk-balancing and risk-adjusting behaviors in detail. Risk-adjusting means that the effects of predation risk are the same regardless of patch qualities. While the quantities of food did not vary in this experiment, the overall patch qualities were manipulated through

turbidity levels. The responses of minnows in this project concurred with the findings of Cerri and Fraser (1983); both results fit the description of a risk-adjusting response.

The results of repeated measures ANOVAs showed the size difference between minnows of 2004 and 2005 did not significantly affect their behaviors; there were also no interactions involving size and the other two factors, except for the interaction between predation risk and size (Table 2.4). But the p values and powers are low, making these results questionable. Generally speaking, against gape-limited predators, fish vulnerability decreases with increasing size. While predator's reactive distance and probability of pursuit increase with prey size and movement (only when the prey is small), the success rate of an attack decreases with size (Howick and O'Brien 1983). But like the dome-shaped mortality proposed by Manderson et al. (2000), the authors suggested that being very small (< 4 cm for bluegill, *Lepomis macrochirus*, against largemouth bass predation) and being very large both can provide a size refuge. However, for individuals caught in between, being larger is still safer. Crucian carp provide an excellent example of size-related vulnerability; they can alter their body morphology to escape size-limited predators (Pettersson and Bronmark 1997, Pettersson et al. 2000). Large fish are able to use more profitable but dangerous open water, while small fish are limited to vegetated areas and suffer poor foraging and low growth rates (Gilliam and Fraser 1987). Abrahams and Cartar (2000) reported that larger individuals of fathead minnows and brook sticklebacks (*Culea inconstans*) were more willing to feed in the presence of a walleye than smaller ones.

Because activity makes prey more detectable to predators (Howick and O'Brien 1983, Utne-Palm 2000), the more active a forager is, the more likely it will be attacked.

But because turbidity reduces reaction range, it may provide cover to active individuals. Sweka and Hartman (2001a) mentioned that although brook trout (*Salvelinus fontinalis*) did not suffer a decreased foraging rate in turbid water, they had to spend more effort. A similar observation was made in juvenile perch (*P. fluviatilis*) (Granqvist and Mattila 2004). For smaller individuals, energy intake is more critical than for larger individuals, as they are less able to withstand starvation and grow faster (Utne et al. 1997, Grand 2000, Krause et al. 2000, Lehtiniemi et al. 2005). It is interesting to note that while not statistically significant, in all treatments but one (turbid, no predator), smaller fish had higher feeding rates (Fig. 2.6).

In the 2005 trials, minnows did not react differently to bullhead and perch, even though the bullhead killed more minnows, especially in turbid water. Prey fish are known to identify predators visually or chemically and respond differently to different species, size, and predator hunger states (Magurran 1990, Light 2000, Kelley and Magurran 2003). Crucian carp did not exhibit significant fright response when exposed to small pike which did not eat prey containing alarm substance. There was also no response to nonpredatory fish. Larger predators elicited stronger response (Pettersson et al. 2000). In turbid water, minnows might not be able to perform inspection and therefore respond differently to different predators; but minnows certainly would detect that a predation event had just taken place. Fathead minnows are able to detect alarm substance released by injured conspecifics (Hartman and Abrahams 2000).

Predation often has a strong impact on community and population structures (Thorp 1986, Paszkowski and Tonn 1994, De Meester et al. 1995). Many times smaller fish are relegated to poorer habitats by predators or competitors. They suffer decreased

growth rate and fitness as their larger/superior cohorts monopolize richer resource (Mittelbach 1986). But turbidity could change that by reducing predation and competition. Berg and Northcote (1985) reported that juvenile coho salmon stopped expressing social hierarchy and defending territories at higher turbidity (30-60 NTU) because of visual isolation among individuals. As a result, the feeding of subordinate fish was no longer suppressed by the dominant fish. Also being restricted to poor habitat heightens the intraspecific competition among small individuals, further decreasing their fitness (Mittelbach 1986). Therefore if the predation risk of the open habitats is lowered by turbidity, small fish can distribute themselves more evenly. This should benefit small individuals by providing access to more food and reducing competition. Similar sized fish of different species may be confined to a common refuge and compete for the same resource; e. g. small bluegills and pumpkinseeds feed in the same vegetated habitats (Mittelbach 1984). Reducing predation allows the species to exploit different resources and reduces interspecific competition. Therefore small fish, such as fathead minnows, may gain additional resources as well as experiencing a reduced risk of predation in turbid habitats.

The strong affinity for turbidity shown by fathead minnows suggested that turbid habitats may be important for small foraging fish as found by Blaber and Blaber (1980) and Cyrus and Blaber (1987a). Both Abrahams and Kattenfeld (1997) and Reid et al. (1999) showed that although the overall mortality remained the same, the mortality of smaller individuals decreased with increasing turbidity. This is the direct benefit of turbidity. Predation risk also often limits smaller fish's activity level and habitat use. Turbidity may also allow the smaller individuals to access additional resources and

reduce competition. These are the indirect benefits of turbidity. Because the results of the lab experiment showed that more of the smaller minnows were killed in turbid water, albeit without statistical verification, it suggests that the indirect benefits are more important than the direct one. Although this project did not conclusively find that a predator's effect on prey was mitigated by turbid water, turbidity still allowed more prey to feed in the presence of a predator. This also agrees with the indirect effects of turbidity. Overall, turbidity appears to be beneficial to small forage fish.

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Chapter 3

Theoretical Models of Predator-Prey Habitat Selection under the Influence of Turbidity

Introduction:

Turbidity is generally negative for many fish (see Chapter 1); yet there are still many species preferring this type of habitat, especially juveniles (Cyrus and Blaber 1987). In Chapter 2, fathead minnows (*Pimephales promelas*) showed a strong preference for turbid habitats regardless of the level of predation risk. As minnows are small and without any defensive structures, they should be vulnerable to predators. Predators can affect a prey's fitness both directly (death) and indirectly (lost feeding opportunities and extra energy expenditure) (Dill 1987, Persson 1993, Abrahams and Kattenfeld 1997).

It has been proposed that turbidity is beneficial to small fish. Blaber and Blaber (1980) found that while juveniles of many species were attracted to turbid estuaries, the adults avoided them. The advantage of turbid water to juvenile fish may be reduced predation pressure. Utne-Palm (2002) described turbidity as fog, affecting long-distance vision, but not the visibility of close objects. Small fish should suffer less loss of visual ability than large fish in turbid water. Because small fish have shorter visual ranges to begin with, the light scattering and absorbing properties of turbidity should have less or even no impact on them; as for large fish, their large visual ranges should be severely affected (Giske et al. 1994, Fiksen et al. 2002, Utne-Palm 2002). As a trade-off, small individuals suffer a relatively small decline of their foraging ability but gain a substantial advantage from reduced predation risk. Small fish may also detect predators at a shorter distance, but this should be more than adequately compensated by the loss suffered by the larger predator. A good example is that even though bluegills' reaction distance decreased rapidly in turbid water, they still always reacted to largemouth bass predators before the predators detected them (Miner and Stein 1996). Ginetz and Larkin (1976)

demonstrated that predation of rainbow trout (*Salmo gairdneri*) on migrant sockeye salmon (*Oncorhynchus nerka*) fry was higher at lower turbidities. Gregory and Levings (1998) found that migrating age-0 Pacific salmon were less likely to be killed by piscivorous fish. These studies supported the idea presented by Utne-Palm (2002): turbidity has strong positive effects on small fish (larvae and planktivores), but not on large fish (piscivores).

The experimental chapter investigated the effects of turbidity on predator-prey interaction from the prey's perspective. While the results did not conclusively find that predation pressure was reduced by turbidity, the strong affinity for turbid habitats by fathead minnows suggests that minnows gained benefit in turbid water. However, the experiment did not measure how predators would have reacted to turbidity as the predators were not allowed to switch habitats. If larger fish indeed avoid using turbid habitats as found by Blaber and Blaber (1980), small fish benefit from reduced predation. Yet, as the density of small fish in a turbid habitat increases, their fitness suffers from increased competition. Similarly, if most of the prey are in turbid habitats, predators will have to follow them into these habitats or starve. Both predators and prey will base their habitat selection not only on the environmental factors, but also on each other – a predator-prey game (Hugie and Dill 1994). This chapter investigates how turbidity affects the interaction between predators and prey, particularly, their habitat use.

Computer models have been widely used for habitat selection and foraging behavior simulation (Isawa 1982, Abrahams 1986, Gabriel and Thomas 1988, Hugie and Dill 1994, Giske et al. 1997, Ward et al. 2000, Holker et al. 2002, Maes et al. 2005). These models are excellent tools for complementing empirical works. They provide a

cheap and convenient way to test hypotheses and help visualize the consequences of predictions.

The models written for this chapter are based on the optimality model, the ideal free distribution (IFD) (Fretwell and Lucas 1970). The original IFD was made with several important assumptions: 1) resources are in patches; 2) resources cannot be depleted; 3) all foragers have perfect information about the distribution of their resources; 4) all foragers are equal; 5) all foragers are free to enter any patch; and, 6) there is no cost to travel between patches. From these assumptions, the IFD predicted: 1) all individuals across patches should have the same energy intake and 2) the distribution of individuals should match the resource level of each patch (Ward et al. 2000).

The IFD is often the foundation for modeling habitat selection and foraging behavior. Based on its assumptions and predictions, an equation of resource-matching can be expressed as:

$$F_1 / N_1 = F_2 / N_2 = \dots = F_n / N_n \quad (1)$$

F_1, F_2, F_n represent the amount of food available in each patch.

N_1, N_2, N_n represent the number of foragers in each patch.

As long as the individuals are getting the same amount of energy across the patches, no individual will leave. However, food availability is the sole determinant of energy intake only when all other factors in the patches are equal. Many other factors affect the profitability of a patch. For example, for ectothermic aquatic organisms, water temperature affects their metabolic rates; strength and direction of current affects how hard they have to swim. Both affect their energy expenditure and, therefore, their net energy gains. These factors will cause the forager distributions to mismatch the resource

distributions. If the resource distributions are known, then the energetic equivalents of these factors can be calculated.

Predators also have a strong effect. Food supply and predation pressure have been shown to influence fish habitat selection (Werner et al. 1983, Gilliam and Fraser 1987, Gotceitas 1990, Goteceitas and Colgan 1989, 1990a & b). With no predators, fish should distribute according to the IFD, as this would maximize individual energy intake (Gotceitas 1990) with more fish selecting the more profitable habitats. Yet, because the more profitable habitats are also often the more dangerous (e.g. lack of cover, frequented by piscivores attracted by foragers), prey frequently face the dilemma of choosing a safe but less profitable vs. a dangerous but more profitable habitat (Mittelbach 1986, Persson 1993, Grand and Dill 1997).

