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## The role of turbidity as a constraint on predator-prey interactions in aquatic environments

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**Abstract** Many of the world's most productive aquatic ecosystems usually contain turbid water. Paradoxically, many fish species that live in these habitats are also those that often rely on vision to detect their predators and their prey. For these fish, turbidity will reduce the distance at which predator-prey interactions occur, and there should be a reduction in the opportunity for behavioural modification to control the risk of predation. Under these conditions, we predict that most antipredator behaviour will become ineffective and that predator-prey interactions in turbid water will be primarily characterised by the direct effects of predator consumption of prey, rather than behavioural modification reducing the growth rates of prey. This hypothesis was tested in two laboratory experiments. The first experiment investigated how water turbidity, risk of predation, and their interaction affect habitat choice decisions by fathead minnows (*Pimephales promelas*). These data demonstrate that fathead minnows reduce their use of dangerous habitats, but that this effect is diminished in turbid water. A second experiment examined mortality patterns when these fish were preyed upon by yellow perch (*Perca flavescens*) in clear and turbid water. Absolute mortality rates were unaffected by visibility, but patterns of mortality were random in turbid water and skewed towards smaller individuals in clear water. Combined, these results support our hypothesis and suggest that the impact of predation risk will be reduced in turbid aquatic ecosystems.

**Key words** Risk of predation · Predator-prey · Turbidity · Fathead minnows · Yellow perch

### Introduction

The nature of predator-prey interactions has long fascinated ecologists, partly because of the importance of these interactions in determining patterns of energy flow within an ecosystem. Traditionally it has been assumed that the primary impact of predators is through the consumption of their prey, and the consequences associated with the reduced densities of these prey species. With greater attention being devoted to understanding the behaviour of prey in relation to the presence of predators, it has become obvious that predators can also generate significant changes in the behaviour of their prey, and that these can have an equally important role in shaping the dynamics of aquatic communities (Dill 1987, Kerfoot and Sih 1987).

The changes in the behaviour of prey generated by the presence of predators are assumed to reduce their probability of being killed by the predator. There are three different levels at which these behavioural changes can operate: the rate of encounter between predator and prey, time spent vulnerable to attack by a predator, and the probability of death given an encounter (Lima and Dill 1990). For behaviour to have an influence in this latter category, fish must be able to precisely locate their predator in space and time. As most fish species have well-developed eyes (Guthrie and Muntz 1993), vision is probably the sense that most reliably provides this information.

In many aquatic ecosystems, the ability of both prey and predator to detect each other is frequently impaired by turbidity. Often this turbidity is highly variable in nature, such as seasonal changes in suspended sediments and algal blooms, and wind-driven suspension of sediments in shallow water. Turbidity can also vary spatially within a lake (Scheffer et al. 1994). In some of these aquatic ecosystems, there are fish species that have developed non-visual means of detecting prey and predators. However, the temporal and spatial variability in turbidity may be sufficient to allow vision to be a reliable

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means of detecting predators most of the time, preventing the displacement of these species by others that rely upon non-visual senses. Here, we seek to determine the influence that turbidity, and hence a reduced ability to detect predators and prey, may have on predator-prey interactions.

The ecological effects generated by the risk of predation are due to behavioural changes by prey species in response to the detected presence of a predator. Miner and Stein (1996) demonstrated that the reactive distance of bluegill sunfish (*Lepomis macrochirus*) to their predator (a largemouth bass, *Micropterus salmoides*) declined from more than 200 cm in clear water to 23 cm in turbid water [10 nephelometric turbidity units (NTU)]. Turbidity will therefore affect risk of predation by reducing the distance at which prey and their predators detect each other. As the effectiveness of antipredator behaviours will diminish the closer a predator gets to the prey (Ydenberg and Dill 1986), the lower will be the potential benefits that are associated with antipredator behaviours. With increasing turbidity, predator-prey encounters will occur at shorter distances with the probability of escape by the prey ultimately being determined by the probability of detecting the predator before the predator detects them.

