

ADAPTIVE RADIATION IN STICKLEBACKS: SIZE, SHAPE, AND HABITAT USE EFFICIENCY¹

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Abstract. I examined habitat use efficiencies of two morphologically distinct threespine sticklebacks (*Gasterosteus* spp.). The species make up one of several coexisting pairs that apparently formed in the past 13 000 yr in coastal British Columbia lakes. Previous comparative work has shown that morphology and habitat use are correlated within and among populations. Sticklebacks occurring alone in lakes are intermediate in morphology and habitat use, suggesting that differences between the sympatric species result from ecological character displacement.

I tested two hypotheses to explain these patterns, and which are implicit in general views of the causes of adaptive radiation: (1) Each resource (habitat) subjects its species to unique selection pressures, owing to the advantages of certain combinations of traits for foraging; (2) Phenotypes intermediate between habitat specialists suffer a competitive disadvantage. These hypotheses were evaluated by measuring the foraging rates of the two species and their interspecific hybrids in the two main habitats (benthos and open water) provided in the laboratory.

Efficiencies of habitat exploitation matched observed morphological differences. In the benthic habitat the larger, deeper bodies species (having also a wide mouth and few short gill rakers) was superior to the smaller, more slender species (having a narrow mouth and many long gill rakers). Success of hybrids was intermediate. This rank order of species efficiencies was reversed in the open water habitat. These results support the hypothesis that different traits are favored in different habitats, and that adaptation to one habitat has occurred at the expense of feeding rate in the other. Average foraging success of hybrids in the two habitats fell near or below the average of the two parental species, suggesting natural selection against intermediate phenotypes. Foraging efficiency in open water was greatest in the smaller size classes of fish, hinting that small size of the open water species is the result of selection for high foraging efficiency. However, size could not explain most differences in feeding efficiency between species, and it is likely that many traits contribute.

Key words: *adaptive radiation; body size; British Columbia; foraging efficiency; habitat selection; morphology–ecology correlation; sticklebacks.*

INTRODUCTION

The evolutionary expansion of a lineage to exploit a variety of new resource types, and the accompanying differences in morphology between new species, are the signatures of adaptive radiation (Futuyma 1986). At least three kinds of processes are thought to be responsible for this phenomenon. (1) Divergent natural selection, whereby each resource type subjects a species to unique selection pressures and favors a distinct combination of traits for foraging. (2) The evolution of reproductive isolation between populations exploiting different resources. (3) Ecological character displacement: competition between similar phenotypes for food drives the divergence to exploit new resources, a process aided by a dearth of competing taxa.

None of these processes is very well understood. For example, the role of competition is still much debated, and clear demonstrations of its role in adaptive radi-

ation remain few (Grant 1972, 1986, Fjeldsa 1983, Schluter and Grant 1984, Schluter et al. 1985, Schluter 1988a, Losos 1990, Schluter and McPhail 1992, Taper and Case 1992). The consequences of divergent selection pressures for the evolution of reproductive isolation also remains controversial (Felsenstein 1981, Butlin 1989, P. R. Grant and B. R. Grant 1989, Wilson 1989). Finally, the form of divergent natural selection has rarely been estimated (Schluter and Grant 1984, Schluter et al. 1985, B. R. Grant and P. R. Grant 1989, Smith 1990, Benkman 1993).

In this paper I examine the relationship between morphology and foraging success in a morphologically distinct pair of coexisting sticklebacks (*Gasterosteus* spp.; Fig. 1). The study is part of a wider investigation into the ecological selection pressures causing diversification in a complex of new freshwater species (McPhail 1992a, Schluter and McPhail 1992). All species are thought to be very recent because they are endemic to coastal lakes that did not form until the late Pleistocene (13 000 yr ago; Mathews et al. 1970).

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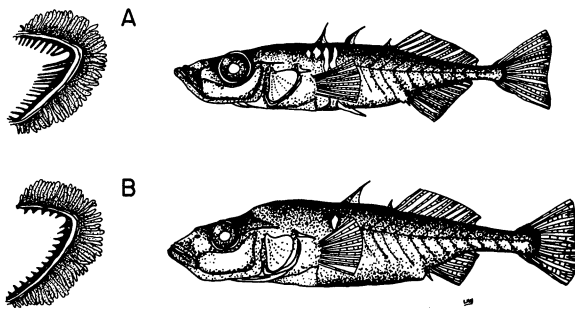


FIG. 1. The Limnetic (upper) and Benthic (lower) species in Paxton Lake. Drawings on left illustrate the first gill arch for each species. The gill rakers are the projections along the inside edge.

Most lakes contain only one species, but some contain two. Preliminary indications based on the geology of the area are that several species pairs have evolved independently (McPhail 1992a, Schluter and McPhail 1992).

An earlier survey of stickleback populations in small lakes revealed that morphology and habitat use are strongly correlated within and among populations, and that sympatric species show character displacement (Schluter and McPhail 1992). In lakes with two species, one (hereafter, the Benthic) forages almost entirely on benthos, whereas the other (the Limnetic) takes mainly plankton from open water, particularly in the non-breeding season (Fig. 2). Benthics are larger and have deeper bodies, wider mouths, and shorter, fewer gill rakers than Limnetics (Fig. 1). Populations occurring alone in small lakes are intermediate in morphology and habitat use. These patterns suggest that sticklebacks are undergoing an adaptive radiation that is as yet in an early phase.