Gilliam and Fraser (1987) and Gotceitas (1990) both presented results supporting a “trade-off” model based on selecting habitats that minimize the ratio between mortality and foraging rate. Prey should neither base their choice solely on maximizing the energy intake nor predator avoidance. Both extreme strategies lead to either a quick death or severely declining fitness. Similarly, Giske et al. (1997), also using a mortality-based ratio, g/M (g = growth rate; M = mortality rate), modeled vertical distribution of copepod under predation risk.

But mortality rate is not necessarily the only consequence of predation. Predators are not always successful; and prey can deploy antipredator strategies to counter the threat. Instead of using the mortality rate-foraging rate ratio to assess predator’s impact, Abrahams and Dill (1989) took another approach. They determined the energetic cost of a cichlid (*Cichlasoma* sp.) predator to a group of 10 guppies (*Poecilia reticula*) using the

deviation of the guppies from the IFD. The presence of the predator caused the dangerous patch to be underused, even though both patches had equal food supplies. Assuming a density-dependant energy intake rate, the fewer individuals in the dangerous patch would have a higher energy intake; but, according to the IFD's prediction, to keep distributions in equilibrium, individuals in both patches must do equally well; therefore, the presence of the predator was offsetting the higher energy intake. The difference between the individual energy intake rates in the dangerous and safe patches was the energetic equivalent of predation which included costs from lost feeding opportunity and increased metabolic rate due to vigilance and stress (Ward et al. 2000). Even in a study showing that the IFD method underestimated predation risk, Kennedy et al. (1994) still reached their conclusion by calculating an associated energetic cost of predation. They did not assume IFD and calculated the risk by measuring the deviations from predator-free baseline distribution.

Lima and Dill (1990) reviewed studies showing that prey, with increasing group size, decreased their response to predators. In a group, there are more eyes to detect approaching danger, therefore, allowing lower individual vigilance, yet still maintaining or achieving a higher overall vigilance. Each individual then suffers fewer penalties associated with vigilance (energy allocated to vigilance and reduced focus on feeding). Mortality-wise, increasing group size also produces a "dilution of risk" effect assuming predators are limited in their ability to attack more than one prey at once. The larger the group is, the lower the probability of an individual being the target of an attack (Lima and Dill 1990, Grand and Dill 1999). Therefore, the cost of predation, like the habitat profitability, was set as density-dependent in the models.

Abrahams and Dill (1989) provided the justification of simulating predation risk in the term of energetic units. This created a common currency linking resource level, predation risk, and net gain. Instead of trying to incorporate the complex mechanisms of predation, such as capture success and handling time, the effect of a predator was simply presented as a number. This helped to simplify the math needed for the models. Moreover, the goal of this project was to observe whether turbidity mitigated predation risk from prey's perspective. Ward et al. (2000) used the same approach in their simulation model of foraging behavior and the effect of predation risk on European hedgehog (*Erinaceus europaeus*). Also factored into the models was a cost of employing some level of antipredator strategy even when predators were absent (Grand and Dill 1999). Just because a predator is not seen does not guarantee that it is not there. Therefore, it is prudent for small animals to always carry some level of wariness. This cost was also assumed to be density-dependent.

Many studies have found that fish's visual ranges are reduced in turbid water, and often, their foraging success as well (Vinyard and O'brien 1976, Berg and Northcote 1985, Barret et al. 1992, Vogel and Beauchamp 1999, Sweka and Hartman 2001b, Asaeda et al. 2002). Miner and Stein (1996) found that bluegill reaction distance declined with increasing turbidity from less than 2 m in clear water to 23 cm at 10 NTU to 9 cm at 50 NTU. Sweka and Hartman (2003) showed that for smallmouth bass, reaction distance decreased from 65 cm in clear water to 10 cm at 40 NTU. A reduced visual range should lead to a reduced ability to detect and assess food supply, thus, reduced foraging efficiency. In the models, this reduction in foraging efficiency in turbid water was expressed as a fraction of the foraging efficiency in clear water. In clear water, the foraging efficiency

was set as 1 (the IFD assumes that foragers have perfect knowledge of all the resource in a patch and are free to maximize intake). The food available in turbid water was the product of the total amount of food and this foraging efficiency factor.

The efficiency factor was different for predator and prey. Utne-Palm (2002) suggested that larger fish with longer visual ranges should be affected more severely than smaller fish with shorter visual ranges. Generally, piscivores are larger than their prey; therefore, in turbid water, predator foraging efficiency should suffer more than prey foraging efficiency.

In the models, predator foraging efficiency was also used to determine how much of a threat a predator was in a given setup; and, hence, the predator's real energetic cost. Because turbidity was expected to make predators less effective (dangerous), I assumed that prey were able to lower their guard to its basic antipredator expenditure (predator absent) by the same fraction.

Model 1 generated distributions from a range of values set for the previously described factors. By matching the empirical distributions (Chapter 2) with the computer-generated distributions, possible values for these factors were identified. These values helped to establish theoretical relationships among predator, prey, and water clarity. Model 2 then applied these values to a more realistic setting (predator movement was not restricted). This model should shed some light on how predators and prey react to each other and turbidity.

Methods:

Model 1:

Both programs were written as Macros embedded in Microsoft Excel using Visual Basic language. Coding for both Model 1 and Model 2 can be found in Appendix 1 and Appendix 2, respectively. Model 1 mimicked the four treatments used in the laboratory experiment of 2004 (see Methods, Chapter 2). The prey was assumed to assess the quality of a habitat by net density-dependent individual energy gain.

For clear water, no predator treatment, the net individual energy gain was calculated as the total food available in the patch minus the cost of employing a basic level of antipredator strategy when the danger was not imminent, then divided by the number of the foragers already in the patch plus the one animal that was doing the assessment:

$$(F_n - \text{NoP}) / (N_n + 1) \quad (2)$$

where: NoP represents the cost of the basic antipredator behavior when predators are absent.

Both individual food intake and individual antipredator energy expenditure had the same denominator (fish already in the habitat plus one inspecting individual).

Both the food available and cost of antipredator strategy should be influenced by the factors of prey foraging efficiency and predator effectiveness. I expected clear water to neither enhance nor decrease prey and predator's foraging abilities; therefore, both factors were set as 1, hence, omitted from the equations. This equation was also used to calculate the qualities of all the "control patches" (see Methods, Chapter 2).

For clear water with a predator, the energetic equivalent of a predator was deducted from the food available:

$$(F_n - P) / (N_n + 1) \quad (3)$$

where: P represents the energetic equivalent of a predator.

Again prey and predator's efficiency factors were omitted.

For turbid water with no predator, the food available to prey was affected by the prey's foraging efficiency and the level of antipredator expenditure was affected by predator's efficiency:

$$[(F_n \times PyT) - (NoP \times PredT)] / (N_n + 1) \quad (4)$$

where: PyT represents prey's foraging efficiency in turbid water.

PredT represents predator's foraging efficiency in turbid water.

For turbid water, no predator treatment, the energetic cost of a predator was affected by the predator's effectiveness in turbid water:

$$[(F_n \times PyT) - (P \times PredT)] / (N_n + 1) \quad (5)$$

Sequentially, each animal was to assess both patches before deciding which one to stay in. If the individual intake rates of both patches were equal, the animal would have an equal chance of randomly picking a clear or turbid patch. There were 10 animals per replicate; 10 replicates were programmed to be run. The average proportions of fish choosing the "treatment (manipulated) patch" (see Methods, Chapter 2) were recorded on the spreadsheet.

The food supplies to both patches were set at 100 energy units and not depletable. Both the energy equivalent of a predator and the cost of basic antipredator expenditure with predator absent were given a range of 0 – 100 energy units at an interval of 10

energy units. Both the prey and predator's efficiency factor in turbid water were given a range of 0 – 1 at an interval of 0.1.

Model 2:

In the laboratory experiment and Model 1, a single predator was restricted to the treatment patch, thus, creating a fixed difference of predation risk. Model 2 gave predator(s) the freedom to move between patches, assess the qualities of both patches based on the availability of prey, and select the most profitable habitat. Because both predator and prey were free to select habitats, their decisions depended on and impacted the other's decisions. This interaction made this model a game situation (Hugie and Dill 1994).

The model first established an initial distribution of prey without predator in both the clear (both patches clear) and the turbid water treatment (1 patch turbid; 1 patch clear) using equations (2) and (4). For the turbid water treatment, the patch containing turbid water was always designated Side 1. Next a predator or predators selected a patch based on the availabilities of prey.

For the clear water patch:

$$N_n / (\text{Pred}N_n + 1) \tag{6}$$

Where: $\text{Pred}N_n$ represent the number of predators in each patch.

For the turbid water patch:

$$(N_n \times \text{Pred}T) / (\text{Pred}N_n + 1) \tag{7}$$

As for prey, if a predator found both patches to be equally profitable, a random choice put the predator into one of the two patches. After the predator or predators established their distributions, a fish, either a prey or a predator, was randomly selected to come out of its

patch, reevaluate both patches, and reselect (see Abrahams 1986 for details). There were 100 resamplings in each replicate.

For a resampling prey, if there was no predator in the clear water patch, equation (2) was used again. If there was at least one predator present:

$$(F_n - P \times \text{Pred}N_n) / (N_n + 1) \quad (8)$$

If there was no predator in the turbid water patch, equation (4) was used again. If there was at least one predator present:

$$[(F_n \times P_{yT}) - (P \times \text{Pred}T \times \text{Pred}N_n)] / (N_n + 1) \quad (9)$$

If the resampling fish was a predator, equation (6) was used for the clear water patch; (7) for turbid. Average proportions of prey and predator using Side 1 were recorded as well as their distributions for each resampling (Fig. 3.1).

All the variables in model 2 can be changed easily from the spreadsheet. The foods in both patches were still set at 100 energy units each. The number of prey was still 10. Model 2 ran simulations for 1 – 4 predators with the combinations of the predator and the baseline antipredator costs and the predator's and the prey's foraging efficiencies as determined by Model 1.

Results:

Model 1:

This model, using the combinations of factors shown in Table 3.1, created 14641 patterns of proportional use of the 4 treatment patches. The combined results from large and small perch trials established an empirical pattern (Table 3.2) for these simulated patterns to be compared to. None of the simulated patterns fell exactly within all four 95% confidence intervals of the empirical distributions, although some came very close.