Antipredator behaviour is known to be costly, both in terms of the energy required, and because this behavior prevents animals from pursuing the more profitable behaviours of seeking mates and foraging. It is generally assumed that behavioural decisions made by animals represent a balance between their costs and benefits. If turbidity functions to reduce or eliminate the potential benefits associated with antipredator behaviour, we predict that animals should reduce or eliminate their antipredator behaviour in turbid water. We tested this hypothesis with two experiments. The first experiment directly tested whether fish exhibit reduced behavioural avoidance of a predator in turbid water. A second experiment examined how turbidity affected the predator's ability to capture prey, and patterns of vulnerability of different size classes of individuals within the prey population.

## Methods

### Collection and holding

The fish used for these experiments were fathead minnows (*Pimephales promelas*), and their predator, the yellow perch (*Perca flavescens*). Both species are commonly observed together in turbid water environments in North America. Fish for these experiments were captured between May and June of 1992 and 1993 from the University of Manitoba field station at Delta Marsh, located at the southern tip of Lake Manitoba. Fathead minnows were collected by minnow trap and yellow perch were captured with a beach seine.

Upon capture all fish were transported to the University of Manitoba Animal Holding facility where they were held in 200-l fibreglass flow-through tanks at 12°C with a 12-h photoperiod. All fish were fed a diet of frozen brine shrimp (*Artemia salina*). The diet of the fathead minnows was supplemented with flake fish food, and

the yellow perch were also fed trout pellets. Prior to experiments, fish were moved to the laboratory and held in 30-l static water aquaria at 18°C with a 12-h photoperiod. The fathead minnows were exclusively fed brine shrimp; yellow perch were fed a live fathead minnow or brook stickleback (*Culaea inconstans*) once a week.

### Experiment 1: the effect of turbidity on antipredator behaviour

To examine the effect of turbidity on antipredator behaviour, we first had to devise a system that would allow us to observe the behaviour of the fish while simultaneously impairing the ability of the predator and the prey to see each other. We resolved this problem by conducting experiments in a large, shallow, aquarium. Turbidity that impaired the ability of predators and their prey to see each other in the horizontal plane still allowed the fish to be monitored by us in the vertical plane by a camera mounted directly above the apparatus.

Trials were conducted in an aquarium (76 cm × 76 cm × 30 cm) that was filled to a constant depth of 20 cm and divided into two habitats by a mesh partition that restricted the predator (a yellow perch) to one half of the aquarium but did not impede the movement of the minnows. The partition was constructed by attaching 3.5-cm stretch mesh within a transparent plexiglas frame. Nylon string was tied to the mesh to reduce its size by one half.

Between trials the perch predator was separated from the fathead minnows by a clear Plexiglas divider. Two fluorescent lights, diffused by a sheet of white Plexiglas, were placed beneath the aquarium and used during both clear and turbid feeding trials. This illuminated white background enhanced the contrast of fish when observed by the overhead video camera. Due to the absence of aquarium gravel in this system, bacterial nitrogen cycling could not be maintained. To remove the metabolic nitrogenous by-products, four Hagen corner filters, containing an ammonia-absorbing Nitra-Zorb filter, were placed in the aquarium. Once every 5 days, 15 ml of Ammo-lock was also added to the water to detoxify ammonia.

Food was provided to fish in this apparatus using automated feeders (see Abrahams 1989 for details). These feeders provided food at a constant rate, and dispensed this food through openings in a 30-cm horizontal bar (feeder bar). One feeder was located on each side of the partition, and the feeder bars were positioned parallel and 10 cm from the mesh partition.

To conduct experiments, equal amounts of brine shrimp (0.25 g per feeding trial per feeder) were provided to the fish uniformly over a 20-min period. Every 30 s, we recorded the positions of fish at the two feeders. We only included fish that swam near or under the feeder bar during the two seconds prior to and after the observation interval. From each experiment, the time series of observations were averaged to provide the mean proportion of fish feeding at the safe and dangerous feeder. For this experiment, we used six groups of 16 similar-sized fathead minnows (Table 1).