The present study has two objectives. First, I test the hypothesis that species differences are the result of natural selection for efficient foraging in alternative habitats (benthos and open water). Ideally, one should measure selection directly, by comparing fitness of individuals of different morphology on each resource type (e.g., Schluter et al. 1985, Smith 1990). I use foraging efficiency as an indirect measure of fitness, and test the hypothesis by measuring performance of both species in the two habitats. If size and shape of Limnetics and Benthics is molded by selection for efficient foraging in contrasting habitats, then differences between the species in feeding efficiency in the two habitats should match their morphological differences.

Second, I estimate the success of phenotypes intermediate between Limnetics and Benthics by measuring the foraging efficiency of their interspecific Hybrids. My purpose was to assess whether intermediate phenotypes suffer a foraging disadvantage in both habitats when compared to the more specialized parental phenotypes. A large reduction in success of intermediate phenotypes would suggest the presence of disruptive

selection against them, as required by the hypothesis of character displacement (Schluter and McPhail 1992) and by models of competitive speciation (Rosenzweig 1978, Wilson 1989).

Speciation in threespine sticklebacks

I treat the sympatric forms of threespine sticklebacks as distinct species, a conclusion supported by several lines of evidence. Morphological differences between the forms are retained when fish are bred for two generations in a common laboratory environment (McPhail 1984, 1992b). F_1 and F_2 hybrids between sympatric forms are morphologically intermediate under the same laboratory conditions (McPhail 1984, 1992b; T. Hatfield, *unpublished data*). A population of Paxton Lake F_1 hybrids established in a small lake in 1981 has remained morphologically intermediate over 10 subsequent years (generations) without recovering the parental phenotypes (J. D. McPhail, *unpublished data*). Hence the differences between sympatric forms are mainly genetic, and probably involve many loci. This result distinguishes the sticklebacks from other examples of trophic polymorphism in fish in which the differences between sympatric forms are environmentally induced during development (e.g., cichlids [Meyer 1987], sunfish [Wainwright et al. 1991], and possibly char [Skúlason et al. 1989]).

There appears to be little gene flow between sympatric morphs. Morphologically intermediate individuals (such as F_1 hybrids) are rare in the natural lakes (McPhail 1984, 1992b). Laboratory experiments have shown very strong assortative mating between the sympatric forms (Ridgway and McPhail 1984). Finally, sympatric forms approach fixation for alternative alleles at one or more enzyme loci (McPhail 1984, 1992b). These data suggest that sympatric forms are true species by the standard biological concept, rather than alternative morphs in a single-species polymorphism.

METHODS

Study populations

The studies were carried out in spring and summer of 1990, on the two species of sticklebacks (Benthic and Limnetic) endemic to Paxton Lake, Texada Island, British Columbia. I used Hybrids between Benthics and Limnetics as the intermediate phenotype. These were preferable to individuals from a solitary population, because Hybrids are morphologically intermediate in every known respect (McPhail 1984, 1992b; T. Hatfield, *unpublished data*). The two species are sufficiently young that artificially created F_1 Hybrids are as viable and fertile as the parental species when raised in the laboratory (McPhail 1992b; T. Hatfield, *unpublished data*). Nevertheless, as a precaution against any possible F_1 Hybrid vigor or inferiority I used individuals from a population established from F_1 individuals 10 yr (generations) previously (Second Lake,

TABLE 1. Body length and estimated body mass of the three species (means \pm 1 SD). (A) Individuals used in the experiments. (B) Individuals in 1989 random samples from Paxton Lake (May and September collections combined). Sample sizes for the three species are (A) $N = 86, 40, 95$, and (B) $N = 80, 91$.

Trait	Benthic	Hybrid	Limnetic
A) Present study			
Length (mm)	45.5 \pm 12.2	44.5 \pm 7.9	41.9 \pm 6.3
Mass (g)	1.48 \pm 1.13	1.12 \pm 0.57	0.81 \pm 0.34
B) Paxton Lake sample			
Length (mm)	46.9 \pm 7.6	...	40.4 \pm 6.5
Mass (g)	1.59 \pm 0.71	...	0.73 \pm 0.34

Texada Island; J. D. McPhail, *personal communication*).

Habitats

Foraging success of individual fish was measured in two habitats, open water and benthos, presented separately in large aquaria (outside dimensions 120 \times 33 \times 53 cm). These are the two main habitats partitioned by species in all lakes where two species of sticklebacks are present (Bentzen and McPhail 1984, Schluter and McPhail 1992).

The experimental open water habitat contained plankton at natural densities. Plankton was collected at dusk from Paxton Lake one or two evenings before each day of experiments. Dusk was chosen for sampling because the major prey in open water (calanoid copepods) migrate to the surface and are easiest to capture then. A tow made of 0.15-mm Nitex mesh was pulled horizontally 0.5–2 m below the lake surface. The volume of water sieved was calculated from the distance towed and tow diameter. Sufficient plankton was added to the aquarium on the morning of the trials to yield ambient (dusk) lake densities when diluted to 180 L.

The benthic habitat consisted of lake sediment distributed evenly over the bottom of the aquarium to a depth of \approx 3 cm. Water was added to bring the total volume in the tank to 180 L. Benthos was collected from Paxton Lake at various depths above the thermocline using an Ekman grab. The total surface area of lake bottom sampled with the grab equalled that of the bottom of the aquarium (\approx 3800 cm²). Sediment was not replaced daily, but was used in a series of trials over 6 d following collection. The aquarium was aerated to minimize mortality of prey.