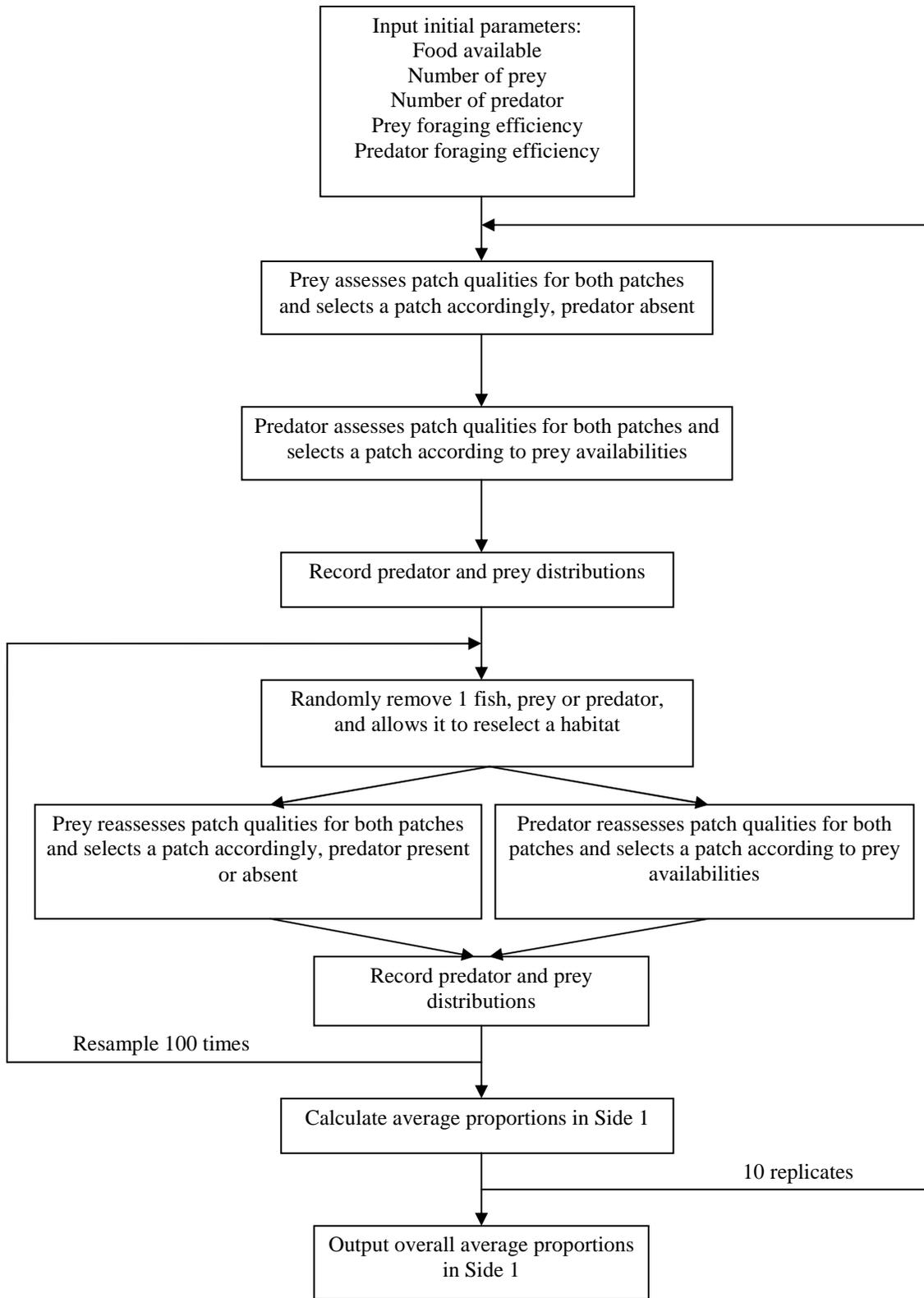


Fig. 3.1: Flowchart of operations in Model 2.

Table 3.1: Summary of variables used in Model 1.

Factors	Value	Interval	Unit
Energetic Cost of a Predator	0 - 100	10	Energy Unit
Antipredator Cost when Predator is Absent	0 - 100	10	Energy Unit
Prey Efficiency in Turbid Water	0 - 1	0.1	N/A
Predator Efficiency in Turbid Water	0 - 1	0.1	N/A
Prey Efficiency in Clear Water	1	N/A	N/A
Predator Efficiency in Clear Water	1	N/A	N/A

Table 3.2: 95% confidence intervals for minnows feeding in the treatment chamber (see Chapter 2) established by combining the perch treatments of 2004 and 2005 and the acceptable ranges used for selecting simulated patterns. Clear = clear water; Turbid = turbid water; None = no predator; Predator = predator present.

	Clear, None	Turbid, None	Clear, Predator	Turbid, Predator
95% C.I.	42.21% - 50.51%	70.23% - 82.24%	24.29% - 34.03%	43.71% - 58.33%
Ranges Acceptable	40.00% - 55.00%	70.00% - 85.00%	20.00% - 35.00%	40.00% - 60.00%

It was decided to slightly extend the acceptable ranges to the nearest multiple of 5% “outward” from the empirical means (Table 3.2). Twelve combinations of the values produced simulated distributions deemed similar to the distribution pattern obtained from the lab experiment (Table 3.3). These 12 combinations of values were used as input variables for Model 2.

Model 2:

This model generated distributions for both prey and predator using the 12 sets of values produced by Model 1. Predator(s) were free to move between the 2 patches and interact with prey. Simulations were run for 2 types of environment settings: both patches containing clear water; one patch containing clear water and one patch containing turbid water. This turbid patch was always designated Side 1 for analysis. Simulations were run for up to 4 predators. When both patches contained clear water, predators and prey used both patches equally (Table 3.4a, b, c, & d). Prey preferred turbid habitats regardless of the level of predation pressure at the prey foraging efficiencies tested (Table 3.3, 3.4a, b, c, & d). But the strength of this preference was influenced by predator efficiencies (Fig. 3.2). As the predator’s efficiency in turbid water decreased, the prey’s preference for turbid habitat increased. Predators’ use of turbid habitats varied greatly (Table 3.4a, b, c, & d). In single predator simulations, the predator’s use of turbid habitat depended on its efficiency factor in turbid water (Table 3.4a, Fig. 3.2). When the efficiency was only slightly reduced (0.8), the predator used only the turbid patch. When the efficiency was reduced further (0.5 and 0.6), the predator used both patches, but still slightly preferred the turbid patch. As the efficiency went down more (0.3 and 0.4), the predator preferred

Table 3.3: Summary of the combinations of factors generating patterns similar to the pattern observed in the laboratory experiment using Model 1. Clear = clear water; Turbid = turbid water; None = no predator; Predator = predator present.

Combination	Energetic Cost of a Predator	Antipredator Cost when Predator is Absent	Prey Efficiency in Turbid Water	Predator Efficiency in Turbid Water
A	80	50	1	0.2
B	80	60	0.9	0.3
C	80	60	1	0.4
D	90	60	0.9	0.3
E	90	60	1	0.4
F	90	70	0.6	0.1
G	90	70	0.7	0.2
H	90	70	0.9	0.5
I	90	70	1	0.6
J	90	80	0.6	0.3
K	90	80	0.7	0.4
L	90	80	1	0.8

Table 3.4: Summary of the average simulated distributions of prey and predator using Side 1 and the shapes of the distribution patterns generated by Model 2.

a) simulations with 1 predator:

Combination	Average Prey Distribution				Average Predator Distribution			
	Clear (%)		Turbid (%)		Clear (%)		Turbid (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
A	52.77	1.99	78.82	1.06	43.27	5.11	10.99	4.50
B	50.97	1.77	71.04	0.82	48.22	3.89	39.21	3.53
C	50.87	1.52	70.47	0.99	47.62	3.48	40.69	4.82
D	51.48	2.74	75.26	1.10	47.13	4.68	35.45	3.49
E	46.73	2.06	72.72	1.03	54.46	3.28	42.18	3.06
F	49.21	2.99	89.03	0.13	51.78	5.07	0.00	0.00
G	51.05	2.19	74.57	0.89	50.10	2.59	38.91	1.72
H	48.11	1.96	69.50	1.24	49.80	3.65	54.26	3.29
I	47.24	3.24	69.07	1.31	52.28	4.93	57.72	3.55
J	52.42	1.74	71.96	0.98	45.84	4.52	31.78	4.36
K	52.56	2.38	71.99	0.85	44.46	5.49	34.06	4.50
L	49.43	1.50	60.13	0.02	52.08	3.97	100.00	0.00

b) simulations with 2 predators:

Combination	Average Prey Distribution				Average Predator Distribution			
	Clear (%)		Turbid (%)		Clear (%)		Turbid (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
A	50.00	0.00	80.36	0.46	50.00	0.00	44.11	1.32
B	50.00	0.00	79.79	0.04	50.00	0.00	50.00	0.00
C	50.00	0.00	79.62	0.10	50.00	0.00	50.00	0.00
D	50.00	0.00	78.62	1.19	50.00	0.00	57.92	2.16
E	50.00	0.00	77.41	0.93	50.00	0.00	58.66	1.22
F	50.00	0.00	88.41	0.53	50.00	0.00	44.90	1.63
G	50.00	0.00	88.45	0.36	50.00	0.00	44.36	1.25
H	50.00	0.00	72.42	1.59	50.00	0.00	57.97	1.82
I	50.00	0.00	73.12	1.61	50.00	0.00	61.68	1.59
J	50.00	0.00	79.57	0.09	50.00	0.00	50.00	0.00
K	50.00	0.00	79.51	0.17	50.00	0.00	50.00	0.00
L	50.00	0.00	67.88	2.51	50.00	0.00	61.19	1.32

c) simulations with 3 predators:

Combination	Average Prey Distribution				Average Predator Distribution			
	Clear (%)		Turbid (%)		Clear (%)		Turbid (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
A	51.20	2.38	84.91	0.55	50.00	1.07	45.48	1.31
B	50.36	1.35	76.48	0.48	50.63	0.71	48.81	0.62
C	48.50	1.99	76.57	0.74	50.86	0.77	49.34	1.56
D	51.52	2.70	79.75	0.26	48.25	0.47	62.90	0.83
E	51.67	1.70	80.88	0.39	49.34	1.28	62.84	0.80
F	45.96	1.65	87.01	1.23	50.10	0.85	38.25	1.82
G	46.40	2.07	83.72	0.50	51.32	0.69	46.01	0.82
H	53.13	2.42	61.41	1.82	49.37	0.78	46.11	1.00
I	47.54	1.83	57.35	1.59	49.64	0.97	46.34	0.75
J	50.38	2.30	68.68	1.17	49.50	1.07	43.80	1.25
K	51.63	2.33	63.60	1.66	49.67	0.94	43.80	1.20
L	55.13	3.62	58.23	3.20	48.81	0.87	48.51	0.61

d) simulations with 4 predators:

Combination	Average Prey Distribution				Average Predator Distribution			
	Clear (%)		Turbid (%)		Clear (%)		Turbid (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
A	55.42	2.63	81.99	0.88	52.00	1.00	50.10	1.13
B	48.69	3.86	79.38	1.07	51.86	1.19	55.67	0.97
C	53.03	3.35	72.30	2.08	50.27	1.46	54.68	1.03
D	46.76	2.39	76.14	0.79	50.67	1.48	55.32	0.72
E	56.45	3.21	75.12	1.57	49.80	1.96	53.94	1.11
F	48.35	3.33	87.86	0.84	50.40	1.35	45.62	1.32
G	51.24	2.55	80.87	0.91	49.26	0.99	49.55	1.33
H	52.02	2.92	71.67	1.77	49.95	1.05	55.99	1.13
I	52.80	3.80	70.64	2.65	52.65	1.29	55.87	0.78
J	50.02	3.71	76.50	1.80	50.59	1.06	53.74	0.84
K	54.62	1.50	71.71	2.08	48.54	1.03	51.88	1.21
L	48.94	2.66	61.89	2.66	49.55	1.36	58.02	0.88

