

Interaction between Young-of-Year Fathead Minnows and Brook Sticklebacks: Effects on Growth and Diet Selection

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Abstract.—The hypothesis that brook sticklebacks *Culaea inconstans* and fathead minnows *Pimephales promelas* are competitors was tested in field enclosures containing young-of-the-year individuals from both species. Growth was monitored for 6 weeks, then final weights and gut contents were examined. Fathead minnows were relatively unaffected by brook sticklebacks. Neither dietary composition nor growth was affected in enclosures containing only fathead minnows or a combination of fathead minnows and brook sticklebacks at similar density. The presence of fathead minnows did, however, stimulate growth of brook sticklebacks; this was possibly related to the relatively higher mortality of fathead minnows within the jointly occupied enclosures and the resulting reduced absolute density of fish. The diet of brook sticklebacks also became more diverse in the presence of fathead minnows. In enclosures containing only sticklebacks, the fish consumed primarily copepods. These data demonstrate that growth of brook sticklebacks may be sensitive to both intra- and interspecific competition. This apparent sensitivity of growth to the presence of fathead minnows may account for the observed spatial distribution and migratory habits of brook sticklebacks.

Brook sticklebacks *Culaea inconstans* and fathead minnows *Pimephales promelas* are common to lakes and streams of central North America. In southwestern Manitoba, at least one of these two species is found in 57% of the lakes and streams surveyed and both species occur together in 35% of them (Manitoba Department of Natural Resources, Fisheries Branch, unpublished data). Both species typically occupy the shallow-water portions of these lakes and streams and are often found living in association with each other (Scott and Crossman 1973).

These species are also similar in many aspects of their natural history. Both species consume many similar food items including zooplankton, insects, fish eggs and larvae, seeds, and blue-green algae (Scott and Crossman 1973; Wootton 1976). In southern Manitoba, both species are vulnerable to the same predators, including piscivorous birds, fishes, insects, amphibians, and reptiles. They also tolerate hypoxic water, which allows them to reside in bogs and marshes (Scott and Crossman 1973).

The species also share other life history characteristics (Table 1), including a similar mating system and male parental care. Male brook sticklebacks build a nest of vegetation in which females deposit their eggs; the male then aerates the eggs and defends them from predators (Wootton 1976). Male fathead minnows establish breeding territories. Females enter the territory and deposit their eggs on the underside of some horizontal surface (Sargent 1989). As with male brook sticklebacks, the male fathead minnow aerates and defends eggs within its nest (Sargent 1989). Females of both species devote a similar proportion of their body weight to egg production (Table 1). They mature at the same age and have the same maximum age. Growth in both species is seasonal; the fish are short lived and achieve similar maximum lengths, although fathead minnows weigh more than brook sticklebacks of similar length.

Morphologically, these species are distinct. Brook sticklebacks possess lateral plates, spines, and a reduced caudal peduncle that characterize species in the family Gasterosteidae. Lack of red muscle in the trunk of brook stickleback limits its ability to sustain long periods of swimming (Wootton 1984; Abrahams, unpublished data). Fathead minnows have a morphology typical of that of a small minnow; they lack armor or plates and have a much better developed caudal peduncle than sticklebacks. Their alimentary canal is much longer than that of sticklebacks, and they have large amounts of red muscle, allowing long periods of aerobic swimming (Abrahams, unpublished data).

Although morphologically distinct, the similarity of their life histories suggests that these species may be direct competitors, although no such evidence exists to directly measure this possibility. Given the wide distribution of this species assemblage within central North America (Lee and Gilbert 1980) and the potential importance of competition, both directly (see Connell 1983; Schoener 1983, 1985) and indirectly by modification of community structure through predation (e.g., Persson 1991; Abrahams 1994; Hughes et al. 1994), it is important to determine whether these species com-

TABLE 1.—Comparison of the life history characteristics of fathead minnows and brook sticklebacks.

