

Risk of Predation and Its Influence on the Relative Competitive Abilities of Two Species of Freshwater Fishes

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Abrahams, M.V. 1994. Risk of predation and its influence on the relative competitive abilities of two species of freshwater fishes. *Can. J. Fish. Aquat. Sci.* 51: 1629–1633.

Experiments were conducted with fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) to determine whether their relative feeding rates were affected by risk of predation. Six groups of both species were observed foraging for food provided by an automated feeder while two parameters were manipulated: the presence or absence of a predator, yellow perch (*Perca flavescens*), and clear or turbid water. It was hypothesized that the armour and spines of brook stickleback would be of greatest benefit during a direct encounter with a predator. I attempted to simulate this condition with turbid water and predator present. Feeding rates of the two species were significantly different, with fathead minnow feeding at a greater rate than brook stickleback in the absence of a predator. In the presence of a predator the feeding rate of fathead minnow declined significantly whereas that of brook stickleback was unaffected. This resulted in similar feeding rates for the two species in the presence of a predator. Results demonstrate that risk of predation can alter the relative competitive abilities of two species in situations where one species possesses a morphological adaptation against predation. In the absence of predators, these traits may be detrimental in interspecific competition for food.

Des expériences ont été menées sur la tête-de-boule (*Pimephales promelas*) et l'épinoche à cinq épines (*Culaea inconstans*) afin de déterminer si leur taux d'alimentation relatif était affecté par le risque de prédation. Pour chacune des espèces, six groupes ont été observés pendant qu'ils cherchaient leur nourriture, fournie par un alimenteur automatique, tandis que l'on manipulait deux paramètres : la présence ou l'absence d'un prédateur, la perchaude (*Perca flavescens*), et la transparence ou la turbidité de l'eau. Notre hypothèse était que la cuirasse et les épines de l'épinoche à cinq épines lui seraient grandement utiles lors d'une confrontation directe avec un prédateur. Nous avons tenté de simuler ces conditions en eau trouble et en présence d'un prédateur. Nous avons observé des taux d'alimentation des deux espèces significativement différents, la tête-de-boule s'alimentant à un taux plus élevé que l'épinoche à cinq épines en l'absence de prédateur. En présence d'un prédateur, le taux d'alimentation de la tête-de-boule diminue significativement, tandis que celui de l'épinoche à cinq épines reste inchangé. On obtient ainsi des taux d'alimentation comparables pour les deux espèces en présence d'un prédateur. Ces résultats démontrent que le risque de prédation peut altérer la compétitivité relative de deux espèces, dans les situations où une espèce seulement est dotée d'une adaptation morphologique la protégeant de la prédation. En l'absence de prédateurs, ces caractéristiques peuvent nuire à la compétition interspécifique pour les aliments.

Received March 3, 1993

Accepted January 17, 1994
(JB832)

Reçu le 3 mars 1993

Accepté le 17 janvier 1994

The presence of predators can cause dramatic alterations in the behaviour of prey (for a review, see Lima and Dill 1990). However, not all prey respond similarly to a threat of predation. Differences in the relative willingness to risk exposure to predators have been observed between species (Brown et al. 1989; McLean and Godin 1989; Kotler et al. 1991; Abrahams and Healey 1993) and between sexes within a species (Abrahams and Dill 1989; Holtby and Healey 1990).

Behaviour or morphology that minimizes vulnerability to predators can allow a species to exploit niches that are too dangerous for other species. One such example exists in terrestrial communities. Brown et al. (1989) and Kotler et al. (1991) have demonstrated that some species of desert rodents are better able to exploit resources in open areas where they are vulnerable to aerial predators. They hypothesized that better-developed auditory bullae in these species is an adaptation that provides a superior ability to detect approaching predators, thereby increasing their probability of escape.