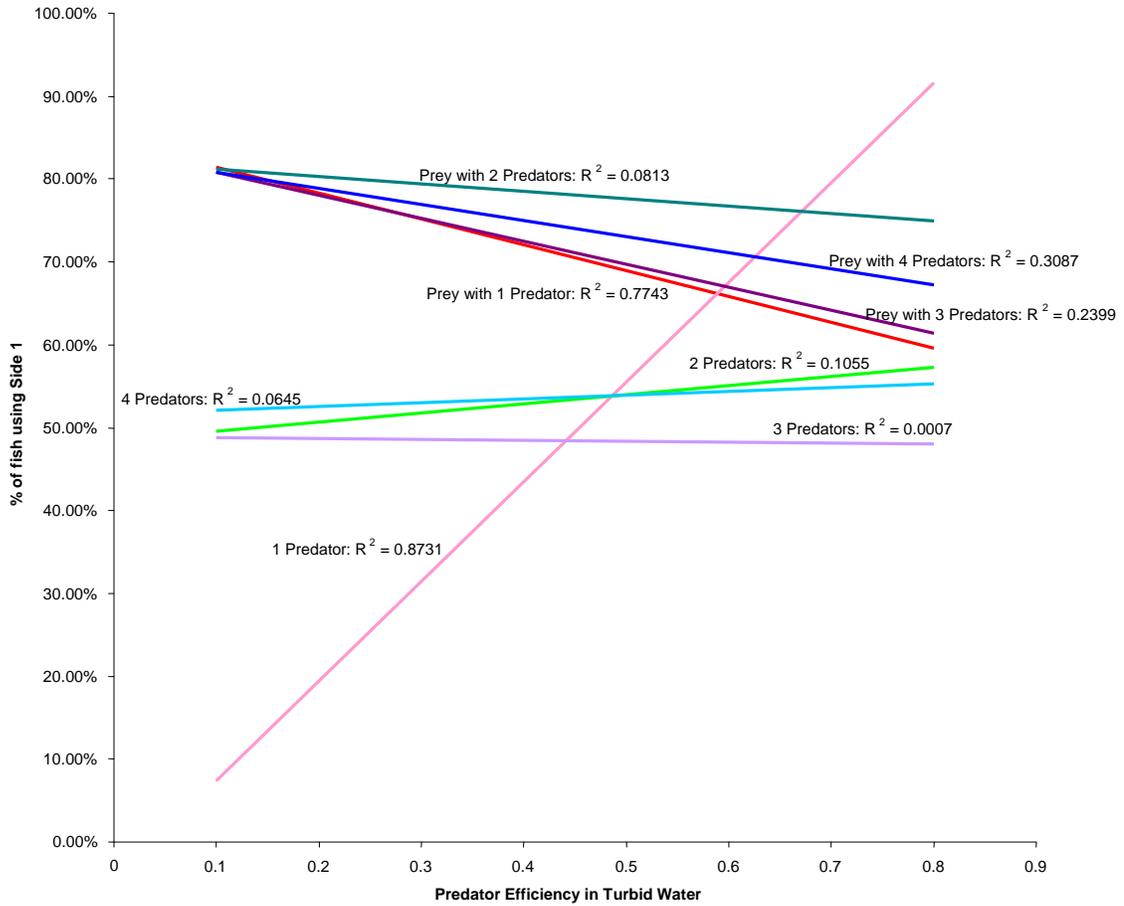


Fig. 3.2: How predator efficiency in turbid water affected both predator and prey use of the turbid habitat. Simulations were run with 1 – 4 predators. Linear regression was determined to provide the best fit (Zar 1996). Predator efficiency only significantly affected predator (ANOVA: $F = 34.31$, $dF = 11$, $p = 0.0002$) and prey ($F = 68.80$, $dF = 11$, $p < 0.0001$) use of the turbid habitat in the single predator simulations.

clear water, but still used both patches. The predator strongly avoided the turbid water patch when its efficiency was greatly reduced (0.1 and 0.2). In 2-predator simulations, the difference in predators' use of the turbid patch was less dramatic. Predators used both clear and turbid patches. Predators showed slight avoidance only when their foraging efficiency was greatly reduced by turbidity (0.1 and 0.2). In 9 out of 12 combinations modeled, the predators did not avoid using the turbid patch (Table 3.4b). In 3-predator simulations, predators used both clear and turbid water patches with a slight preference for clear water in 9 of the 12 combinations. They showed preference for turbidity only in combinations D and E (Table 3.4c). Again, 4-predator simulations found that predators used both patches with a slight preference for the turbid patch in most combinations (Table 3.4d).

Discussion:

Ecology:

Model 1 produced 12 combinations of predation risk, predator, and prey foraging efficiencies deemed possible for generating the distribution patterns observed in the laboratory experiment. The energetic equivalent of a predator was 80% - 90% of the energy available in the patch, and the cost of the basic antipredator behavior when the predator was absent was 50% - 80% of the energy available in the patch. Both values are very high, particularly for the predator absent situation. Numerous field and lab studies have clearly established that predation is one of the major factors determining habitat usage (Mittelbach 1984, Gotceitas 1990b, Harvey 1991, Whitehead et al. 2002). So this high cost of predation pressure agrees with that predation can make a potentially profitable habitat less attractive. The energetic equivalent of a predator was calculated

from the results presented by Abrahams and Dill (1989); the cost of predation in their experiments ranged from 22% to 1675% of the food supplied to the safe patch. The costs generated by Model 1, while high, are still possible. In their experiment, they manipulated resource level (amount of food provided), risk level (distance of food source from cover), and prey physical attributes and life history (sex). The varying costs of predation were the results of the combinations of these factors. It suggests that energetic cost of predation is very specific; the cost of predation changes with various factors, e.g. prey and predator size, prey and predator hunger state, and distance to refuge (Light 1989, Lima and Dill 1990, Pettersson et al. 2000). The simulated basic antipredator cost in the absence of predator was high. Nevertheless, for small fish like fathead minnows which lack physical defenses such as spines or armor, their only defense may be behavioral and they can not afford to let their guard down.

The predators' and prey's foraging efficiencies in turbid water generated by Model 1 also showed wide variations. One general trend can be observed: predators always suffered a more severe reduction than prey in the same combination. While a predator's turbid water efficiency ranged from 10% to 80% of its efficiency in clear water, 9 out of the 12 values were below 50%. So in most cases, predators suffered a very severe reduction in foraging efficiency entering turbid water. On the contrary, 8 out of 12 efficiency values generated for prey were equal to or greater than 90% of prey's foraging efficiency in clear water. These values suggested that turbidity favored the prey. Predator's ability to hunt prey was greatly compromised while prey's ability to forage remained quite effective. This supports the idea that smaller fish with shorter visual range are less impacted by turbidity. As a trade-off, small individuals suffer relatively small

declines in their foraging ability but gain a substantial advantage from reduced predation risk (Giske et al. 1994, Fiksen et al. 2002, Utne-Palm 2002). Besides suffering a reduction in foraging efficiency, small fish may also detect predators at a closer distance in turbid water than in clear water, but this should be compensated by the loss in foraging efficiency suffered by the larger predator. For example, although bluegill reaction distance decreased rapidly in turbid water, they still always reacted to largemouth bass first (Miner and Stein 1996).

Model 2 was an attempt to apply the findings from Model 1 in a more realistic situation. Experimentally, it is difficult to modify the apparatus (see Methods, Chapter 2) to allow unrestricted movement of a predator. Enlarging the tunnels to accommodate predators would weaken the pressure screen and allow bentonite to disperse over to the clear side. Simulation may be a good alternative; although simulation can not replace empirical data completely, it provides a chance to test and visualize predictions and generates insights for future projects.

Model 2 also generated some very surprising results. The clear water only simulations produced the expected baseline. Both predators and prey used both patches equally as the 2 clear patches held the same level of profitability in conformation to the IFD. When one of the patches was turbid, prey preferred using the turbid water patch in most situations, which agreed with Hugie and Dill's (1994) prediction that prey distribution is affected by the inherent "riskiness" of each habitat. Only in single predator simulations, the predators showed strong avoidance of turbid water in some combinations. In most cases, predators used clear and turbid patches almost equally. This is surprising because it was expected that larger predatory fish would avoid the turbid area (Blaber and

Blaber 1980). Hugie and Dill (1994) predicted that predator distribution matches not the prey distribution but the distribution of the prey's food (patch productivity). As both patches were set to have equal amounts of energy for the prey, most of the simulations agree with this prediction. Only when the predator's efficiency was extremely high or extremely low in turbid water, did the predator show strong preference or avoidance of turbid water. When the predator's efficiency become too low in the turbid water, although there were more prey in the turbid patch, it was still not as profitable as the clear patch for the predator. When the predator's ability was not impeded severely by turbid water, it would be attracted to the patch with more prey. As the numbers of predators increased, the predators used both patches more equally. Because the total number of prey was fixed in Model 2, increasing the number of predators increased the competition among predators. As the prey were divided evenly among the predators (an assumption of the IFD), the more predators there were, the lower the benefit was for each predator. The individual benefit difference between the turbid and clear patch got smaller as well. Therefore, both patches were used more equally.

Hugie and Dill (1994) predicted that prey distribution was determined by the inherent riskiness of a habitat, not by resource level and predator distribution. My data seem to agree with this prediction. Prey preferred turbid water even when predators did not avoid it; but turbid water reduced predator's efficiency making it less risky. The use of the turbid patch by the prey was the lowest when the predator's turbid water efficiency was the highest (combination L). While the food supplies of both habitats were equal, turbidity reduced the food available in the turbid water patch by reducing the prey's foraging efficiency; but this reduction did not seem to affect the prey's preference for the

turbid patch. Hugie and Dill (1994) also found in their model that prey distribution was not affected by the availability of food. Giske et al. (1997) reached a different conclusion from their model. They found that with increasing prey density, predation eventually became a non-factor as they factored in predator satiation. Prey would distribute themselves according to food distribution. In this project, predation risk was modeled as density-dependent as well. The cost of predation pressure to each individual prey decreased with increasing prey population. Because both energy intake rate and predation risk were density-dependent in Model 2, changing prey density will not change the weights of both factors in habitat selection decisions (both factors divided by the same denominator) in my model. Also I did not factor in predator satiation and prey mortality. Giske et al. (1997) stated that, in their model, increased competition led to higher sensitivity toward resource input. Their model incorporated prey (copepod) and resource (phytoplankton) growth rates, interference, resource depredation (starvation). That model took a more complete and longer term view at survival and growth, while my model was only intended to focus on how risk of predation affected immediate habitat usage.