Character	Fathead minnow	Brook stickleback
Parental care	Male guards eggs that are adhered to surfaces (Markus 1934; Scott and Crossman 1973)	Male guards eggs that are laid in its nest (Wootton 1976)
Mating system	Polygynous (Markus 1934; Scott and Crossman 1973)	Polygynous (Wootton 1976)
Spawning season	Spawning commences when water temperature is approximately 15.5°C and continues until the temperature falls below this value (typically from early June to August) (Scott and Crossman 1973)	When water temperature is rising from 8°C to 19°C (May to mid-June) (Scott and Crossman 1973)
Repeat spawning by females	Yes (Markus 1934)	Yes (Wootton 1976)
Average egg size	1.15 mm with some variation depending on size and source of female (Markus 1934)	1.3 mm with some variation depending on size and source of female (Weselowski 1974)
Age at maturity	After 1 year (Scott and Crossman 1973)	After 1 year (Scott and Crossman 1973)
Sexual dimorphism	Males change morphology during breeding season (develop barbels and alter color); males larger than females (Markus 1934)	Sexually dimorphic; both males and females change color during breeding season (Wootton 1976)
Mortality	High after spawning (about 80%) (Markus 1934)	Population demographics suggest mortality pattern similar to that of fathead minnows (Weselowski 1974)
Maximum age	3 years (Markus 1934)	3 years (Weselowski 1974)
Maximum size	83 mm (Scott and Crossman 1973)	87 mm (Scott and Crossman 1973)
Female gonadosomatic index	13–17% (Carlson 1967)	10–20% (Braekvelt and McMillan 1967)

pete in the wild. This knowledge will provide a greater understanding of the mechanisms that are important in regulating and shaping the numerous aquatic communities in which this species assemblage occurs. In my study, I sought evidence for competition between brook sticklebacks and fathead minnows by rearing young of year within enclosures that contained single or mixed species groups at a common density.

Methods

Experiments were conducted between 25 July and 16 September 1992 at the University of Manitoba's field station at Delta Marsh at the southern tip of Lake Manitoba. These experiments were conducted in a section of the marsh known as the blind channel, which is an open body of water within the marsh with an average depth of 150 cm but may fluctuate by up to 30 cm because of wind driven seiches.

Species interactions were measured within fifteen 20-L enclosures. Enclosures were constructed from 20-L plastic pails. Most of the sides and the bottom were removed, leaving the remnants of the pail to serve as a plastic frame. These frames were covered with a 6.5-mm 210/9 knotless nylon mesh that was attached to the pail with silicone sealant and metal staples. Elastic cord was used to attach the same fine mesh to the top of the pail, providing access via a removable cover.

The enclosures were suspended just beneath the

water, evenly spaced (2 m apart) along three sides of a floating platform (i.e., five enclosures on each of three sides of the floating platform). Rocks were placed in the bottom of each enclosure to maintain constant orientation. These enclosures restricted the fish to a 20-L volume, and the mesh construction allowed food items (e.g., suspended phytoplankton and zooplankton) to enter at densities that naturally occur within this section of the marsh. Because the enclosures were suspended, the fish in this study did not have access to benthic organisms. The three treatments—sticklebacks only, fathead minnows only, and fathead minnows plus sticklebacks—were divided evenly among the 15 enclosures (5 enclosures/treatment) and assigned randomly to locations around the floating platform. Thirty young-of-the-year fish were placed in each enclosure, representing a density of 250 g of fish/m³ of water (approximating the natural density of fish within this section of Delta Marsh: Acere 1971; Suthers 1984). Enclosures that were selected for mixed species pairs contained 15 fathead minnows and 15 brook sticklebacks.

Fish used in this experiment were captured by seine and dip net in the vicinity of the enclosures. These fish were immediately placed in buckets and returned to a laboratory at the University of Manitoba field station within the marsh. Fish were anesthetized with 2-phenoxyethanol, and their lengths (fork length for fathead minnows, total length for brook sticklebacks) and wet weights (brook stick-

lebacks only) were determined. Fathead minnows at this age are very delicate and die easily when handled. To avoid direct handling of these fish, I removed them from nets with drinking glasses and placed them directly into buckets of water. Fork lengths of these fish were determined after they were drawn into transparent cylinders (disposable 5-mL syringes that had the tapered end removed). Wet weight for the fathead minnows was determined later through interpolation from a length-weight regression for fish that perished during capture.