Experimental benthos did not include vegetation, a second substrate exploited by the Benthic species, and hence did not fully duplicate the natural habitat. Nevertheless, the diet of the Benthic species in the experiments was similar to that in the lake (see *Foraging experiments*), suggesting that sediment is the major substrate exploited in the wild.

Aquaria were kept indoors and illuminated from above with 15-W fluorescent lights, and were surrounded on three sides with brown paper to minimize disturbance from outside. Water temperature was kept between 17° and 20°C. Only one habitat type was set

up on any one day, and I alternated open water and benthos experiments at 1–2 wk intervals. A duplicate aquarium was available at all times, and was used to familiarize fish with the experimental conditions prior to testing, as described below.

Foraging experiments

Fish from Paxton and Second Lakes were collected using dip nets and minnow traps 3 d prior to testing, and placed in 10–20 L aquaria. Only juvenile and adult fish in their second summer or older were used (i.e., no young of the year were tested). Each fish was allowed to feed in the experimental habitat (duplicate aquarium) for 1 h on each of the two days prior to testing. Prey were regularly replenished to minimize depletion. Most fish fed readily; those that did not were not used. Large Benthics and small Limnetics were the least responsive classes of fish, so that the size difference between the species was less in the experiments than in the wild (Table 1). As a result the experiments would tend to underestimate differences between species in foraging efficiency, if these differences are determined in part by size. To check this possibility I tested for effects of size on feeding efficiency.

An experimental trial consisted of releasing a fish into the test aquarium with a dipnet and observing it for 15 min after foraging had begun. The observer sat behind a blind and recorded behaviors on a laptop computer programmed as an event recorder. Unfortunately, it was not possible by direct observation to determine accurately the success of strikes at prey or the sizes of items consumed. As a result, it was necessary to dissect each fish immediately after testing it in order to count and measure prey. This prevented us from assessing an individual's performance in both habitats or over a sequence of trials. To minimize depletion, prey items consumed by each fish in the experimental aquarium, as judged by inspection of its gut contents, were replaced with similar items before the next fish was tested.

Foraging success was highly variable among trials within a habitat. Two sources of sampling error were probably the main cause of this variability. First, the duration of feeding trials was short (\leq 15 min), and two fish of the same size and species tested in sequence in the same aquarium would usually have very different

foraging successes. Second, since prey were provided at natural densities, which could vary from sample to sample, I could not ensure that each fish was tested under identical prey densities or distributions. Unfortunately, it was not possible to quantify these errors directly, since repeated measurements could not be made on the same individual fish. Another possible source of variability was a change in prey distribution between successive trials (e.g., through mortality or increased concealment of prey). Foraging efficiency indeed declined weakly with successive experiments on any given day, but this effect accounted for <3% of the variability between trials.

I attempted to obtain as large a sample of fish as possible to minimize the effect of variability. As a result, and because proper laboratory facilities were lacking at the field site, I was not able to provide fish with a pre-trial experience of longer than 2 d (2 h total). Experiments by Mittelbach (1981) suggested that foraging rate of an individual bluegill may improve for 7 d following introduction to experimental conditions, but his trials were more brief than mine (0.5–3.0 min). The problem of familiarity with experimental conditions should be less in the present study because I used natural prey mixtures and densities.

Nevertheless, I carried out a second experiment in spring 1991 to test for effects of additional learning on foraging rates. The study was done only in the open water habitat, on the reasoning that effects of unfamiliarity should be greatest there: both Limnetics and Benthics forage on benthos in the wild but only Limnetics exploit open water to any degree (Schluter and McPhail 1992: Fig. 2). Fish were held together in 200-L aquaria for 1 wk prior to the start of testing, by which time they had ceased to be alarmed by observers or dipnets. Testing continued for an additional 10 d. Fish were fed plankton for 2 h every 2nd d throughout their captivity. Afterward, and in the intervening days, the fish were fed with frozen brine shrimp and bloodworms. Fish were starved 24 h before testing.

Analysis

Length and width of prey items were measured (millimetres) using an ocular micrometer on a dissecting microscope. Prey volume was estimated as $\pi \times (\text{width}/2)^2 \times \text{length}$. To minimize sampling error, my analysis used only fish that had made at least 10 strikes at prey during a trial.

I calculated four measures of foraging success: (1) *Capture success* is the volume of prey obtained per strike, and was computed as (total volume of prey)/(total number of strikes). (2) *Between-strike interval* is the median time between successive strikes at prey by an individual fish. This includes prey handling time and search time. (3) *Intake rate* is the volume of prey obtained per minute, and was computed as (total volume of prey)/(total number of strikes \times between-strike interval). Differences between species were virtually

identical for (1) and (3), and so I mainly present results on capture success only.

(4) The fourth measure was *net energy intake*, the rate of energy consumed in excess of metabolic requirements. I was able to compute this only approximately. First, I converted the length of each prey item (l , in millimetres) to dry mass (m , in milligrams) using Mittelbach's (1981) formula $m = 0.005^{2.16}$, which is based on a variety of prey types. Second, prey dry mass was converted to energy using the constant 22 J/mg and assuming an assimilation fraction of 70% (Mittelbach 1981). Third, I used routine respiration rate (r , in joules per minute) as my measure of metabolic requirement. It was calculated as a function of fish mass (W , in grams) and ambient temperature (T , in degrees Celsius) from the example values for threespine sticklebacks (*Gasterosteus aculeatus*) in Wootton's (1984) Table 5.1: $r = \exp(0.741 \ln(W) + 0.77T - 3.762)$. I used the summer mean $T = 19^\circ\text{C}$. Net energy intake was then computed for an individual as the energy intake from prey minus r .