The results from both models show that although predator's foraging efficiency is reduced by turbid water, in most instances, they do not shy away from turbid habitats. Therefore turbid habitats are unlikely to act as a physical barrier which separates predators and prey. While the model did not simulate mortality, Abrahams and Kattenfeld (1997) found that prey had the same mortality rates in clear and turbid water. It is likely that turbid habitats provide indirect benefits to prey in terms of reducing energy expended on antipredator behavior. For predators, the results suggested that as predator density increases, the profitability of clear water habitat decreases; and predators are forced to

use turbid habitats. Because there are more prey in the turbid habitat, even with reduced efficiency, predators in turbid water should have similar energy intake with their clear water peers, but predators may have to work harder to achieve the intake rate (Sweka and Hartman 2001a).

Model:

These two models represent a theoretical approach toward completely quantifying effects of water clarity on predator-prey interaction with energetic flow. While there have been precedents of modeling predator-prey interaction and environmental factors (e.g. Hugie and Dill 1994, Giske et al. 1997, Ward et al. 2000), I have not come across any publication taking the same purely energetic approach. Taking a novel approach certainly carries risks and questions with it; but the mathematics and key assumptions used in the models are backed up with literature or modified based on the observations from laboratory experiments.

The original concept called for giving the effect of turbidity a fixed energy value as it has been well established that turbidity is detrimental to fish and causes physiological stress (see Chapter 1 for details). Fathead minnows, however, showed strong affinity for turbid water even without a predator present. This overuse of turbid water suggested that turbidity may be beneficial to them. It was also observed that minnows stayed closer to food sources and stayed for longer durations in turbid water (see Chapter 2). This might be caused by minnows' reduced visual range. Alternatively, fatheads could perceive it as a safer environment and be more active. Based on the observations, I made the assumption that turbidity did not carry a fixed cost; instead, it reduced the foraging efficiencies of both prey and predators.

The observation of minnows preferring to use turbid water even in the absence of predator also strongly suggested that the fish gained more benefit in turbid water than in clear water. It may be prudent for animals to assume danger until it is proven otherwise; therefore, prey may not perceive zero risk in the absence of a predator (Lima and Dill 1990). This concept was incorporated into the model by designating a basic antipredator cost in the absence of a predator. Because predators are expected to be less of a threat due to their diminished foraging efficiency, prey should be able to lower the energy expended on antipredator behavior. In the models this decrease was directly linked to the predator's efficiency factor. This may be an oversimplification, but theoretically prey should evolve a better knowledge of predator's capabilities as this leads to the most optimal strategy. On the other hand, this very specific approach may be difficult to achieve when prey face predator species with different hunting strategies and tolerances.

The level of protective measure should be in step with the level of threat. Light (1989) demonstrated that Trinidadian guppies (*Poecilia reticulata*) were flexible in their response to satiated and hungry predators. Pettersson et al. (2000) showed that crucian carp (*Carassius carassius*) reacted stronger to larger predators. Over-protectiveness wastes energy that could be allocated to growth and reproduction. Under-protectiveness may lead to death. Individuals that have developed the ability to accurately assess threat will have an advantage in fitness. Experimentally, it may be difficult to create a environment where prey perceive zero risk. In experiments involving predator exclusion habitat, it may be preferable to label patches as high and low risk instead of risky and risk-free. However, most literature does not account for this situation when performing IFD-based predation risk/habitat selection experiment. While it is difficult to measure

zero risk, not accounting for this basic level of antipredator cost could underestimate the impact of a predator.

Besides the assumptions dictated by the IFD (perfect knowledge and free movement), two other simplifying assumptions were made when creating the models. I assumed that both density-dependent energy intake rate and predation risk are related linearly. I ignored the effect of interference (which was incorporated in Hugie and Dill 1994, Giske et al. 1997, and Ward et al. 2000). By ignoring interference, I essentially assumed the interference coefficient as 1. A coefficient larger than 1 will lead to an accelerating decrease in feeding rate with increasing forager density (Ward et al. 2000). Ward et al. (2000) used an interference coefficient of 1.17 in their model. For the sake of simplicity and in the absence of any parameter values, this factor was ignored. Similarly, assuming a linear relationship for risk dilution was due to the difficulty of determining the exact mathematical relationship between group size and antipredator effectiveness (increased group size leads to reduced risk and increased competition). I also decided to use random resampling to establish the distributions of predators and prey.

The original version of Model 2 used a very rigid method of establishing distributions. Prey would, one by one, always establish their distribution free of predators first; followed by predators, one by one, selecting a patch according to prey distributions. Then all of the prey reestablished their distribution taking both food and predators into account; then all of the predators reselected habitats accordingly. This obviously is a totally artificial process which created a very rigid cycle of decision making. By using random resampling, I attempted to break this rigid cycle. As any individual, predator or prey, could be selected to reselect a patch at any given time, the rigid prey and predator

decision-making phases were broken. Random resampling made the decision making process more realistic; but in reality, decisions will not be made in sequence, the processes overlap (Ward et al. 2000). However, a model that can perform simultaneous multiple habitat selections may be too complicated and require extensive computing power; thus, random resampling should be an acceptable compromise.

This project attempted to apply game theory to the question of how predator and prey respond to each other when a turbid habitat is available. The models used a purely energetic approach to predict the habitat uses of prey and predator. Based on the assumptions made, the models predicted that prey will always prefer turbid habitats, but predators seem to be deterred when their foraging ability was severely reduced by turbidity. This prediction is only intended for visual predators, non-visual predators should not be affected by turbidity. The model is flexible as more trophic levels can be added, making it a multi-layer interaction game. By adding more measurable details such as change in activity level and escape/successful attack rate, this can be made more accurate. But while theoretical models are imperfect abstractions of reality (Giske et al. 1997) and can and should never replace laboratory and field experiments; it is a great tool for complementing empirical work. For example, the assumption of these models is that vision is the primary sense used in predator-prey interactions. Future models can relax this assumption and incorporate sensory compensation and how it is affected by environmental change. This process may ultimately provide insight into how changing environment can affect aquatic communities.

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Chapter 4

Conclusion

This thesis examined the effect of turbidity on predator-prey interaction and habitat selection decisions. Chapter 2 examined fathead minnow habitat selection under different levels of water clarity and predation risk. Minnows showed a strong preference for turbid habitats regardless of the level of predation risk. The experiment did not find conclusively that turbidity reduced prey's response to predation risk. Chapter 3 used the information provided by these experiments to understand the dynamic relationships between prey, predators, and turbid environments. The computer model predicted that while prey strongly preferred turbid habitat, predator distributions were driven primarily by the distribution of their prey.

Turbidity has been described to have negative effects on fish ((Bruton 1985, Newcombe and MacDonald 1991), yet, it has also been associated with abundances of fish, particularly, smaller individuals (Blaber and Blaber 1980, Cyrus and Blaber 1987). These studies attributed this to reduced predation pressure in turbid habitats. As turbidity increases, a predator's visual range decreases, and prey should be harder to detect; once attacked, prey should have an increased chance to escape. Abrahams and Kattenfeld (1997) proposed an alternative hypothesis. Turbidity does not reduce the direct cost of predation, mortality rate, but it renders prey's antipredator behaviors ineffective. As both predators' and prey's visual ranges decrease in turbid water, their encounters happen more by chance and at a shorter distance at which prey's behavioral modifications bring no benefit. Therefore, in turbid water, prey should reduce their antipredator behavior and allocate the energy to other vital needs, such as growth. Both hypotheses (turbidity reduces predator effectiveness and turbidity reduces prey antipredator behavior expenditure), although different in how turbidity shapes predator-prey interactions, agree

that turbid habitats are beneficial to prey under the threat of predation. This creates a trade-off situation: prey should balance the adverse effects of turbidity and the antipredator benefit it offers when selecting habitats.

The results from both laboratory experiments and computer models showed that turbidity was preferred by prey regardless of the level of predation risk, and it may be even more beneficial than originally expected. This suggests that predators have a huge impact on the habitat use of small fish lacking morphological defenses. They may be so vulnerable to predation that they do not perceive zero risk even when they do not detect the presence of a predator. The same observation may also imply that the cost of antipredator behavior may be extremely high; so high that the cost of the basic level of antipredator behavior can not be outweighed by the benefit of better visibility and search efficiency in clear water. Surprisingly, the reduction of antipredator response (reduction in feeding activity) in turbid habitats observed by Abrahams and Kattenfeld (1997) was not conclusively found in this experiment. In the laboratory experiments, no significant interaction between water clarity and predation risk was found, implying a predator's effect on prey was the same whether in turbid or clear water. Water clarity and predation risk were affecting fathead minnow habitat selection independently, albeit with weak statistical power.

Fathead minnow's ability to identify different types of predators was also tested for and not found. The minnows did not respond differently to a visual predator (yellow perch) and to a chemical predator (black bullhead). Bullheads should be more dangerous in turbid water as they do not rely on vision. Yet, minnows responded to a bullhead with the same magnitude as they responded to a yellow perch. Prey might not recognize they

were facing different types of predators because they lost the ability to inspect or stopped inspection altogether in turbid water.

While the larger minnows of 2004 did not behave differently from the smaller minnows of 2005 and both size classes had similar feeding rates across all treatments, turbidity has been suggested to favor smaller individuals (Utne-Palm 2002). Smaller fish are vulnerable to more gape-limited predators. They also have shorter detection range and poorer escape ability. As a result, they may need to spend more energy in antipredator behaviors and may be prevented from performing other vital activities (e.g. feeding and mating) more compared to their larger conspecifics. These disadvantages, however, may be eliminated by turbid water as predators encounter prey by chance at a short distance in turbid water and lose their preference for smaller prey (Abrahams and Kattenfeld 1997).

The computer models simulated habitat selection of both predators and prey under the influence of turbidity. Model 1 determined possible parameters based on observations for the lab experiment. These parameters suggested that threat of predation has a huge impact on prey. Even when the predator is absent, prey still allocate substantial energy to antipredator behavior. Turbidity has a stronger adverse effect on predator foraging than prey foraging. Model 2 utilized these parameters to determine the outcome of a game between predators and prey. From the model, it is clear that turbidity generally does not act as a physical barrier to keep predators away. Prey strongly preferred turbid habitats, even though predators were not repulsed by turbidity until their foraging efficiency was severely reduced. Predators' preference of turbidity varied greatly with foraging efficiency and may response discontinuously to changing turbidity.