After weights and lengths were determined in the laboratory, fish were placed in their appropriate group and transported to the enclosure within the marsh. Three days were required to obtain and measure all fish that were used in this experiment. I checked for mortalities 24 h after the fish were handled, and any dead fish were replaced. After that time, weekly checks were made for each enclosure to ensure fish were still alive and that no holes had appeared in the enclosures.

At the end of this experiment, fish were killed by an overdose of 2-phenoxyethanol, remeasured, and preserved in 10% formalin. The stomach contents were determined for a subsample of brook sticklebacks from each enclosure. For fathead minnows, the contents of the gut posterior of the esophagus and anterior of the small intestine were removed. Because of extensive mechanical grinding by the pharyngeal teeth of the fathead minnows, it was very difficult to assess the specific composition of their diet. Instead, the gut contents were digested with cellulase (an enzyme that digests cellulose), which allowed the proportion of their gut contents that was cellulose to be determined. This proportion was used as an index for the amount of plant material in their diet. This index was then used to determine whether exposure to brook sticklebacks altered the proportion of plant material that appeared in their diet.

Results

Growth of the two species differed significantly during this experiment (Figure 1; two-way analysis of variance, ANOVA: $F = 19.62$; $df = 1, 14$; $P < 0.001$). Species composition within enclosures had a significant effect on brook stickleback growth ($F = 8.95$; $df = 1, 14$; $P < 0.01$), but no effect upon the growth of fathead minnows (Figure 1). Thus, a significant species by enclosure interaction existed with these data ($F = 9.33$; $df = 1, 14$; $P < 0.01$).

During this experiment, the average mortality

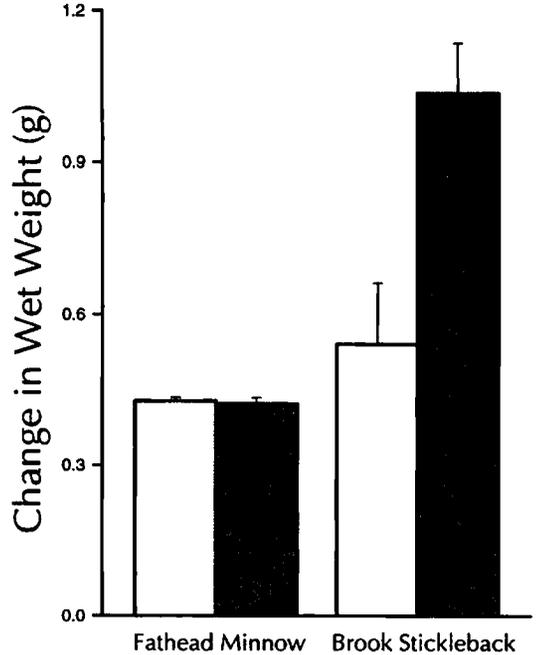


FIGURE 1.—Average growth for fathead minnows and brook sticklebacks that were held in either single species (open bars) or mixed species (shaded bars) enclosures. Error bars correspond to 1 SE.

for fathead minnows was six fish per enclosure that contained only fathead minnows and four fish per enclosure that contained both fathead minnows and brook sticklebacks. Brook stickleback mortality was much lower: 0.8 fish were lost from enclosures that contained only sticklebacks and 0.5 fish were lost from mixed enclosures. Mortality was significantly different between species in these enclosures (two-way ANOVA: $F = 24.63$; $df = 1, 14$; $P < 0.001$) but was not significantly affected by competition ($F = 1.72$; $df = 1, 14$; $P > 0.05$) or the interaction between competition and species ($F = 0.94$; $df = 1, 14$; $P > 0.05$).