Distributions of foraging success in each habitat and for each species were often highly skewed, and I mainly used medians of individuals rather than the mean to describe results. Standard errors for medians were calculated using a bootstrap procedure (Efron 1982) as follows. N observations were randomly sampled (with replacement) from the given data set and the new median was computed, where N is original sample size. This process was repeated 200 times. The standard error is obtained as the standard deviation of the 200 resampled medians. Other statistical comparisons were carried out using nonparametric procedures whenever possible. When parametric tests were necessary (e.g., to obtain regression slopes), measurements were first \ln -transformed; zero values were assigned the smallest positive value in the data set before transforming.

I assume that each fish provided a single independent measurement. Slight daily and seasonal trends in foraging success were detected, but correcting for them made no difference to the results.

Fish size and shape

Body length, maximum depth and mouth width were measured on all experimental fish, as described in Lavin and McPhail (1985). Number and length of gill rakers were measured on the first gill arch (Fig. 1) in a random sample of 40 individuals from each species (only 34 Hybrids were available). Techniques are described in Lavin and McPhail (1985). I used these measurements to summarize shape differences between species. Body depth, mouth width, and gill raker length were regressed separately on body length, and used to calculate means for each species adjusted to a common length of 42 mm (results are similar if other lengths are used). Number of gill rakers varied independently of size, and I used the unadjusted means for each species. Finally, body mass was estimated using regres-

TABLE 2. Shape differences between species. Values are species means (± 1 SD) scaled to a body length of 42 mm using regression. $N = 40, 34, 40$.

Trait	Benthic	Hybrid	Limnetic
Body depth (mm)	9.5 \pm 0.4	9.0 \pm 0.5	8.1 \pm 0.5
Mouth width (mm)	3.7 \pm 0.3	3.4 \pm 0.3	2.9 \pm 0.3
Gill raker number	18.3 \pm 1.2	20.3 \pm 1.4	23.3 \pm 1.3
Gill raker length (mm)	0.6 \pm 0.2	0.9 \pm 0.1	1.2 \pm 0.2

sions of mass on body length obtained in later studies (D. Schluter, *unpublished data*).

RESULTS

Fish size and shape

The Benthic species was larger on average than the Limnetic, as indicated by body length and estimated body mass (Table 1). The difference between the means of these two species was slightly less in experimental fish than in a random sample of fish from the same lake. Hybrids were intermediate in body size. Table 2 compares the dimensions of species scaled to a common body length. Benthics had deeper bodies and wider mouths than Limnetics of the same length, whereas Limnetics had longer and more numerous gill rakers. Hybrids were intermediate in all respects.

Foraging behaviors

Sticklebacks used remarkably different feeding techniques to capture prey in the two habitats. When attacking calanoid copepods in open water (the dominant prey, see below) a fish would doubly bend its body laterally into an S-shape and then straighten it rapidly to produce a single forward thrust ("S-start"; e.g., Webb 1976) culminating in a strike. This action was performed as often as 5–10 times per minute. Benthics appeared to be much more stiff-bodied than Limnetics when performing this action, particularly the largest individuals, and the amplitude of their S-shape was noticeably less. This difference remains to be quantified.

Foraging on benthos was accomplished mainly by a

series of pauses to horizontal swimming motion. During these pauses a fish would hover motionless 1–3 cm above the benthos, with the head oriented downward and the gaze fixed at the substrate. This was often followed by a strike in which the fish would engulf a mouthful of sediment, sometimes burying its entire head in the effort. The fish would then spit out the captured sediment, and occasionally a prey item, which was then reingested. The majority (87%) of strikes by Benthics were of this type. Remaining strikes by Benthics were at prey clinging to the sides of the aquarium (6%), prey in open water (4%), or prey in the 1-cm layer immediately above the sediment (3%). Limnetics made fewer strikes at the benthos (54%) than did Benthics, and more strikes at prey in the other three locations (20, 17, and 10%, respectively). Hybrids were similar to Benthics (86, 7, 4, and 5%).

Diets

Calanoid copepods were the main prey of all three stickleback species in the experimental open water habitat (Table 3). This is similar to the diet of wild Limnetics when planktivorous, especially from midsummer through fall (Fig. 2). For example, calanoids made up 87% of prey items in the stomachs of Limnetics caught in Paxton Lake in July 1991. The calanoids consumed in the experiments were uniform in size, and mean sizes of prey taken by the three species were identical (Table 3; $F_{2,83} = 0.73$, $P = .48$).

The three species consumed dissimilar prey types in the experimental benthic habitat (Table 3). Chironomid larvae, gammarids, and ostracods were the main

TABLE 3. Diet proportions in the experimental habitats. All foods are listed that constituted $\geq 10\%$ of items of any species* N is the total number of items. Prey size is the mean (± 1 SE) of means for individual fish.

Open water habitat							
Species	Calanoids	Other	N	Prey size (mm ³)			
Limnetic	0.95	0.05	1048	0.072 \pm 0.006			
Hybrid	0.99	0.01	470	0.073 \pm 0.006			
Benthic	0.95	0.05	395	0.072 \pm 0.007			
Benthic habitat							
Species	Chironomids	Gammarids	Ostracods	Cyclopoids	Other	N	Prey size
Limnetic	0.06	0.03	0.06	0.76	0.09	459	0.48 \pm 0.14
Hybrid	0.11	0.03	0.14	0.54	0.18	35	1.50 \pm 0.62
Benthic	0.27	0.17	0.30	0.03	0.23	150	7.79 \pm 3.74

* Calanoid copepods were the main prey in open water. Prey from benthos included chironomid larvae, gammarids (Amphipoda), ostracods, and cyclopoid copepods.