This thesis supports that turbid environments are important for the well-being of small and juvenile fish. By reduction of direct (consumption) or indirect (energy expended on antipredator behavior) effects of predation, turbidity enhances the survival of small fish. Turbidity also allows small fish to use more profitable habitats and focus more on feeding. This reduces competition and increases food intake. Turbid habitats may also be high in food. Blaber and Blaber (1980) have mentioned that turbidity might stimulate zooplankton concentration near the surface in estuaries. Turbid lakes also can have high zooplankton density (Jacobsen et al. 2004). Sweka and Hartman (2001) mentioned increasing invertebrate drift associated with increasing turbidity. As many fish are zooplanktivores in their early life stages (larvae, fry, and juveniles), increasing zooplankton abundance should provide substantial benefit to these small fish.

While it's generally accepted that turbidity is harmful to fish, especially to the large fish, a system that is uniformly clear may not be the most ideal as well. Small fish form the bottom layers of food chain to feed commercially valuable large fish; and many of the small fish are actually the juveniles of these large fish. As turbid habitats enhance the survival of small fish, it may be important to conserve or re-create some turbid habitats when carrying out habitat restoration projects. Large scale and/or chronic turbidity decreases biodiversity, but the existence of localized turbidity may be beneficial and could be an interesting topic for future investigations.

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Appendices

Appendix 1: Model 1 Code

Option Explicit

Dim counter, PreyClear, PreyTurbid, PredatorClear, PredatorTurbid, Predator,
NoPredator As Integer

Dim Outflow, PerceptionLimit, Food1, Food2, Fish1, Fish2 As Integer

Dim r, f, TotalFish1C, TotalFish2C, TotalFish1T, TotalFish2T As Integer

Dim TotalFish1CP, TotalFish2CP, AvgFish1CP, TotalFish1TP, TotalFish2TP As Integer

Dim Fish1C, Fish2C, Fish1T, Fish2T, Fish1CP, Fish2CP, Fish1TP, Fish2TP As Integer

Dim Energy1, Energy2, u, AvgFish1C, AvgFish2C, AvgFish1T, AvgFish2T,

AvgFish2CP, AvgFish1TP, AvgFish2TP As Double

Dim ProportionC, ProportionT, ProportionCP, ProportionTP As Double

Sub CommandButton1_Click()

counter = 2 'Keep tracking all results and printing them in the proper rows.

PreyClear = 1 'Prey foraging efficiency in clear water.

PredatorClear = 1 'Predator foraging efficiency in clear water.

Food1 = 100 'Energy available to prey in patch 1.

Food2 = 100 'Energy available to prey in patch 2.

Outflow = 0 'Cost of the current generated by outflow of excess water from the tank.

PerceptionLimit = 0 'Prey's ability to detect the difference in the energies available.

For Predator = 0 To -100 Step -10 'Range of the energetic cost of a predator.

For NoPredator = 0 To -100 Step -10 'Range of the energetic cost of employing the basic
level of antipredator behavior in the absence of predators.

For PreyTurbid = 0 To 1 Step 0.1 'Range of prey foraging efficiency in turbid water.

For PredatorTurbid = 0 To 1 Step 0.1 'Range of predator foraging efficiency in turbid
water.

counter = counter + 1

TotalFish1C = 0

TotalFish2C = 0

TotalFish1T = 0

TotalFish2T = 0

TotalFish1CP = 0

TotalFish2CP = 0

TotalFish1TP = 0

TotalFish2TP = 0

For r = 1 To 10 'Run simulations for 10 replicates.

Call C 'Subroutine for clear-clear, no predator trial.

TotalFish1C = TotalFish1C + Fish1C

TotalFish2C = TotalFish2C + Fish2C

AvgFish1C = TotalFish1C / r

AvgFish2C = TotalFish2C / r

ProportionC = AvgFish1C / (AvgFish1C + AvgFish2C)

Call T 'Subroutine for clear-turbid, no predator trial. Chamber 1 holds turbid water.

TotalFish1T = TotalFish1T + Fish1T

TotalFish2T = TotalFish2T + Fish2T

AvgFish1T = TotalFish1T / r

AvgFish2T = TotalFish2T / r

ProportionT = AvgFish1T / (AvgFish1T + AvgFish2T)

Call CP 'Subroutine for clear-clear, predator trial.

TotalFish1CP = TotalFish1CP + Fish1CP

TotalFish2CP = TotalFish2CP + Fish2CP

AvgFish1CP = TotalFish1CP / r

AvgFish2CP = TotalFish2CP / r

ProportionCP = AvgFish1CP / (AvgFish1CP + AvgFish2CP)

Call TP 'Subroutine for clear-turbid, no predator trial. Chamber 1 holds turbid water.

TotalFish1TP = TotalFish1TP + Fish1TP

TotalFish2TP = TotalFish2TP + Fish2TP

AvgFish1TP = TotalFish1TP / r

AvgFish2TP = TotalFish2TP / r

ProportionTP = AvgFish1TP / (AvgFish1TP + AvgFish2TP)

Cells(16 + r, 1) = r

Next r

Cells(2, 5) = AvgFish1C

Cells(2, 6) = AvgFish2C

Cells(3, 5) = AvgFish1T

Cells(3, 6) = AvgFish2T

Cells(4, 5) = AvgFish1CP

Cells(4, 6) = AvgFish2CP

Cells(5, 5) = AvgFish1TP

Cells(5, 6) = AvgFish2TP

Worksheets("Sheet2").Activate

Sheet2.Cells(counter, 6) = AvgFish1C

Sheet2.Cells(counter, 7) = AvgFish2C

Sheet2.Cells(counter, 8) = AvgFish1T

```
Sheet2.Cells(counter, 9) = AvgFish2T
Sheet2.Cells(counter, 10) = AvgFish1CP
Sheet2.Cells(counter, 11) = AvgFish2CP
Sheet2.Cells(counter, 12) = AvgFish1TP
Sheet2.Cells(counter, 13) = AvgFish2TP
Sheet2.Cells(counter, 15) = ProportionC
Sheet2.Cells(counter, 16) = ProportionT
Sheet2.Cells(counter, 17) = ProportionCP
Sheet2.Cells(counter, 18) = ProportionTP
```

```
Sheet2.Cells(counter, 4) = PredatorTurbid
Sheet2.Cells(counter, 3) = PreyTurbid
Sheet2.Cells(counter, 2) = NoPredator
Sheet2.Cells(counter, 1) = Predator
```

Next PredatorTurbid

Next PreyTurbid

Next NoPredator

Next Predator

End Sub

Sub C()

Fish1 = 0

Fish2 = 0

Fish1C = 0

Fish2C = 0

For f = 1 To 10

Energy1 = (Food1 * PreyClear + Outflow + NoPredator * PredatorClear) / (Fish1 + 1)

'Calculating the net energy available to a prey in chamber 1.

Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2 + 1) 'Calculating
the net energy available to a prey in chamber 2.

If Energy1 - Energy2 > PerceptionLimit Then 'Comparing the energies offered by
chamber 1 and chamber 2 and making habitat choice accordingly.

Fish1 = Fish1 + 1

Else

If Abs(Energy2 - Energy1) <= PerceptionLimit Then

u = Rnd

If u > 0.5 Then

Fish1 = Fish1 + 1

```

    Else
        Fish2 = Fish2 + 1
    End If
Else
    Fish2 = Fish2 + 1
End If
End If

Next f

Fish1C = Fish1C + Fish1
Fish2C = Fish2C + Fish2

Cells(16 + r, 3) = Fish1C
Cells(16 + r, 4) = Fish2C

End Sub

Sub T()

Fish1 = 0
Fish2 = 0
Fish1T = 0
Fish2T = 0

For f = 1 To 10

Energy1 = (Food1 * PreyTurbid + Outflow + NoPredator * PredatorTurbid) / (Fish1 + 1)
Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2 + 1)

If Energy1 - Energy2 > PerceptionLimit Then
    Fish1 = Fish1 + 1
Else
    If Abs(Energy2 - Energy1) <= PerceptionLimit Then
        u = Rnd
        If u > 0.5 Then
            Fish1 = Fish1 + 1
        Else
            Fish2 = Fish2 + 1
        End If
    Else
        Fish2 = Fish2 + 1
    End If
End If

Next f

```

```
Fish1T = Fish1T + Fish1
Fish2T = Fish2T + Fish2
```

```
Cells(16 + r, 6) = Fish1T
Cells(16 + r, 7) = Fish2T
```

```
End Sub
```

```
Sub CP()
```

```
Fish1 = 0
Fish2 = 0
Fish1CP = 0
Fish2CP = 0
```

```
For f = 1 To 10
```

```
Energy1 = (Food1 * PreyClear + Predator * PredatorClear + Outflow) / (Fish1 + 1)
Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2 + 1)
```

```
If Energy1 - Energy2 > PerceptionLimit Then
```

```
    Fish1 = Fish1 + 1
```

```
Else
```

```
    If Abs(Energy2 - Energy1) <= PerceptionLimit Then
```

```
        u = Rnd
```

```
        If u > 0.5 Then
```

```
            Fish1 = Fish1 + 1
```

```
        Else
```

```
            Fish2 = Fish2 + 1
```

```
        End If
```

```
    Else
```

```
        Fish2 = Fish2 + 1
```

```
    End If
```

```
End If
```

```
Next f
```

```
Fish1CP = Fish1CP + Fish1
Fish2CP = Fish2CP + Fish2
```

```
Cells(16 + r, 9) = Fish1CP
Cells(16 + r, 10) = Fish2CP
```

```
End Sub
```

```

Sub TP()
Fish1 = 0
Fish2 = 0
Fish1TP = 0
Fish2TP = 0

For f = 1 To 10

Energy1 = (Food1 * PreyTurbid + Predator * PredatorTurbid + Outflow) / (Fish1 + 1)
Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2 + 1)

If Energy1 - Energy2 > PerceptionLimit Then
    Fish1 = Fish1 + 1
Else
    If Abs(Energy2 - Energy1) <= PerceptionLimit Then
        u = Rnd
        If u > 0.5 Then
            Fish1 = Fish1 + 1
        Else
            Fish2 = Fish2 + 1
        End If
    Else
        Fish2 = Fish2 + 1
    End If
End If

Next f

Fish1TP = Fish1TP + Fish1
Fish2TP = Fish2TP + Fish2

Cells(16 + r, 12) = Fish1TP
Cells(16 + r, 13) = Fish2TP

End Sub

```

Appendix 2: Model 2 Code

Option Explicit

Dim PreyClear, PreyTurbid, PredatorClear, PredatorTurbid, Predator, NoPredator, Food1, Food2, Replicate, PerceptionLimit, Fish1, Fish2 As Integer

Dim r, f, NumPrey, NumPredator, p, TotalFish1C, TotalFish2C, TotalFish1T, TotalFish2T As Integer

Dim TotalFish1CP, TotalFish2CP, TotalFish1TP, TotalFish2TP, PredatorCost1, PredatorCost2 As Integer

Dim Fish1C, Fish2C, Fish1T, Fish2T, Fish1CP, Fish2CP, Fish1TP, Fish2TP As Integer

Dim Energy1, Energy2, u As Double

Dim AvgFish1C, AvgFish2C, AvgFish1T, AvgFish2T, AvgFish1CP, AvgFish2CP, AvgFish1TP, AvgFish2TP As Double