Because some fathead minnows died, some enclosures contained different densities of fish for part of the experimental period. I determined whether total mortality (and hence density of fish in the enclosures) had a significant impact on the observed growth of fathead minnows and sticklebacks. Regression analysis showed that growth of fathead minnows was unaffected by the density of fish in the enclosures (Figure 2; $F = 0.526$; $df = 1, 7$; $P > 0.05$; $r^2 = 0.0699$). Mortality, however, had a significant impact on the growth of brook sticklebacks ($F = 6.396$; $df = 1, 7$; $P < 0.05$) and accounted for a substantial proportion of the vari-

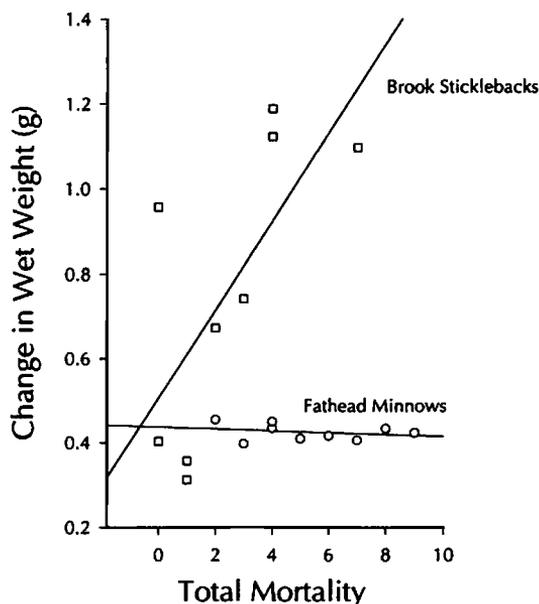


FIGURE 2.—Effect of total mortality within enclosures on the observed growth of fathead minnows (open circles) and brook sticklebacks (open squares).

ation in observed growth rates ($r^2 = 0.4775$). Because mortality of brook sticklebacks was low relative to that of fathead minnows, the sticklebacks that were held with fathead minnows were also held at lower densities within their enclosures. Therefore, the increased growth of the sticklebacks in the presence of the fathead minnows may have been caused by the reduced fish densities associated with this treatment.

Despite the differences in growth, no significant difference was observed in the number of food items in the sticklebacks' stomachs as a function of the experimental treatment (analysis of covariance, ANCOVA: $F = 0.08$; $df = 1, 6$; $P > 0.05$). The composition of the food items, however, changed considerably. Stickleback diet was summarized as a single number by describing the gut contents with the Brillouin diversity index. Analysis of dietary composition with enclosure position as a covariate demonstrates that species composition within the enclosure had a significant effect on dietary composition for sticklebacks (ANCOVA: $F = 17.82$; $df = 1, 6$; $P < 0.01$). As illustrated in Figure 3, the main effect upon dietary composition was a change in the proportion of copepods. When both species occupied these enclosures, copepods accounted for approximately 40% (by number) of the stomach contents of the sticklebacks; however, in enclosures that contained

only sticklebacks, copepods accounted for over 65% of the stomach contents. The covariate, enclosure position, also had a statistically significant effect upon dietary composition ($F = 10.80$; $df = 1, 6$; $P < 0.05$).

In the enclosures containing only fathead minnows as well as in those containing both species, enzymatic digestion of cellulose removed less than 10% of the dry weight of the stomach contents of fathead minnows, and species composition in the enclosure had no effect upon this measure. Thus, at this level of resolution, the sticklebacks appeared to have no effect on the diet of fathead minnows.

Discussion

These data demonstrated that the presence of brook sticklebacks exerted no obvious effect upon either the growth of juvenile fathead minnows or the amount of plant material in their diet. Sticklebacks held in enclosures containing fathead minnows, however, grew more rapidly than their counterparts held in enclosures containing only sticklebacks. The mechanism responsible for this increased growth may be the increased mortality of the fathead minnows and the associated reduction in fish density (see below). In addition, dietary composition becomes more diverse in the presence of fathead minnows. Groups consisting only of brook sticklebacks consumed primarily copepods, whereas in the presence of fathead minnows, their diet contained higher proportions of cladocerans, ostracods, and dipteran larvae.