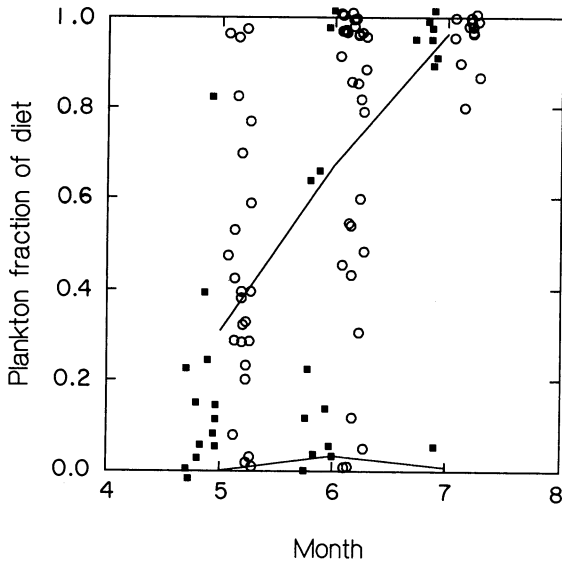


FIG. 2. Seasonal trend in plankton fraction of the diet of the Limnetic species in Paxton Lake in 1991. Data are for males (■) and females (○). Symbols were displaced to reduce overlap. The upper line connects overall monthly means. For comparison, the lower line indicates mean plankton fraction in the diet of Benthics in the same three months. Limnetics continue to concentrate on open water plankton through the late summer and fall (Larson 1976, Schluter and McPhail 1992).

prey of Benthics, which is similar to their diet in nature. For example, spring, summer, and fall stomach samples of Benthics taken during 1989–1991 revealed that other dipteran larvae and small clams are the only additional prey consumed as frequently in the wild (except stickleback eggs; D. Schluter, unpublished data). These additional prey types were also eaten by Benthics in the experiments, but made up <10% of the items. In contrast, Limnetics in the benthic habitat ate mainly cyclopoid copepods, a prey type largely ignored by Benthics (Table 3). The diet of Hybrids was intermediate, but more similar to Limnetics than to Benthics. Prey sizes also differed between species, being smallest in Limnetics and largest in Benthics, with Hybrids again intermediate ($F_{2,60} = 19.46$, $P < .001$).

Foraging efficiency

1990 vs. 1991.—Capture success in open water by the three species in 1990 was virtually identical to that observed in 1991, when a protracted learning period preceded the trials (Fig. 3). This suggests that the standard pre-trial period in the main set of experiments (1990) was sufficient to permit quantitative comparisons of foraging success between species.

Benthos.—The three species differed greatly in their foraging efficiency on benthos (Fig. 4; Kruskal–Wallis [K–W] test, $\chi^2 = 7.724$, $df = 2$, $N = 91$, $P = .021$). Capture success (median volume of food obtained per strike) by Benthics was nearly six times that of Lim-

netics. The greater success of Benthics is entirely attributable to their consumption of larger prey (Table 3), since the Limnetics captured more prey per strike (medians ± 1 SE: 0.086 ± 0.016 vs. 0.148 ± 0.029 individuals per strike). Capture success by Hybrids was intermediate, although closer to Limnetics than to Benthics (Fig. 4).

Time between strikes was least in Limnetics (Table 4); nevertheless its intake rate on benthos (volume of prey ingested per unit foraging time) remained much lower than that of Benthics (0.19 ± 0.03 vs. 0.64 ± 0.28 mm³/min). Intake rate of Hybrids was intermediate, although closest to Limnetics (0.22 ± 0.11 mm³/min).

The pattern of differences between species in estimated net energy intake (Fig. 5) was similar to that in capture success (Fig. 4), although the differences were not significant ($\chi^2 = 3.82$, $df = 2$, $N = 91$, $P = .148$). Net energy intake incorporates the energy content of prey after subtracting the routine metabolic costs per unit time spent foraging. Benthics were again the superior foragers despite their larger size and hence higher total metabolic requirements. Hybrids were slightly but not significantly worse than Limnetics (Fig. 4). Median net energy intake on benthos was positive in all three species.

Open water.—The rank order of species' foraging efficiencies in open water was the reverse of that observed on benthos (Figs. 4 and 5). Capture success of Benthics was about one-third that of Limnetics and of Hybrids (K–W test, $\chi^2 = 6.653$, $df = 2$, $N = 112$, $P = .036$). Time between strikes tended to be least in Limnetics and greatest in Benthics, with Hybrids intermediate (Table 4). Species differences were also large