Dim FinalTotalFish1C, FinalTotalFish2C, FinalTotalFish1T, FinalTotalFish2T As Double

Dim FinalAvgFish1C, FinalAvgFish2C, FinalAvgFish1T, FinalAvgFish2T As Double

Dim Predator1, Predator2, Predator1CP, Predator2CP, Prey1CP, Prey2CP, TotalPredator1CP, TotalPredator2CP As Integer

Dim Loops, l, PrePerLim, Predator1TP, Predator2TP, Prey1TP, Prey2TP, TotalPredator1TP, TotalPredator2TP As Integer

Dim FoodPrey1, FoodPrey2 As Double

Dim AvgPredator1CP, AvgPredator2CP, AvgPredator1TP, AvgPredator2TP As Double

Dim FinalAvgPredator1CP, FinalAvgPredator2CP, FinalAvgPredator1TP, FinalAvgPredator2TP As Double

Dim FinalTotalPredator1CP, FinalTotalPredator2CP, FinalTotalPredator1TP, FinalTotalPredator2TP As Double

Dim NumFish As Integer

Dim NumPredator1CP, NumPredator2CP, NumPredator1TP, NumPredator2TP As Double

Dim counter1, counter2 As Integer

Dim InitialFish1C, InitialFish2C, InitialFish1T, InitialFish2T As Integer

Dim AvgInitialFish1C, AvgInitialFish2C, AvgInitialFish1T, AvgInitialFish2T As Double

Dim InitialPredator1CP, InitialPredator2CP, InitialPredator1TP, InitialPredator2TP As Integer

Dim AvgInitialPredator1CP, AvgInitialPredator2CP, AvgInitialPredator1TP, AvgInitialPredator2TP As Double

Dim AvgTotalFish1C, AvgTotalFish2C, AvgTotalFish1T, AvgTotalFish2T As Double

Dim AvgTotalPredator1CP, AvgTotalPredator2CP, AvgTotalPredator1TP, AvgTotalPredator2TP As Double

Sub CommandButton1_Click()

Call WipeData 'Clear old results from the spreadsheet.

PreyClear = Cells(8, 2) 'Prey foraging efficiency in clear water.

PreyTurbid = Cells(9, 2) 'Prey foraging efficiency in turbid water.

PredatorClear = Cells(8, 3) 'Predator foraging efficiency in clear water.
 PredatorTurbid = Cells(9, 3) 'Predator foraging efficiency in turbid water.
 Predator = Cells(2, 2) 'The energetic cost of a predator.
 NoPredator = Cells(3, 2) 'The energetic cost of employing the basic level of antipredator behavior in the absence of predators.
 Food1 = Cells(4, 2) 'Energy available to prey in patch 1.
 Food2 = Cells(5, 2) 'Energy available to prey in patch 2.
 Replicate = Cells(11, 2) 'How many times the simulation will be repeated.
 PerceptionLimit = Cells(6, 2) 'Prey's ability to detect the difference in the energies available.
 NumPrey = Cells(13, 2) 'The number of prey present.
 NumPredator = Cells(14, 2) 'The number of predator present.
 Loops = Cells(16, 2) 'How many times a random predator or prey resample and reselect a patch.
 PrePerLim = Cells(18, 2) 'Predator's ability to detect the difference in the numbers of prey available.

NumFish = NumPrey + NumPredator 'The total number of fish in the simulation.

Call ClearVariables 'Clear all values from the previous simulation.

For r = 1 To Replicate 'Run simulations for all the replicates.

Call C 'Subroutine for establishing the initial prey distribution in clear water with no predator.

InitialFish1C = InitialFish1C + Fish1C
 InitialFish2C = InitialFish2C + Fish2C
 AvgInitialFish1C = InitialFish1C / Replicate
 AvgInitialFish2C = InitialFish2C / Replicate

Call T 'Subroutine for establishing the initial prey distribution in turbid water with no predator.

InitialFish1T = InitialFish1T + Fish1T
 InitialFish2T = InitialFish2T + Fish2T
 AvgInitialFish1T = InitialFish1T / Replicate
 AvgInitialFish2T = InitialFish2T / Replicate

Call PredationCP 'Subroutine for establishing the initial predator distribution in clear water.

InitialPredator1CP = InitialPredator1CP + Predator1CP
 InitialPredator2CP = InitialPredator2CP + Predator2CP
 AvgInitialPredator1CP = InitialPredator1CP / Replicate
 AvgInitialPredator2CP = InitialPredator2CP / Replicate

Call PredationTP 'Subroutine for establishing the initial predator distribution in turbid water.

InitialPredator1TP = InitialPredator1TP + Predator1TP
 InitialPredator2TP = InitialPredator2TP + Predator2TP
 AvgInitialPredator1TP = InitialPredator1TP / Replicate
 AvgInitialPredator2TP = InitialPredator2TP / Replicate

counter1 = 1 'Keeping track of the number of resampling prey.
 counter2 = 1 'Keeping track of the number of resampling predators.

For l = 1 To Loops 'Run resampling.

u = Rnd 'Randomly picking a predator or prey for resampling.

Dim thisFish As Integer

thisFish = Int(u * NumFish + 1)

If thisFish <= NumPrey Then

 If thisFish <= Fish1C Then

 Fish1C = Fish1C - 1

 Else

 Fish2C = Fish2C - 1

 End If

 If thisFish <= Fish1T Then

 Fish1T = Fish1T - 1

 Else

 Fish2T = Fish2T - 1

 End If

 Call PreyResample 'Subroutine for prey resampling.

Else

 If (thisFish - NumPrey) <= Predator1CP Then

 Predator1CP = Predator1CP - 1

 Else

 Predator2CP = Predator2CP - 1

 End If

 If (thisFish - NumPrey) <= Predator1TP Then

 Predator1TP = Predator1TP - 1

 Else

 Predator2TP = Predator2TP - 1

 End If

 Call PredatorResample 'Subroutine for predator resampling.

End If

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 2) = 0

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1 + 1, 2) = 1

Next l

FinalTotalPredator1CP = FinalTotalPredator1CP + AvgTotalPredator1CP
FinalTotalPredator2CP = FinalTotalPredator2CP + AvgTotalPredator2CP
FinalAvgPredator1CP = FinalTotalPredator1CP / Replicate
FinalAvgPredator2CP = FinalTotalPredator2CP / Replicate

FinalTotalPredator1TP = FinalTotalPredator1TP + AvgTotalPredator1TP
FinalTotalPredator2TP = FinalTotalPredator2TP + AvgTotalPredator2TP
FinalAvgPredator1TP = FinalTotalPredator1TP / Replicate
FinalAvgPredator2TP = FinalTotalPredator2TP / Replicate

FinalTotalFish1C = FinalTotalFish1C + AvgTotalFish1C
FinalTotalFish2C = FinalTotalFish2C + AvgTotalFish2C
FinalAvgFish1C = FinalTotalFish1C / Replicate
FinalAvgFish2C = FinalTotalFish2C / Replicate

FinalTotalFish1T = FinalTotalFish1T + AvgTotalFish1T
FinalTotalFish2T = FinalTotalFish2T + AvgTotalFish2T
FinalAvgFish1T = FinalTotalFish1T / Replicate
FinalAvgFish2T = FinalTotalFish2T / Replicate

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 1) = r

Call ClearSomeVariables 'Clear some vvalues from the previous loop.

Next r

Cells(2, 5) = AvgInitialFish1C
Cells(2, 6) = AvgInitialFish2C
Cells(3, 5) = AvgInitialFish1T
Cells(3, 6) = AvgInitialFish2T
Cells(4, 5) = FinalAvgFish1C
Cells(4, 6) = FinalAvgFish2C
Cells(5, 5) = FinalAvgFish1T
Cells(5, 6) = FinalAvgFish2T
Cells(2, 9) = AvgInitialPredator1CP
Cells(2, 10) = AvgInitialPredator2CP
Cells(3, 9) = AvgInitialPredator1TP
Cells(3, 10) = AvgInitialPredator2TP
Cells(4, 9) = FinalAvgPredator1CP
Cells(4, 10) = FinalAvgPredator2CP
Cells(5, 9) = FinalAvgPredator1TP
Cells(5, 10) = FinalAvgPredator2TP

End Sub

Sub WipeData()

Range("A23:o40001").Select
Selection.ClearContents
Selection.Font.ColorIndex = 1

End Sub

Sub C()

Fish1C = 0

Fish2C = 0

For f = 1 To NumPrey 'Each of the prey will make a habitat choice.

Energy1 = (Food1 * PreyClear + NoPredator * PredatorClear) / (Fish1C + 1) 'Calculating
the net energy available to a prey in chamber 1.

Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2C + 1) 'Calculating
the net energy available to a prey in chamber 2.

If Energy1 > Energy2 And Abs(Energy1 - Energy2) > PerceptionLimit Then 'Comparing
the energies offered by chamber 1 and chamber 2 and making habitat choice accordingly.

Fish1C = Fish1C + 1

Else

If Abs(Energy2 - Energy1) <= PerceptionLimit Then

u = Rnd

If u > 0.5 Then

Fish1C = Fish1C + 1

Else

Fish2C = Fish2C + 1

End If

Else

Fish2C = Fish2C + 1

End If

End If

Next f

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 4) = Fish1C

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 5) = Fish2C

TotalFish1C = TotalFish1C + Fish1C

TotalFish2C = TotalFish2C + Fish2C

AvgTotalFish1C = TotalFish1C

AvgTotalFish2C = TotalFish2C

End Sub

Sub T()

Fish1T = 0

Fish2T = 0

For f = 1 To NumPrey

Energy1 = (Food1 * PreyTurbid + NoPredator * PredatorTurbid) / (Fish1T + 1)

Energy2 = (Food2 * PreyClear + NoPredator * PredatorClear) / (Fish2T + 1)

If Energy1 > Energy2 And Abs(Energy1 - Energy2) > PerceptionLimit Then

 Fish1T = Fish1T + 1

Else

 If Abs(Energy2 - Energy1) <= PerceptionLimit Then

 u = Rnd

 If u > 0.5 Then

 Fish1T = Fish1T + 1

 Else

 Fish2T = Fish2T + 1

 End If

 Else

 Fish2T = Fish2T + 1

 End If

End If

Next f

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 10) = Fish1T

Cells(22 + r * (Loops + 1) - (Loops - 1) - 1, 11) = Fish2T

TotalFish1T = TotalFish1T + Fish1T

TotalFish2T = TotalFish2T + Fish2T

AvgTotalFish1T = TotalFish1T

AvgTotalFish2T = TotalFish2T

End Sub

Sub PredationCP()

Predator1CP = 0

Predator2CP = 0

Prey1CP = Fish1C

Prey2CP = Fish2C

For p = 1 To NumPredator 'Each of the predator will make a habitat choice.