The observed changes in stickleback growth are possibly a consequence of the observed fathead mortality; that is, changes in growth appear to be generated primarily by changes in fish density, not in fish composition. Interestingly, growth of fathead minnows was unaffected by changes in fish density. The sensitivity of stickleback growth to fish density may be due to relatively higher energy demands associated with their specialized morphology (Abrahams 1995). Their relatively short gut may limit the range of food items that can be profitably consumed, and their armor, reduced caudal peduncle, and lack of red muscle may make movement relatively more energetically expensive.

The sensitivity of brook stickleback's growth to the density of a potential competitor may account for some of its unusual characteristics. In particular, this species is notorious for its extensive spring migrations into ephemeral habitats. If this species is sensitive to competition with fathead minnows, then migration may be a strategy to reduce competition. Possibly this behavior may be

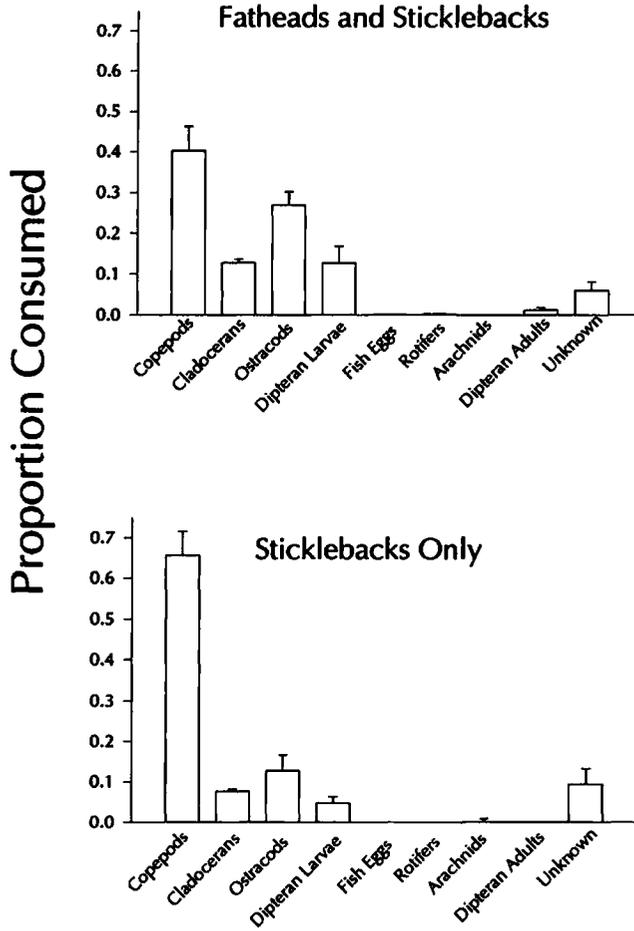


FIGURE 3.—Composition of stomach contents (proportion by number) for brook sticklebacks held in single-species enclosures or in enclosures with fathead minnows. Error bars correspond to 1 SE ($N = 5$).

generated if there is some substantial cost to maintaining the antipredator morphology of the sticklebacks (either direct energetic costs, or indirect costs because of impairment of swimming ability generated by the morphology).

Abrahams (1994) demonstrated that in the absence of predators, brook sticklebacks feed at a relatively slow rate compared to that of fathead minnows. In the presence of a predator, however, the fathead minnows adjust their behavior considerably and have a slower feeding rate. The sticklebacks do not adjust their behavior to the same extent and consequently have a feeding rate higher than the fathead minnows in the presence of a predator.

In summary, these data indicate that brook stickleback growth is affected by the presence of fathead minnows, whereas the growth of fathead minnows appears to be unaffected by the presence of

sticklebacks. If this is the case, then sticklebacks should do relatively well only in habitats where they are at a competitive advantage. This advantage would be generated by allowing them to exploit habitats that contain few competitors, either by migrating rapidly to new habitats generated by spring flooding or by exploiting areas that are relatively dangerous for other species. In the absence of such adjustments, modifications in brook stickleback life histories may be expected. Future research will determine whether morphological variation in the brook stickleback is generated by habitats that do not allow sticklebacks to benefit from their antipredator morphology.

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