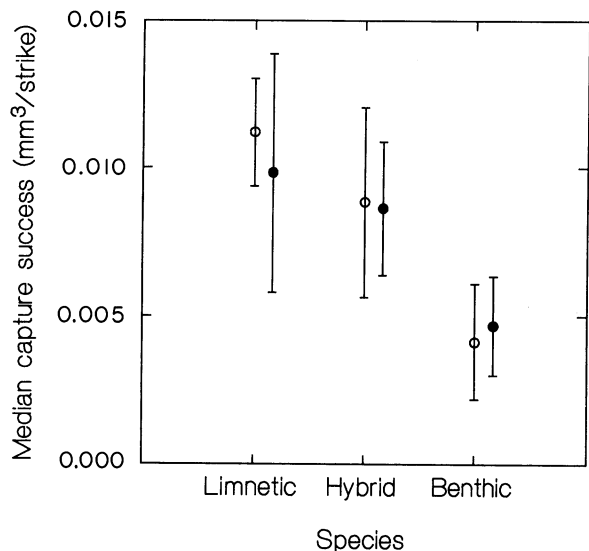


FIG. 3. Median prey capture success of the three species in the open water habitat in 1990 (○) and 1991 (●). Values are prey volume per strike (± 1 SE) in mm³. $N = 50, 27, 27, 25, 35, 18$.

TABLE 4. Time between strikes at prey in the two habitats, in seconds. Values are medians (± 1 SE) of individual median times. Sample sizes are given in the legend to Fig 3. χ^2 is the K-W test statistic.

Habitat	Limnetic	Hybrid	Benthic	χ^2	<i>P</i>
Open water	7.0 \pm 0.5	8.0 \pm 1.7	11.0 \pm 2.2	5.06	.08
Benthos	14.5 \pm 1.3	19.5 \pm 4.3	18.5 \pm 1.5	7.12	.03

when net energy intake rates were compared ($\chi^2 = 16.95$, $df = 2$, $P < .001$). Only Limnetics appeared to have a positive median net energy intake in the open water habitat (Fig. 5).

Trade-offs.—The reversal in the rank order of species' foraging efficiencies between open water and benthic habitats implies a cost to specialization: morphological adaptation to improved efficiency in one habitat has occurred at the expense of feeding success in the other. This is emphasized by the negative slope to the line connecting Benthic and Limnetic medians in Figs. 4 and 5, and by the large species \times habitat interaction term in an analysis of variance of capture success (ln-transformed data, $F = 6.311$, $df = 2,197$, $P = .002$) and of net energy intake ($F = 4.08$, $df = 2,197$, $P = .02$). Hybrids tended to fall below the line, although never significantly (all $P > .10$).

Benthics were much more successful in benthos than in open water, as measured by net energy intake (Fig. 5; Mann-Whitney *U* test, $P = .005$). However, Limnetics were not apparently better off in the open water habitat than on benthos: net energy intake by this species was slightly higher on benthos than in open water, although not significantly (*U* test, $P = .24$). Hybrids were also better on benthos than in open water, but not significantly (*U* test, $P = .39$).

Body size.—Size is among the most noticeable of

differences between Limnetics and Benthics (Table 1), and it is of interest to know whether size alone can account for their differences in foraging efficiency. I examined various measures of size (body length, estimated body mass, and the within-population principal axis of variation) with similar results. I could detect no association between feeding rate and size in the benthos habitat. For example, the effect of body mass on prey capture success (ln-transformed) was not significant in an analysis of covariance ($F = 0.003$, $df = 1,87$, $P = .96$), whereas the differences between species in capture success remained after size was accounted for ($F = 3.574$, $df = 2,87$, $P = .036$).

Relationships between size and foraging efficiency in open water were more interesting, although variability was high (Fig. 6). Capture success (ln-transformed) appeared to diminish steadily with increasing mass of Benthics (regression slope = -0.54 , $R^2 = 0.06$, $N = 35$, $P = .17$) and of Benthics and Hybrids combined (slope = -0.64 , $R^2 = 0.07$, $N = 63$, $P = .02$). Capture success appeared to reach an optimum at intermediate size in Limnetics (Fig. 6), a trend supported by a significant nonlinear term in a quadratic regression of ln capture success on body mass (coefficient = -2.80 , $N = 50$, $R^2 = 0.17$, $P = .02$). Limnetics were superior to Benthics at all but the smallest sizes.

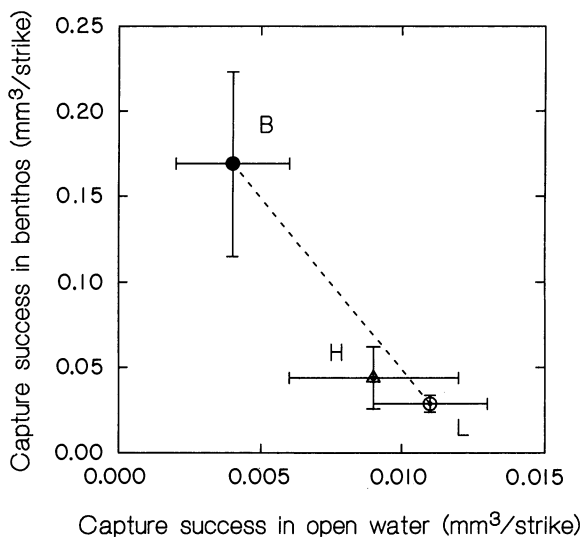


FIG. 4. Prey capture success (prey volume obtained per strike [median ± 1 SE]) in benthic and open water habitats. Symbols indicate Benthics (●), Limnetics (○), and Hybrids (Δ). Dashed line connects medians of parental species.