FoodPrey1 = Prey1CP * PredatorClear / (Predator1CP + 1) 'Calculating the number of prey available to a predator in chamber 1.

FoodPrey2 = Prey2CP * PredatorClear / (Predator2CP + 1) 'Calculating the number of prey available to a predator in chamber 2.

If FoodPrey1 - FoodPrey2 > PrePerLim Then 'Comparing the prey offered by chamber 1 and chamber 2 and making habitat choice accordingly.

 Predator1CP = Predator1CP + 1

Else

 If Abs(FoodPrey2 - FoodPrey1) <= PrePerLim Then

 u = Rnd

 If u > 0.5 Then

 Predator1CP = Predator1CP + 1

 Else

 Predator2CP = Predator2CP + 1

 End If

 Else

 Predator2CP = Predator2CP + 1

 End If

End If

Next p

Cells(22 + (r * (Loops + 1) - (Loops - 1)) - 1, 7) = Predator1CP

Cells(22 + (r * (Loops + 1) - (Loops - 1)) - 1, 8) = Predator2CP

TotalPredator1CP = TotalPredator1CP + Predator1CP

TotalPredator2CP = TotalPredator2CP + Predator2CP

AvgTotalPredator1CP = TotalPredator1CP

AvgTotalPredator2CP = TotalPredator2CP

End Sub

Sub PredationTP()

 Predator1TP = 0

 Predator2TP = 0

 Prey1TP = Fish1T

 Prey2TP = Fish2T

For p = 1 To NumPredator

 FoodPrey1 = Prey1TP * PredatorTurbid / (Predator1TP + 1)

 FoodPrey2 = Prey2TP * PredatorClear / (Predator2TP + 1)

```

If FoodPrey1 - FoodPrey2 > PrePerLim Then
  Predator1TP = Predator1TP + 1
Else
  If Abs(FoodPrey2 - FoodPrey1) <= PrePerLim Then
    u = Rnd
    If u > 0.5 Then
      Predator1TP = Predator1TP + 1
    Else
      Predator2TP = Predator2TP + 1
    End If
  Else
    Predator2TP = Predator2TP + 1
  End If
End If

Next p

Cells(22 + (r * (Loops + 1) - (Loops - 1)) - 1, 13) = Predator1TP
Cells(22 + (r * (Loops + 1) - (Loops - 1)) - 1, 14) = Predator2TP

TotalPredator1TP = TotalPredator1TP + Predator1TP
TotalPredator2TP = TotalPredator2TP + Predator2TP
AvgTotalPredator1TP = TotalPredator1TP / Loops
AvgTotalPredator2TP = TotalPredator2TP / Loops

End Sub

Sub PreyResample()

Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 7) = Predator1CP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 7).Font.ColorIndex = 3
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 8) = Predator2CP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 8).Font.ColorIndex = 3

PredatorCost1 = Predator
PredatorCost2 = Predator

If Predator1CP = 0 Then
  NumPredator1CP = 1
  PredatorCost1 = NoPredator 'If there is no predator in chamber 1, prey still has to
perform some basic caution.
Else
  NumPredator1CP = Predator1CP
End If

```

```

If Predator2CP = 0 Then
    NumPredator2CP = 1
    PredatorCost2 = NoPredator 'If there is no predator in chamber 2, prey still has to
perform some basic caution.
Else
    NumPredator2CP = Predator2CP
End If

Energy1 = (Food1 * PreyClear + NumPredator1CP * PredatorCost1 * PredatorClear) /
(Fish1C + 1) 'Calculating the net energy available to the resampling prey in chamber 1.
Energy2 = (Food2 * PreyClear + NumPredator2CP * PredatorCost2 * PredatorClear) /
(Fish2C + 1) 'Calculating the net energy available to the resampling prey in chamber 2.

If Energy1 > Energy2 And Abs(Energy1 - Energy2) > PerceptionLimit Then
    Fish1C = Fish1C + 1
Else
    If Abs(Energy2 - Energy1) <= PerceptionLimit Then
        u = Rnd
        If u > 0.5 Then
            Fish1C = Fish1C + 1
        Else
            Fish2C = Fish2C + 1
        End If
    Else
        Fish2C = Fish2C + 1
    End If
End If

Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 4) = Fish1C
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 5) = Fish2C

Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 13) = Predator1TP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 13).Font.ColorIndex = 3
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 14) = Predator2TP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (1 - 1), 14).Font.ColorIndex = 3

PredatorCost1 = Predator
PredatorCost2 = Predator

If Predator1TP = 0 Then
    NumPredator1TP = 1
    PredatorCost1 = NoPredator
Else
    NumPredator1TP = Predator1TP
End If

```

```

If Predator2TP = 0 Then
    NumPredator2TP = 1
    PredatorCost2 = NoPredator
Else
    NumPredator2TP = Predator2TP
End If

Energy1 = (Food1 * PreyTurbid + NumPredator1TP * PredatorCost1 * PredatorTurbid) /
(Fish1T + 1)
Energy2 = (Food2 * PreyClear + NumPredator2TP * PredatorCost2 * PredatorClear) /
(Fish2T + 1)

If Energy1 > Energy2 And Abs(Energy1 - Energy2) > PerceptionLimit Then
    Fish1T = Fish1T + 1
Else
    If Abs(Energy2 - Energy1) <= PerceptionLimit Then
        u = Rnd
        If u > 0.5 Then
            Fish1T = Fish1T + 1
        Else
            Fish2T = Fish2T + 1
        End If
    Else
        Fish2T = Fish2T + 1
    End If
End If

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 10) = Fish1T
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 11) = Fish2T

TotalFish1C = TotalFish1C + Fish1C
TotalFish2C = TotalFish2C + Fish2C
TotalFish1T = TotalFish1T + Fish1T
TotalFish2T = TotalFish2T + Fish2T
counter1 = counter1 + 1
AvgTotalFish1C = TotalFish1C / counter1
AvgTotalFish2C = TotalFish2C / counter1
AvgTotalFish1T = TotalFish1T / counter1
AvgTotalFish2T = TotalFish2T / counter1

End Sub

Sub PredatorResample()

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 4) = Fish1C
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 4).Font.ColorIndex = 3

```

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 5) = Fish2C
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 5).Font.ColorIndex = 3

Prey1CP = Fish1C
Prey2CP = Fish2C

FoodPrey1 = Prey1CP * PredatorClear / (Predator1CP + 1) 'Calculating the number of prey available to the resampling predator in chamber 1.
FoodPrey2 = Prey2CP * PredatorClear / (Predator2CP + 1) 'Calculating the number of prey available to the resampling predator in chamber 2.

If FoodPrey1 - FoodPrey2 > PrePerLim Then '
 Predator1CP = Predator1CP + 1
Else
 If Abs(FoodPrey2 - FoodPrey1) <= PrePerLim Then
 u = Rnd
 If u > 0.5 Then
 Predator1CP = Predator1CP + 1
 Else
 Predator2CP = Predator2CP + 1
 End If
 Else
 Predator2CP = Predator2CP + 1
 End If
End If

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 7) = Predator1CP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 8) = Predator2CP

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 10) = Fish1T
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 10).Font.ColorIndex = 3
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 11) = Fish2T
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 11).Font.ColorIndex = 3

Prey1TP = Fish1T
Prey2TP = Fish2T

FoodPrey1 = Prey1TP * PredatorTurbid / (Predator1TP + 1)
FoodPrey2 = Prey2TP * PredatorClear / (Predator2TP + 1)

If FoodPrey1 - FoodPrey2 > PrePerLim Then
 Predator1TP = Predator1TP + 1
Else
 If Abs(FoodPrey2 - FoodPrey1) <= PrePerLim Then
 u = Rnd
 If u > 0.5 Then

```

        Predator1TP = Predator1TP + 1
    Else
        Predator2TP = Predator2TP + 1
    End If
Else
    Predator2TP = Predator2TP + 1
End If
End If

```

```

Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 13) = Predator1TP
Cells(22 + (1 + r) + ((r - 1) * Loops) + (l - 1), 14) = Predator2TP

```

```

TotalPredator1CP = TotalPredator1CP + Predator1CP
TotalPredator2CP = TotalPredator2CP + Predator2CP
TotalPredator1TP = TotalPredator1TP + Predator1TP
TotalPredator2TP = TotalPredator2TP + Predator2TP
counter2 = counter2 + 1
AvgTotalPredator1CP = TotalPredator1CP / counter2
AvgTotalPredator2CP = TotalPredator2CP / counter2
AvgTotalPredator1TP = TotalPredator1TP / counter2
AvgTotalPredator2TP = TotalPredator2TP / counter2

```

```
End Sub
```

```
Sub ClearVariables()
```

```

InitialFish1C = 0
InitialFish2C = 0
AvgInitialFish1C = 0
AvgInitialFish2C = 0

```

```

InitialFish1T = 0
InitialFish2T = 0
AvgInitialFish1T = 0
AvgInitialFish2T = 0

```

```

InitialPredator1CP = 0
InitialPredator2CP = 0
AvgInitialPredator1CP = 0
AvgInitialPredator2CP = 0

```

```

InitialPredator1TP = 0
InitialPredator2TP = 0
AvgInitialPredator1TP = 0
AvgInitialPredator2TP = 0

```

FinalTotalPredator1CP = 0
FinalTotalPredator2CP = 0
FinalAvgPredator1CP = 0
FinalAvgPredator2CP = 0

FinalTotalPredator1TP = 0
FinalTotalPredator2TP = 0
FinalAvgPredator1TP = 0
FinalAvgPredator2TP = 0

FinalTotalFish1C = 0
FinalTotalFish2C = 0
FinalAvgFish1C = 0
FinalAvgFish2C = 0

FinalTotalFish1T = 0
FinalTotalFish2T = 0
FinalAvgFish1T = 0
FinalAvgFish2T = 0

TotalPredator1CP = 0
TotalPredator2CP = 0
TotalPredator1TP = 0
TotalPredator2TP = 0

TotalFish1C = 0
TotalFish2C = 0
TotalFish1T = 0
TotalFish2T = 0

AvgTotalFish1C = 0
AvgTotalFish2C = 0
AvgTotalFish1T = 0
AvgTotalFish2T = 0

AvgTotalPredator1CP = 0
AvgTotalPredator2CP = 0
AvgTotalPredator1TP = 0
AvgTotalPredator2TP = 0

End Sub

Sub ClearSomeVariables()

TotalPredator1CP = 0
TotalPredator2CP = 0

TotalPredator1TP = 0
TotalPredator2TP = 0

TotalFish1C = 0
TotalFish2C = 0
TotalFish1T = 0
TotalFish2T = 0

AvgTotalFish1C = 0
AvgTotalFish2C = 0
AvgTotalFish1T = 0
AvgTotalFish2T = 0

AvgTotalPredator1CP = 0
AvgTotalPredator2CP = 0
AvgTotalPredator1TP = 0
AvgTotalPredator2TP = 0

End Sub