For each group of fish, a preliminary experiment was conducted to examine how their spatial distribution was affected by the spatial distribution of food within the apparatus in clear water. If the fish were sensitive to the spatial distribution of food, this would be consistent with the habitat-matching prediction of the ideal free distribution and indicate that feeding rates were negatively affected

**Table 1** The mean fork length and wet weight for each group of fathead minnows used in experiment 1

Group	Fork length (mm)		Wet weight (g)	
	Mean	SE	Mean	SE
1	42.5	6.6	0.8	0.4
2	53.1	4.9	1.4	0.3
3	50.6	6.3	1.4	0.6
5	49.3	3.5	1.2	0.3
6	47.2	5.5	1.1	0.3

by the number of fish feeding at a feeder. It would then be reasonable to assume that the spatial distribution of the fish would represent a trade-off between the availability of food and the perceived risk of predation (*sensu* Abrahams and Dill 1989).

A total of 0.5 g of brine shrimp was distributed between the two automated feeders at a 1:1, 2:1, or 1:2 ratio. Three trials were conducted per day (0900, 1200, and 1500 hours) and each combination was provided over 2 consecutive days (i.e., six trials). Data were recorded as described below. The order of the treatments was determined randomly.

Habitat choice decisions by fathead minnows were recorded while manipulating two parameters, the presence or absence of a predatory yellow perch (one of two fish was used, with fork lengths of 114 and 121 mm) and water treatment (clear or turbid). The turbid water treatment was produced by suspending 4.5 g, generating a turbidity value of 13 NTU. Settling and filtration was compensated by the daily addition of 2 g of bentonite.

The order of trials was determined by first randomly selecting the water treatment. All predator treatments (predator left, right, or no predator) were then conducted in a random order within the selected water treatment. Once a treatment combination was selected, trials were conducted three times per day (0900, 1200, and 1500 hours) for two consecutive days. Twelve days were required to complete an experiment for each group of fish. Data in the form of proportions were arc-sine square-root transformed prior to statistical analysis.

Experiment 2: the effect of turbidity on the mortality of fathead minnows due to predation by yellow perch

Two water conditions were tested in this experiment, clear (< 1 NTU) and turbid (mean = 11.01 ± 0.34 (SE) NTU). The turbidity levels were selected to match approximately the levels in the first experiment and were created as described above with 8 g of suspended bentonite. Each test aquarium was equipped with a sub-gravel filter and two Hagen corner filters in order to keep the water well circulated. Pebbles (approximately 1 cm in diameter) were used as the substratum on the aquarium bottom to minimize the amount of bentonite removed by the subgravel filters. An additional 0.4 g of bentonite was added each day to compensate for settling and filtration.

Trials were conducted in two aquaria (76 × 30 × 30 cm) that were divided into two habitats by a mesh partition. The larger habitat (56 × 30 × 30 cm) contained both a predator (a yellow perch) and a feeder. The remaining space was a refuge that provided no food.

Trials were conducted in pairs, with one aquarium containing clear water and the other containing turbid water. The two predators lived permanently within the aquarium and were moved between the aquaria between trials in such a manner that they were each involved in an equal number of turbid water and clear water treatments. To begin an experiment, two groups of 16 fathead minnows each were anaesthetized with 2-phenoxyethanol and their wet weight and fork length determined. These fish were allowed to recover from the effects of the anaesthetic overnight, and the following morning were placed into the two experimental aquaria. For three days, the fathead minnows were kept within the experimental tank and were fed 0.5 g of frozen brine shrimp by automated feeders, three times per day (0900, 1200, and 1500 hours). Prior to each feeding trial, a water sample was taken from the tanks and the current turbidity level measured. The turbidity values for each feeding trial were averaged to estimate the turbidity level for the experiment. After 3 days, the surviving fathead minnows were removed and their wet weight and fork length were recorded.

Mortality by the different predators was standardized by dividing the number of fathead minnows consumed in a single experiment by the total number of fathead minnows consumed by that predator from all ten groups (five clear and five turbid water treatments per predator). In this way, we eliminated experimental error that was generated by the different consumption rates of the predators.

Size selectivity by the predators was determined using Ivlev's electivity index (Krebs 1989):

$$E_i = \frac{(r_i - n_i)}{(r + n)}$$

where  $r_i$  is the percentage of size class  $i$  fish in the diet, and  $n_i$  is the percentage of size class  $i$  fish in the environment. This index ranges from -1 (highly avoided) to +1 (highly preferred).