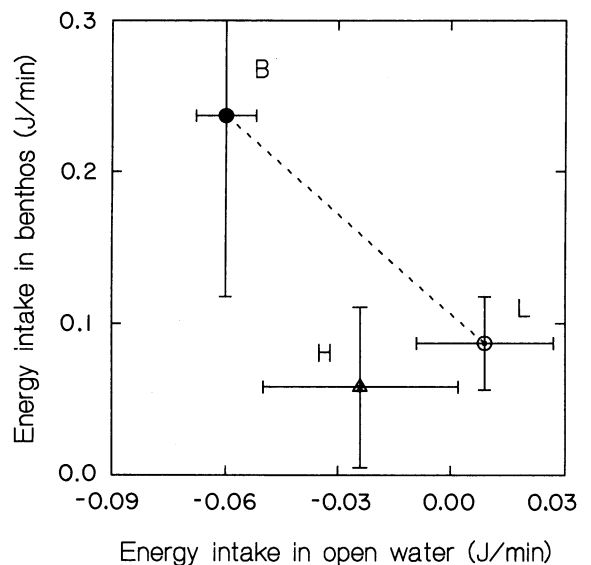


FIG. 5. Net energy intake (median ± 1 SE) in benthic and open water habitats. Symbols indicate Benthics (B, ●), Limnetics (L, ○), and Hybrids (H, Δ). Dashed line connects medians of parental species.

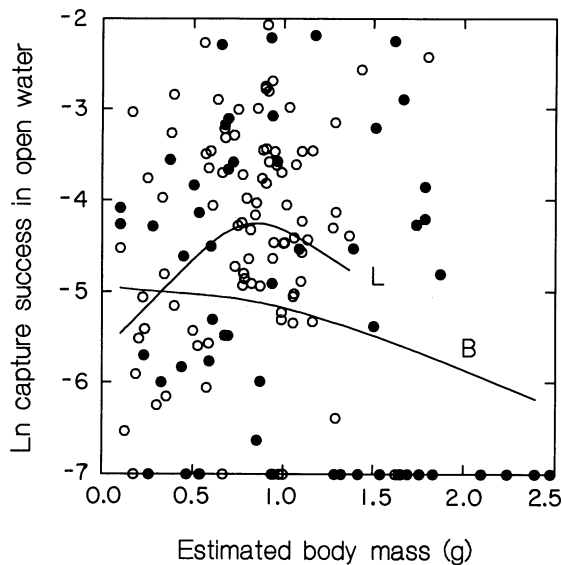


FIG. 6. Prey capture success as a function of estimated body mass in Limnetics (O, upper line) and Benthics (●, lower line). Capture success was ln-transformed to reduce skew; original units are $\text{mm}^3/\text{strike}$. Curves were fitted using non-parametric regression (the cubic spline; see Schluter 1988b).

DISCUSSION

Size, shape, and habitat use efficiency

The morphological divergence of freshwater sticklebacks in coastal British Columbia lakes has been accompanied by major shifts in habitat and foraging behavior. The present study has sought to test the hypothesis that each habitat favors a unique suite of traits for foraging, and hence that the alternative selection pressures in different habitats have directed evolutionary transitions.

The results suggest that morphological differences between Limnetics and Benthics strongly affect their habitat use efficiency. On benthos, foraging success of Benthics was much greater than that of Limnetics. Conversely, Limnetics were the superior foragers in open water. The conclusion that morphology is directly responsible for species differences in feeding efficiency is strengthened by the observation that foraging success of Hybrids (which are morphologically intermediate between Limnetics and Benthics) tended to be intermediate between the parental species in both habitats.

Foraging success of Limnetics was roughly similar between the two habitats, although it may have been slightly higher in benthos than in open water (Fig. 5). Conversely, foraging success of Benthics was much higher on benthos than in open water. This difference between species in the absolute habitat rankings accords well with habitat choices observed in the wild: Benthics are specialized on benthos and rarely exploit open water, whereas Limnetics are more generalized and may exploit benthos seasonally (Fig. 2; Larson

1976, Bentzen et al. 1984, Schluter and McPhail 1992). The use of benthos by Limnetics in spring may stem in part from their breeding requirements, since males build and defend nests on sediment inshore, and gravid females seek them out. However, seasonal shifts in the relative profitabilities of habitats are probably also a factor. In my experiments, prey capture success on benthos (ln-transformed) tended to decline with advancing date (measured as days since 1 May; pooled slope = -0.009), whereas capture success in open water tended to increase (pooled slope = 0.007). The difference between these opposite slopes was marginally significant (analysis of covariance; $F = 3.61$, $df = 1, 197$, $P = .059$), and awaits further confirmation. The habitat flexibility of Limnetics shows that they are not completely specialized on plankton, and raises the possibility that their morphology is partly designed to take advantage of benthos seasonally.

Limnetics and Benthics differ morphologically in many traits (Fig. 1, Tables 1 and 2), and a difficult task will be to determine which set is chiefly responsible for habitat use efficiency. Overall size appears to be a factor (Fig. 6). Capture success of Benthics in open water decreased steadily with size. Capture success of Limnetics in open water was maximized at ≈ 0.8 g. This latter result does not take into account the metabolic costs of feeding, which are necessarily higher in larger individuals. I therefore repeated the analysis on Limnetics using net energy intake; the optimum was shifted leftward as expected, to near 0.7 g. Mean size of Limnetics is close to this optimum (Table 1). This result is strong indication that the relatively small size of Limnetics compared to Benthics results directly from the effect of size on foraging efficiency in open water.