Teleost fishes possess diverse morphologies, ranging from

streamlined bodies to bodies with armour and spines. Armour and spines are probably an adaptation to reduce vulnerability to predators (Hoogland et al. 1957) and therefore may allow more efficient exploitation of dangerous areas (McLean and Godin 1989).

Two mechanisms may be responsible for allowing fish to exploit dangerous areas. First, predators prefer to attack unarmoured prey. Reist (1980) demonstrated that a predatory northern pike (*Esox lucius*) preferred to attack morphs of the brook stickleback (*Culaea inconstans*) that had reduced armour compared with the fully armoured morph. Second, armoured fish need to rely less on antipredator behaviours (Benzie 1966; McLean and Godin 1989), providing them more time for other activities. Spending less time watching for predators or deferring a response to a predator is analogous to an alteration in the foraging–fleeing trade-off proposed by Ydenberg and Dill (1986).

These benefits of armour may come at a cost. Many armoured invertebrates have lower feeding, growth, or reproductive rates than similar species that do not possess armour

TABLE 1. Mean wet weight (g) and total length (mm) of the fathead minnow and brook stickleback in each of the six groups used in the study.

Group	Fathead minnow		Brook stickleback	
	Weight	Length	Weight	Length
1	1.25	52.7	2.68	57.3
2	0.56	41.7	0.48	37.3
3	0.72	45.3	1.01	44.8
4	0.59	38.3	0.59	36.2
5	0.87	42.3	0.70	45.7
6	0.71	44.7	0.85	45.7

(Dodson 1984; Havel 1987). Furthermore, the positive correlation between the degree of armour and spines possessed by threespine stickleback (*Gasterosteus aculeatus*) and the ambient level of predation risk (Gross 1978) suggests that this morphology is expensive. Such a relationship is expected because a phenotypic adaptation should be conserved when the fitness-related benefits exceed the cost. For some populations, this may no longer be true and could therefore lead to a reduction in armour.

Clearly, the net value of armour as measured by relative competitive abilities will be determined by predation risk. In the presence of predators, armour may render one species competitively superior whereas in the absence of predators, it may become inferior.

This mechanism may operate in aquatic communities that contain brook stickleback (armoured with plates and spines) and unarmoured fathead minnow (*Pimephales promelas*). These species are common to southwestern Manitoba; they are found in 57% of surveyed streams and lakes and occur together in 35% of them (Manitoba Department of Natural Resources, Fisheries Branch, unpublished data). Armoured brook stickleback are less susceptible to attack by a predator than fathead minnow (Robinson 1989). These species appear to be potential competitors because of overlap in their diet (both consume small aquatic invertebrates (Scott and Crossman 1973), although the elongated intestine of the fathead minnow allows it to include lower quality food items in its diet) and because they co-occur in the same microhabitat at the same time (M.V. Abrahams, unpublished data). Furthermore, enclosure experiments have demonstrated that the presence of fathead minnow reduces the growth rate of brook stickleback (M.V. Abrahams, unpublished data).

In the current study, I measured the relative feeding rates of fathead minnow and brook stickleback while manipulating two ecological variables: the presence of a predator and water transparency. These species are often found in turbid water and I hypothesized that water clarity will determine the distance at which prey can detect a predator (and vice versa) and the relative effectiveness of antipredator behaviours. Clear water will allow a predator to be detected while it may still be avoided. Under these conditions, the relative effectiveness of behavioural avoidance and antipredator morphology may be similar. However, in turbid water where the predator is only detected when avoidance is impossible, armour may be the more effective strategy.

The experiments reported in this paper test the prediction that antipredator morphology improves a species' competitive ability when feeding in the presence of a predator.

Furthermore, I also tested the prediction that the relative benefit of armour should further increase in turbid water due to the reduced effectiveness of behavioural antipredator strategies under this condition.