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## Results

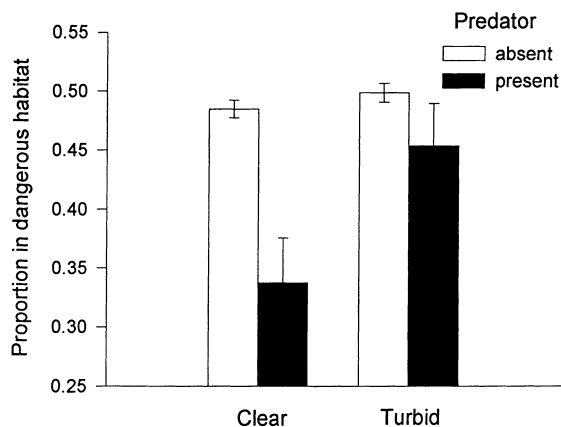
### Experiment 1

We observed numerous encounters between predator and prey during the feeding trials as the predator would often hunt in the area near the feeder bar where the minnows were actively foraging. Many chases occurred, both in clear and in turbid water. Therefore, we are confident that the fathead minnows were able to detect the presence of the predator in both the clear and the turbid water treatments. However, for one group the predator became inactive. As the predator did not present a threat to these fish, this group was excluded from analysis.

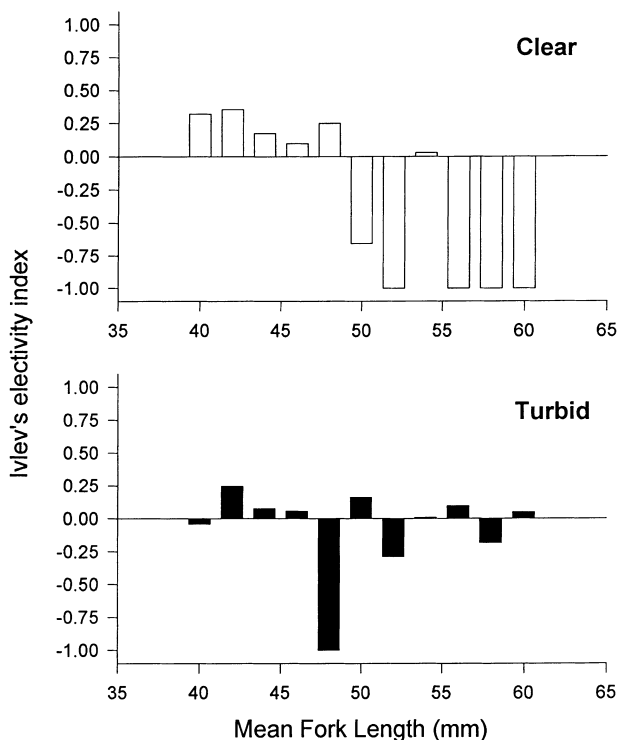
Preliminary experiments demonstrated that the spatial distribution of fish was affected by the spatial distribution of the food. Separate regressions of the relation between the distribution of food and foragers yielded a mean slope of 0.539, a value that was significantly greater than 0 ( $t_5 = 3.193$ ,  $P = 0.006$ ). This result demonstrates that the spatial distribution of these fish is sensitive to the spatial distribution of their food, and is consistent with the assumption that feeding rates will be negatively affected by the number of competitors at a feeder. Movement away from a feeder generated by a predator should create an opportunity for increased feeding rates by individuals that do elect to feed in the presence of the predator.

During these experiments, an average of 1.1 (SE = 0.33) fathead minnows were consumed by the predator per group of experimental fathead minnows. This relatively low mortality rate was due to the close proximity of the feeder to the mesh partition, allowing prey to easily escape attack by the predator. The mortality data from this experiment were insufficient to determine whether fish were more vulnerable to attack by the predator in turbid water. This was examined in more detail in experiment 2.