However, size does not explain most of the differences between species in feeding success. For example, capture success of plankton by Limnetics was higher than that by Benthics at most sizes (Fig. 6). Instead, it is likely that many traits are involved, and that different traits have their greatest effects on different components of foraging success. Mouth width constrains maximum prey size (e.g., Werner 1977, Bentzen and McPhail 1984, Lavin and McPhail 1986, Wainwright 1988, Norton 1991) and the large mouth of the Benthic species may have contributed greatly to its high foraging success on benthos compared to Limnetics or Hybrids (Figs. 4 and 5). Mouth size may also limit the volume of sediment that can be engulfed during a strike at benthic prey, and hence affect the probability of prey capture. However, a small mouth may enhance capture success of open water plankton, particularly when suction is used (e.g., Werner 1977).

Capture success in open water may also be enhanced by the flexible, elongate body of Limnetics and their relatively extended medial fins (Fig. 1) by providing greater thrust and reduced drag during frequent S-starts (Webb 1984). Finally, long and numerous gill rakers may enhance retention of small items of plankton fol-

lowing capture (Hyatt 1979, Mittelbach 1984, Lavin and McPhail 1986, Mummert and Drenner 1986).

Fitness of intermediate phenotypes

Divergent natural selection, and competition between species, are thought to drive adaptive diversification. This is the hypothesis of character displacement, and it predicts that intermediate phenotypes between sympatric species should have relatively low fitness. A second motivation for the present study was thus to gain insight into the fitness of intermediate phenotypes, by looking at foraging success of interspecies Hybrids.

My experimental habitats provided prey at natural densities from Paxton Lake, representing a food supply that may be depleted to some degree by Benthics and Limnetics. Under these circumstances competition against intermediate phenotypes is expected to be greatest, and the fitness of intermediate phenotypes should be least (e.g., Wilson 1989).

Foraging efficiency of Hybrids was intermediate between Benthics and Limnetics (Figs. 4 and 5). They tended to be less efficient than Limnetics in open water and poorer than Benthics on benthos. This does not necessarily translate into lower Hybrid fitness if the relative profitability of habitats fluctuates enough seasonally that Hybrids can opportunistically exploit the best habitat at all times. Such a long-term Hybrid advantage is unlikely here. Limnetics are opportunistic themselves, and are little worse than Hybrids when foraging on benthos, but are better in open water. Also, net energy intake by Hybrids was sufficiently low that the trade-off between foraging success in the two environments appeared linear (as would be the case if hybrids fall on the dashed line in Fig. 5) or possibly slightly concave (if hybrids are below the line). The conditions under which such a large disadvantage could be overcome are probably stringent. The hypothesis that intermediate phenotypes are selected against is thus supported by the results, although the evidence is indirect.

Most other small lakes possess only a single species of stickleback, which is morphologically intermediate between Limnetics and Benthics (Schluter and McPhail 1992). The foraging disadvantage that intermediate phenotypes appear to suffer then raises the question: why should solitary sticklebacks ever be morphologically intermediate? A possible answer is that intermediate phenotypes are selected against when the more specialized Limnetics and Benthics are present, but they are favored when the more specialized parental extremes are absent (e.g., because food abundance is less depressed). Alternatively, solitary forms may indeed experience disruptive selection, but a single intermediate form persists indefinitely in the absence of morphologically based assortative mating.

Interestingly, this second situation might eventually favor the evolution of assortative mating, and ultimately

lead to the formation of two specialized species (Wilson 1989). It is conceivable that the Limnetic and Benthic species pairs formed precisely in this way, although the available evidence suggests that they formed in allopatry, and that lakes with two species have been colonized twice from the sea (McPhail 1992a, Schluter and McPhail 1992). Another possibility is that selection against intermediates would favor the evolution of a single-species trophic polymorphism such as is found in sunfish (Ehlinger and Wilson 1988), cichlids (Kornfield et al. 1982, Meyer 1987), char (Skúlason et al. 1989), and an African finch (Smith 1987, 1990). A comparison of foraging success and fitness of Limnetics, Benthics, and Hybrids in one- and two-species lakes would be a fruitful way to further explore divergent selection and its evolutionary consequences.

Repeatable patterns of diversification

This stickleback system displays features seen in other examples of niche diversification in fish, and that may characterize adaptive radiations generally. These include a strong link between morphology and feeding performance, and trade-offs in feeding ability accompanying morphological specialization (Werner 1977, Liem and Kaufman 1984, Bentzen and McPhail 1984, Lavin and McPhail 1986, Vrijenhoek et al. 1987, Wainwright 1988, Meyer 1989, Ehlinger 1990, Norton 1991).

The resemblance is especially striking between the sticklebacks and other fish taxa inhabiting post-glacial lakes. For example, salmonids frequently show two (or more) closely related, sympatric forms that differ in size, number of gill rakers and other morphological traits, and that are ecologically segregated between benthos and open water habitats (Behnke 1972, Skúlason et al. 1989; J. D. McPhail, *personal communication*). In some cases these morphs may represent a single-species polymorphism (e.g., char; Vrijenhoek et al. 1987, Skúlason et al. 1989), but in others the forms are probably separate species, as in the sticklebacks (e.g., whitefish; Bernatchez and Dodson 1990). Morphological differences tend to be greater in sympatry than allopatry (Schluter and McPhail 1992; J. D. McPhail, *personal communication*), but this tendency is as yet poorly documented.

The apparent repeatability of patterns of divergence between fish lineages is extraordinary and begs further investigation. Because of their recency and simplicity, situations like the sticklebacks present some of the greatest opportunities for direct study into the ecological processes controlling adaptive radiation.

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