Methods

For these experiments, juveniles fathead minnow and brook stickleback were collected by seine net and minnow trap from the marsh at the University of Manitoba's field station (located at the southern tip of Lake Manitoba, approximately 125 km west of Winnipeg) during the summer of 1991. These fish were taken to the University of Manitoba where they were held in 150-L fibreglass flow-through tanks and maintained on a diet of Tetra Min™ flakes and frozen brine shrimp (*Artemia salina*).

Experiments were conducted in a 200-L glass aquarium that was divided in half by a clear Plexiglas partition. A removable opaque partition covered the transparent partition. In one half of the aquarium, a feeder provided 0.5 g (wet weight) of freshly thawed adult brine shrimp delivered uniformly over a 24-min period (see Abrahams 1989 for a detailed description of these feeders). This feeder was located so that food was delivered 3 cm from the transparent partition and just below the surface of the water. The food immediately sank, unconsumed food collecting in a food trap beneath the feeder.

Six groups were used for these experiments. Three individuals from each species constituted each group. Individuals were selected so that mean sizes within a group (Table 1) were similar (within 5 mm total length). The six fish from each group were placed together in the apparatus and trained to use the feeder for 1 wk prior to beginning experiments. The feeder served as their only source of food.

Presence or absence of a predator and water turbidity were used to generate four different treatment combinations that were presented in a random order to each group. Foraging trials for a given fish group at a given treatment combination were conducted over 3 successive days, three times per day, with each trial separated by 3 h. Between trials, an opaque cover was placed over the transparent partition and was removed just prior to each trial. A 120-W halogen bulb shone light through an opening in a piece of matboard to illuminate the area under the feeder. This allowed the fish to be observed and videotaped under all treatment conditions with a High Band 8-mm video camera.

The predator used in the experiments was a 112-g (19.5 cm fork length) yellow perch (*Perca flavescens*). This fish was also collected at Delta marsh and was capable of consuming fathead minnow and brook stickleback in captivity. The yellow perch was placed behind the transparent Plexiglas partition in the experimental aquarium. Because of this partition, the experimental fish could not be captured by the predator but had to feed in close proximity to it. Turbid water was created by adding 3.8 mL of each of blue, red, and green food dyes to the aquarium. Using the untreated water as the blank, this treatment resulted in absorbance readings of 0.0034 at 450 nm, 0.0030 at 500 nm, and 0.0034 at 650 nm. The water in the aquarium was changed following the turbidity treatment.

Each trial lasted 24 min. To measure relative competitive abilities of the fish within each trial, I recorded from the video tapes the number of food items eaten by individuals of

TABLE 2. Summary of regression analyses to determine whether fish habituated to the treatment combinations. This was tested by determining whether the observed slope between the number of unconsumed food items and order within a treatment combination was significantly different from 0. Reduced error degrees of freedom for two treatments were due to missing data.

Treatment	Observed slope	Error df	F	P
No predator, clear	0.368	50	1.600	0.212
No predator, turbid	0.181	52	0.604	0.440
Predator, clear	-0.289	52	0.395	0.533
Predator, turbid	-0.578	50	0.662	0.420

TABLE 3. Summary of one-way repeated measures ANOVA to examine the effect of time within an experiment on the observed proportion of food consumed by each species for each treatment combination. Data were arc-sin square-root transformed prior to analysis. Degrees of freedom for all reported F-values are 2,10.

Treatment	F	P
No predator, clear	0.19	0.833
No predator, turbid	0.30	0.748
Predator, clear	0.95	0.420
Predator, turbid	2.33	0.148

each species for the first, middle, and final 5-min sections of each trial. The average of these three observations represented the results for a single trial.

For each trial, I determined the proportion of food obtained by each species, and the amount of food that was not consumed. For statistical analysis, groups were considered as independent observations. Therefore, the mean of nine observations (three observations per day for 3 d) was used as a single observation to describe the results of each treatment combination for each group. Statistical analysis employed a randomized-block ANOVA with fish group as blocks.