In clear water, the presence of the predator caused a significant reduction in the proportion of fathead minnows feeding within the dangerous habitat (one-tailed paired  $t$ -test,  $t_4 = 3.17$ ,  $P = 0.004$ ) (Fig. 1). This effect was not observed in turbid water (one-tailed paired  $t$ -test,  $t_4 = 1.24$ ,  $P = 0.14$ ). To compare the strength of the response to the predator in both clear and turbid water, we subtracted the number of feeding fathead minnows in the presence of the predator from the number in the control (predator absent). These data demonstrated that



**Fig. 1** Mean proportion of fathead minnows feeding in the dangerous habitat for each experimental treatment (clear, predator; clear, no predator; turbid, predator; turbid, no predator). Error bars represent 1 SE,  $n = 5$



**Fig. 2** Ivlev's electivity index values for the various size classes of fathead minnows, indicating which sizes of prey are preferentially consumed or avoided. Positive values indicate a preference for a particular size class, while negative values indicate avoidance. The frequency distribution was calculated using 320 fathead minnows

the magnitude of the response was greater in clear water than in turbid water (one-tailed  $t$ -test,  $t_4 = 2.41$ ,  $P = 0.037$ ).

## Experiment 2

Turbidity did not have a significant effect on the proportion of fathead minnows consumed (two-tailed  $t$ -test,

$t_{18} = 0.787$ ,  $P = 0.442$ ; data were arcsin square-root transformed prior to analysis). In the clear water treatments, the yellow perch predators consumed an average proportion of 0.102 (SE = 0.003,  $n = 10$ ) fathead minnows per 3 days of exposure to the predator, compared to 0.098 (SE = 0.006,  $n = 10$ ) in turbid water.

Ivlev's electivity index indicates a pattern of size-related mortality in clear water. Small fish suffered disproportionately high mortality rates while large fish had disproportionately low mortality rates (Fig. 2). In turbid water, index values are much closer to zero (no preference) and no patterns are readily discernible (Fig. 2). These data indicate that size-selective predation occurs in clear water, but not in turbid water.

Changes in size-selective predation should also be evident by changes in the mean group size of the fathead minnows before and after the experiment. Prior to the experiment, the mean group fork length of the fathead minnows in the clear water (49.87 mm, SE = 0.37,  $n = 160$ ) and turbid water (50.37 mm, SE = 0.52,  $n = 160$ ) treatments did not vary significantly (two-tailed  $t$ -test,  $t_{18} = -0.791$ ,  $P = 0.44$ ) but did differ significantly after the experiment (two-tailed  $t$ -test,  $t_{18} = 2.12$ ,  $P = 0.048$ , 51.58 mm, SE = 0.39; 50.49 mm, SE 0.34 in the clear and turbid water, respectively). This shift in mean size further demonstrates a pattern of selective mortality on smaller individuals that was eliminated by turbid water.

## Discussion

In Experiment 1, the fathead minnows exhibited a greater level of avoidance of a dangerous feeding area in clear water than in turbid water. While behavioural observations from this experiment indicated that the predator was detected by the fathead minnows in both the clear and the turbid water treatments, it was possible that the reduced behavioural response observed in the turbid water treatment may have been due to a reduced level of perceived predation risk. There are several reasons why this was not likely to have been the mechanism responsible for our results. Fathead minnows and other species belonging to the superorder Ostariophysi are also able to detect predators through an alarm pheromone (*Schreckstoffe*) released from epidermal cells when the skin of fathead minnows is mechanically damaged (Chivers and Smith 1994; Mathis and Smith 1993). Using this alarm pheromone, fish are able to detect regions of their habitat that are dangerous, regardless of turbidity levels. Fish that were killed during this experiment would have released this alarm substance into the water, providing a non-visual cue that a predator was present. However, it should be noted that the type of information provided by the alarm pheromone is significantly different from that obtained visually. To be effective, an alarm pheromone must persist in the environment for some time before decaying. Furthermore, there must be

some diffusion of this chemical through the water. As a consequence, this cue should provide information that a predator is present, but limited detail regarding specific location or time.

Furthermore, experiment 2 demonstrated very similar mortality rates in both clear and turbid water. Assuming that mortality rates are an accurate measure of predation risk, then there was no measurable change in predation risk associated with turbid water. Vandenbyllaardt et al. (1991) also found that overall mortality rates of fathead minnows, when preyed upon by small walleye, *Stizostedium vitreum* (those less than 75 mm fork length), were not affected by ranges of turbidity from 0 to 100 NTU. Similarly, manipulated turbidity levels had no effect upon the mortality rates of four species of pacific salmonids being preyed upon by adult cutthroat trout (*Oncorhynchus clarkii*; Gregory and Levings 1996). The increased preference by our yellow perch for small prey in experiment 2 is also consistent with field data. Paszkowski and Tonn (1994) noted that yellow perch predators (those greater than 190 mm total length) consumed significantly more small than large fathead minnows when preying upon mixed size populations, presumably because in clear water the larger fathead minnows were more effective at escaping predation. That our predators were equally likely to capture fathead minnows of any size category only in the turbid water treatment further supports our hypothesis of a reduced effectiveness of antipredator behaviour in turbid water and not that these results were due to a reduced level of perceived predation risk.

