

TRADE OFFS IN HABITAT-SPECIFIC FORAGING EFFICIENCY AND THE NASCENT ADAPTIVE DIVERGENCE OF STICKLEBACKS IN LAKES

by

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Summary

I assessed habitat-specific foraging efficiency of shallow-water and open-water forms from a morphologically variable population of threespine sticklebacks. Individuals sampled from open-water or shallow-water habitats tend to be morphologically divergent, although the morphology of the modal form is intermediate between the better-known benthic and limnetic pairs of stickleback species that coexist in other local lakes. I tested two hypotheses about this intraspecific variation. First, that heritable genetic variation in body form exists between forms. Morphological differences occurred between progeny reared under common laboratory conditions indicating that heritable genetic variation contributes to morphological variation. Second, that open-water and shallow-water forms face trade offs involving foraging on habitat-specific prey. The foraging efficiency of both forms was measured in two types of habitat (benthos and open-water) simulated in lab aquaria. Foraging efficiency was related to morphological differences between morphs. Relative morph efficiencies were reversed between habitats in a predictable fashion. More streamlined open-water forms consumed *Artemia* nauplii at a higher rate and with fewer bites than more robust shallow-water morphs. Conversely, shallow-water morphs required fewer bites to capture and consume more and larger amphipods than open-water forms. An asymmetry in the trade offs indicates that

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shallow-water types may be the more specialized form. These results are consistent with a hypothesis that trade offs in habitat use efficiency can be involved early in the adaptive divergence of sticklebacks into different lake environments. Similar trade offs exist for the coexisting pairs of stickleback species, suggesting that trade offs are more likely a cause, rather than a consequence, of speciation in sticklebacks that colonize lakes.

Introduction

Adaptive radiation is identified by the rapid divergence of populations simultaneously with respect to morphology and resource use to the extent that they become ecologically specialized, and largely reproductively isolated. Recent research has focused on the operation and importance of two factors involved in this processes: (1) the evolution of reproductive isolation (Rice & Hostart, 1993; Liou & Price, 1994), and (2) divergent environmentally based natural selection (Schluter, 1996). Recent interest in the evolution of reproductive isolation has focused on the role played by sexual selection (Andersson, 1994, Seehausen *et al.*, 1998). However, at least three circumstances are thought to favor divergent selection. Because adaptive radiation predominantly occurs in species-poor environments, one condition appears to be the availability of multiple environmental niches (Robinson & Wilson, 1994; Schluter, 1998; Robinson & Schluter, 2000). Interspecific competition resulting in ecological character displacement is a second condition that can amplify divergent selection (Schluter & McPhail, 1992, 1993; Schluter, 1994, 1998). Finally, divergent selection is favored when trade offs involving fitness arise because an organism is faced with performing different tasks. The focus of this study is on the role that trade offs play early on in adaptive divergence and radiation.

Trade offs can occur when performance on one task (such as feeding on resource X) results in a cost to performance and fitness on a second task (feeding on resource Y). They are expected to play a role in adaptive divergence and radiation because trade offs are an important factor in the evolution of specialization (Schluter, 1995; Robinson *et al.*, 1996; other factors that influence the evolution of specialization are reviewed in Wilson & Yoshimura, 1994). Severe trade offs can result in divergent selection that favors resource specialization and divergence (Levins, 1962). Relaxed trade offs can create stabilizing or directional selection that favors a more generalist type that uses both resources to some extent, thereby constraining adaptive divergence (although see Robinson & Wilson, 1998).

For trade offs to be a factor in adaptive radiation, at least three conditions must be met. First, we must rule out the possibility that trade offs are a consequence, rather than a cause, of divergence for nonadaptive reasons, such as drift or founder effects (Futuyma & Moreno, 1988; Robinson & Wilson, 1996). Evidence that trade offs exist at the earliest as well as the later stages of divergence would satisfy this criterion. Second, phenotypic variation functionally linked to the trade off must be heritable. Third, trade offs must be severe enough for the fitness of generalists averaged over both resources to be less than the fitness of specialists (Levins, 1962; Schluter, 1995, Robinson *et al.*, 1996). This paper focuses on testing predictions arising from the first two conditions.

In this paper, I examine the relationship between body shape and foraging efficiency in a morphologically variable lake population of threespine sticklebacks (*Gasterosteus aculeatus*). I focus on testing two hypotheses. First, that the morphological divergence of shallow- and open-water forms within the population results from divergent natural selection for efficient foraging in each lake habitat. I assume that foraging efficiency is an important component of fitness (Stephens & Krebs, 1986). I predict that each form is most efficient at foraging in its respective habitat, and that each faces a cost in the form of reduced performance in the other habitat. I also predict that foraging efficiency will be correlated with morphological variation for functional reasons (Schluter & McPhail, 1992; McPhail, 1994). Specifically, that foraging efficiency on pelagic plankton will be positively related to gill raker traits (length, number, or spacing of these comb-like projections), and not related to mouth or body size traits. While foraging efficiency on larger benthic prey will be positively related to mouth and body size traits, and independent of gill raker traits (Lavin & McPhail, 1986). Second, I test the hypothesis that morphological differences between shallow- and open-water forms are partially heritable by rearing progeny in a common environment.