Results

In these experiments, the test fish were exposed to the same treatment combination for nine sequential trials (three trials per day for 3 d). A concern with this experimental design was that the fish may habituate to a particular treatment combination, particularly since the predator was separated from the fish by a Plexiglas partition and therefore did not pose a real threat to the fish. The expected antipredator response would be avoidance of the feeder resulting in reduced feeding rates and an increase over time in the number of food items arriving in the food trap. Habituation should result in a sequential reduction in avoidance and therefore a sequential reduction in the number of food items in the food trap at the end of each trial. For each of the four treatment combinations, no sequential change was observed in the number of unconsumed food items (Table 2). Therefore, pooling data over the nine sequential trials per fish group is justified.

The proportion of food consumed by fathead minnow and brook stickleback during the first, middle, and final 5-min

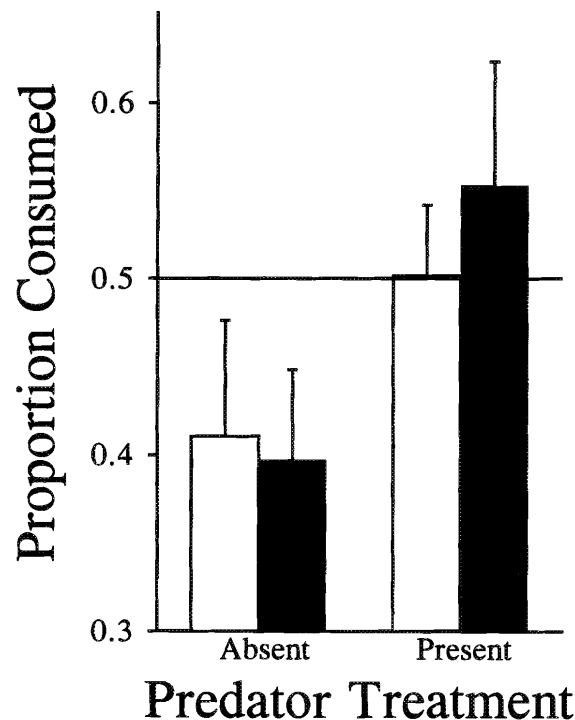


FIG. 1. Proportion of food consumed by brook stickleback under the four different treatment combinations used in this experiment. The open bars represent the clear water treatments and the shaded bars represent the turbid water treatments. Error bars correspond to 1 SE.

intervals was not significantly different (Table 3), indicating that the relative behaviour of the two fish species did not change through time within these experiments. Therefore, the mean value of these three observation periods should accurately describe the result of each experiment.

A further concern with this experiment was that the turbidity treatment would limit my ability to accurately observe the food items consumed by the two species. If this was the case, then the relationship between the total number of food items consumed and the number collected in the food traps should differ between the turbid and clear water treatments (e.g., reduced feeding rates in the turbid water treatment would be due to an inability to observe all food items consumed, not an actual reduction in feeding rate). A comparison of the regression equations for this relationship yielded no significant difference in the slope ($F_{1,104} = 2.268$, $P = 0.135$) or the intercept ($F_{1,104} = 0.078$, $P = 0.78$). Therefore the turbid water treatment did not impair my ability to accurately observe feeding behaviour in these experiments.

The presence or absence of the predator had a significant influence on the relative amount of food captured by each fish species (two-way ANOVA; $F_{1,15} = 4.85$, $P = 0.0437$). In the absence of the predator, brook stickleback obtained 40.4% ($\pm 4\%$ SE) of the consumed food, which was significantly less than that consumed by fathead minnow (Fig. 1). Adding a predator to the apparatus increased the brook stickleback's share of consumed food to 52.7% ($\pm 4\%$ SE), which was not significantly different from the consumption rate of fathead minnow (paired t -test, $t_5 = 0.576$, $P > 0.50$). Varying the turbidity of the water had no effect on the relative feeding rates of the two species (two-way ANOVA; $F_{1,20} = 0.17$, $P = 0.68$), nor was there an interaction between these two treatments (two-way ANOVA; $F_{1,20} = 0.32$, $P = 0.58$). The