Other studies have also reported reduced antipredator behaviour with increasing turbidity. Gradall and Swenson (1982) observed that increased turbidity caused brook trout (*Salvelinus fontinalis*) and creek chub (*Semotilus atromaculatus*) to decrease their use of some antipredator behaviours: use of overhead cover and time spent in association with the bottom. Gregory (1993) also noted that juvenile chinook salmon (*Oncorhynchus tshawytscha*) tended to be distributed more uniformly throughout the water column in turbid water compared to their concentration in deeper water when the water was clear. While these authors have attributed their results to mechanisms associated with intraspecific interactions (Gradall and Swenson, 1982) and enhanced feeding abilities (Gregory 1993), both results are consistent with our hypothesis that animals reduce the extent of antipredator behaviour in turbid water.

In a similar study, Miner and Stein (1996) found that in turbid water bluegill sunfish were more likely to feed in areas where they would ordinarily be susceptible to their predator, the largemouth bass. They interpreted their results as being evidence that turbidity reduced the probability of encountering a predator, and hence made these open-water areas less dangerous. This interpretation is supported by the reduced reactive distances and reduced activity levels of the predators associated with

increased turbidity. In their study, they noted that at all turbidity levels, the bluegills responded before the predator, indicating that turbidity provided a detection advantage. It is unlikely that this mechanism occurred in our experiments as absolute mortality rates were not affected by water visibility.

As alterations in behaviour while feeding inevitably result in reduced net feeding rates, a reduction in anti-predator behaviour under turbid water conditions should have a compensatory increase in feeding rates. While we were not able to quantify feeding rates in our apparatus, a number of published studies have observed this result. Gregory and Northcote (1993), while investigating how turbidity and the presence of avian predator models influenced the foraging behaviour of juvenile chinook salmon, also found that feeding rates for surface and benthic prey increased with intermediate turbidity levels, but ultimately declined at the very highest turbidity values (150 NTU). Boehlert and Morgan (1985) also recorded enhanced feeding rates for larval pacific herring (*Clupea harengus pallasii*) feeding at intermediate turbidity levels (500–1000 mg l<sup>-1</sup>).

He and Kitchell (1990) introduced pike (*Esox lucius*) into a lake. They found that in late May and June, many prey fish responded behaviourally to the presence of the predators by emigrating out of this lake. At the same time, water clarity was at its highest (0.7 m Secchi depth) and capture rates by the predators were relatively low. Later in the year, as turbidity in the lake increased (Secchi depths of 0.2–0.4 m), the predators were capable of capturing more prey, and fewer prey exhibited a behavioural response to the presence of these predators by migrating. Again, these results are consistent with our hypothesis, that in turbid water systems, the direct effects of predation are significantly more important than the indirect effects which result from behavioural responses by prey.

In summary, the results of our experiments, and those of other published studies, are consistent with our hypothesis that turbidity can function to constrain predator-prey interactions. If turbidity causes prey to detect predators at distances where they should have initiated escape, then most antipredator behaviours will have become ineffective. Under these conditions, predator-prey interactions will primarily be characterised by the rate at which predators and their prey encounter each other. The failure of antipredator behaviour to incur any significant benefit will mean that much of the prey's behaviour will be unconstrained by the presence of the predators. From a community perspective, variation in the density of predators will directly result in increases in mortality rates of the prey (Marti et al. 1993; Werner and Gilliam 1984). This would contrast with clearer water situations where prey would have the opportunity to modify their behaviour to limit their mortality rates. As a consequence, variation in predator density in such cases should result in limited increases in mortality rates, but with associated reductions in growth rate (Werner and Gilliam 1984).

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