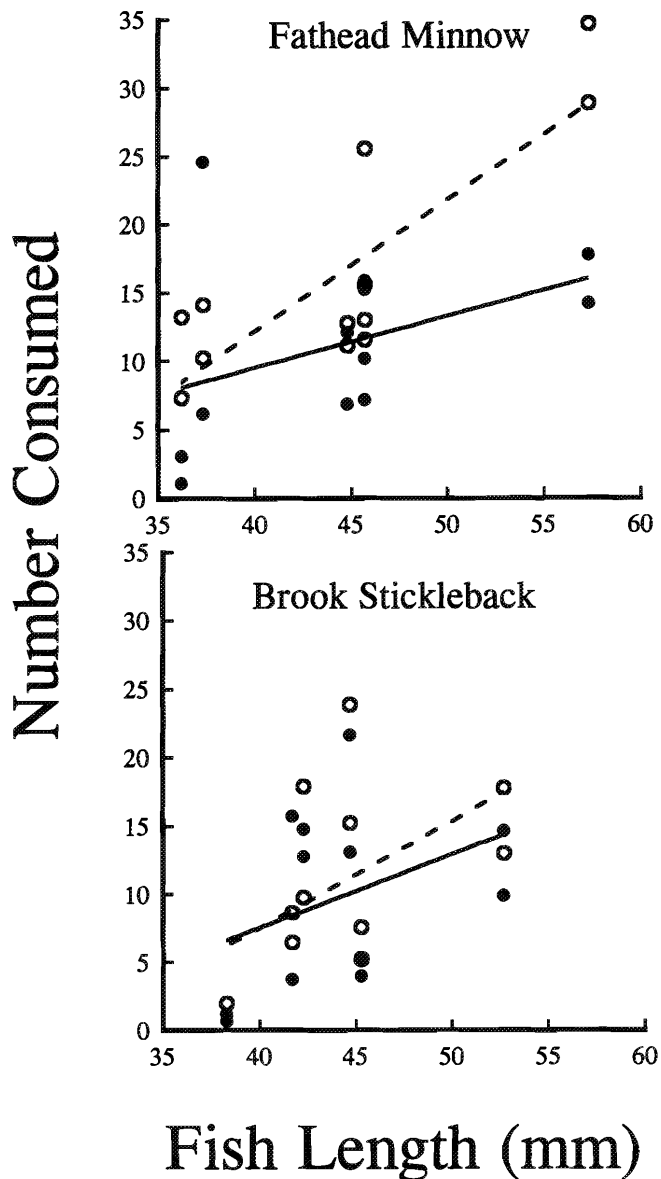


FIG. 2. Number of food items captured by the fathead minnow and brook stickleback as a function of their size and the presence (solid circles) or absence (open circles) of a predator. Data have been pooled for both turbidity treatments. The broken and solid lines indicate the lines of best fit for experiments with no predator present and with a predator present, respectively.

blocking factor (group) had no significant influence on this result ($F_{5,15} = 1.09$, $P = 0.4036$).

For both species, the absolute number of food items captured differed significantly among groups (two-way ANOVA; fathead minnow: $F_{5,12} = 4.54$, $P = 0.015$; brook stickleback: $F_{5,12} = 8.96$, $P = 0.001$). However, the presence of the predator only affected the feeding rate of fathead minnow (Fig. 2). In the presence of the predator, their absolute feeding rates declined significantly (two-way ANOVA; $F_{1,12} = 5.42$, $P = 0.038$). The number of food items captured by brook stickleback did not change in response to this treatment (two-way ANOVA; $F_{1,12} = 0.34$, $P = 0.569$). Therefore, the relative improvement in the food rate of brook stickleback in the presence of a predator was not due to an increase in their absolute feeding rate, but to a reduction in the absolute feeding rate of fathead minnow.

Discussion

These data demonstrated that the relative feeding rates of fathead minnow and brook stickleback were affected by the presence of a predator. In the absence of a predator, fathead minnow consumed proportionately more food than brook stickleback. Adding a predator resulted in both species consuming approximately similar quantities of food. Variation in the response to risk of predation appears to be the mechanism responsible for the change. In these experiments, fathead minnow were sensitive to risk of predation and reduced their feeding rate in the presence of the predator. Brook stickleback did not appear to modify their foraging behaviour in response to risk of predation resulting in feeding rates similar to fathead minnow in the presence of a predator.

The spines and armour of brook stickleback may benefit them in encounters with predators and therefore allow them to minimize their behavioural modification in response to the risk of predation. Reduced vulnerability to predators should allow brook stickleback to postpone their response and therefore not have to forego as many feeding opportunities. Indeed, McLean and Godin (1989) have demonstrated that fishes with increasing amounts of defensive armour are less likely to flee and reduce their reactive distance to an approaching predator. With direct encounters, the predator is detected at a distance requiring an immediate response by the prey. The armour and spines provide brook stickleback a finite probability of escape even if captured by the predator. In the absence of these defenses, I assume there would be no probability of escape. For this reason, I assumed that the combination of turbid water and the presence of a predator would be of the greatest relative benefit to brook stickleback. Manipulating water turbidity had no significant influence on the relative competitive abilities of these two species. Therefore, a postponed response to a predator is likely to be the most important reason for the shift in relative competitive abilities.

Werner (1991) has also demonstrated that competitive abilities can be altered by the presence of a predator. He examined the growth rates and competitive abilities of two species of anuran larvae (*Rana catesbeiana* and *R. clamitans*). In the absence of a predator, both species grew at similar rates and were similar in competitive abilities. However, in the presence of predatory odonate larvae (*Anax junius*), *R. catesbeiana* became competitively superior and achieved higher growth rates than *R. clamitans*. The interaction between brook stickleback and fathead minnow is the reverse of this system. Rather than the risk of predation causing an asymmetry in competitive abilities, it generates equivalence. Therefore, the presence of brook stickleback in some aquatic ecosystems may be dependent on the presence of predators.

Persson (1990) has also observed that predators reversed the relative competitive abilities of roach (*Rutilus rutilus*) and European perch (*Perca fluviatilis*) by altering their use of habitats. In the absence of predators, both species occupy open-water areas, where roach are competitively superior. However, in the presence of predators, juveniles of both species were forced into structurally complex refuges. In this habitat, the swimming performance of roach was impaired, resulting in a reversal of competitive abilities. In the absence of a predator-free control, it is difficult to deter-

mine whether a similar situation applies to the fathead minnow and brook stickleback in this study. However, both species were collected in open water in an environment that contains predators, suggesting that the size class of individuals used in these experiments does not shift habitats in response to predation risk.

Possession of traits specific to reducing susceptibility to predators must have some cost, and this may contribute to polymorphisms observed in threespine stickleback populations (for a review, see Bell 1976). Several potential costs have been proposed. Reimchen (1980) and Reist (1980) have demonstrated that spines make sticklebacks more susceptible to capture by predatory grasping invertebrates. Nelson (1969) suggested that elimination of body armour allows for streamlining and more efficient escape responses through dense vegetation. If these hypotheses are true, animals that possess morphological antipredator adaptations suffer from bearing these traits in the absence of predators. Only in the presence of predators should these traits confer any advantage to their bearer.

Acknowledgements

Alvin Dyck, Keith Jackson, and David Wilson provided patient assistance collecting the data. The University of Manitoba statistical advisory service provided assistance with some of the analysis. I am most grateful to Larry Dill and two anonymous referees for providing comments on an earlier draft of this manuscript. Financial support for this research was provided by an operating grant from the Natural Sciences and Engineering Research Council of Canada.

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