This research complements experimental tests of whether natural selection is a major cause of divergence in a complex of new species of sticklebacks in freshwater environments (reviewed in Schluter & McPhail, 1992; Bell & Foster, 1994; McPhail, 1994). Freshwater stickleback species have originated relatively recently in British Columbia because they are endemic to small coastal lakes that were formed approximately 12,500 years ago (McPhail, 1992, 1993, 1994). Most lakes contain only one species although six contain two. Studies indicate that these unusual species pairs have

evolved independently (Taylor & McPhail, 1999). Morphology is strongly related to habitat use within and among populations, and sympatric species pairs show character displacement (Schluter & McPhail, 1992; McPhail, 1994; Schluter, 1994). Populations found alone in small lakes are generally intermediate in morphology and habitat use between the sympatric species pairs. In the two-species lakes, one species (referred to as the 'benthic') forages almost exclusively on larger invertebrates at the bottom in shallow littoral habitat, whereas the other (the 'limnetic') consumes small zooplankton from the water column. Benthics are larger, have deeper bodies, wider mouths, and fewer, shorter gill rakers than limnetics; variation that is partially heritable (McPhail, 1994; Hatfield, 1997). Experiments have demonstrated that the benthic and limnetic species face strong trade offs in foraging efficiency and growth rate across habitats, and that intermediate phenotypes may be inferior to either specialist (Schluter, 1993, 1995). Variation in morphology and resource use within solitary stickleback populations while not as pronounced, can sometimes parallel the divergence observed between benthic and limnetic species pairs (Schluter & McPhail, 1992; Cresko & Baker, 1996; Robinson, unpubl. data). Such solitary populations may exhibit the very earliest stages of divergence and adaptation to pelagic and benthic environments, and provide an opportunity to study what factors are involved early in divergence.

This study also complements research into the evolution of trophic or resource polymorphisms (Robinson & Wilson, 1994; Skulason & Smith, 1995; Smith & Skulason, 1996). I define a resource polymorphism as an association between diet and phenotype among members of a single phenotypically variable population. The niche-based phenotypic variation is usually greater than the norm as judged by the authors that have described them (Robinson & Wilson, 1994; Robinson & Schluter, 2000). Trophic polymorphisms can reflect underlying genetic differences (Smith, 1990; Skulason *et al.*, 1993), developmental plasticity (Meyer, 1987; Wainwright *et al.*, 1991; Wimberger, 1991, 1992), or a combination of both mechanisms (Robinson & Wilson, 1996). Many populations of northern freshwater fishes exhibit discrete or continuous resource polymorphism related to divergence between benthic and pelagic environments (Robinson & Wilson, 1994; Robinson & Schluter, 2000). Despite the obvious role that resources play in trophic polymorphisms, trade offs that affect the foraging efficiency of slightly divergent forms in solitary vertebrate populations are rarely

tested (Ehlinger & Wilson, 1988; Meyer, 1989; Robinson *et al.*, 1996). Furthermore, no studies assessing the form and magnitude of foraging based trade offs have been made in a single system where trade offs below and above the species threshold can be compared, as here in the threespine stickleback.

Methods

Collection of sticklebacks

This research was performed in the fall of 1996 on lab-reared juvenile progeny of adult sticklebacks collected the previous spring from Cranby Lake in British Columbia, Canada. Cranby Lake is a single basin lake that is found along with two lakes containing sympatric species pairs on Texada Island along the south coast of BC. The lake is approximately one-kilometer long, 750 m wide, with a maximum depth of 12.5 m, found at 73 m above sea level. An artificial earthen dam installed at the east end of the lake in 1962 has raised the lake level 1.5 m above its original height. Adult sticklebacks were collected May 23-24 from benthic and pelagic sites using overnight sets of minnow traps placed respectively inshore in less than 0.5 m of water, or suspended just below the surface from a floating line out in the pelagic habitat of the lake.

Fish for both sets of experiments came from artificial crosses of shallow- and open-water adults collected from the field (Shallow \times Shallow, $N = 30$ crosses; and Open \times Open, $N = 57$ crosses). I made crosses by combining eggs and macerated testes in a petri dish with a small volume of freshwater for approximately 20 minutes at a temporary field station on the island. Fertilized eggs were placed in 250 ml mesh-bottomed hatching cups suspended in 102 l aquaria filled with sea water diluted to 15% with freshwater, and aerated from below using an airstone. Clutches were then flown to the University of British Columbia on May 25 before hatching and placed in aquaria with crushed limestone substrate as described above. Six stock aquaria containing multiple clutches were maintained for each progeny type.

Rearing

Juveniles began hatching June 30 (hereafter day 1), wriggled through the mesh in the hatching cups, and sank to the bottom of the tank. Hatchlings were fed for the first five days on infusoria cultures which was slowly replaced by diets of live first instar *Artemia* nauplii. After 24 days the stock populations of shallow- and open-water progeny were thinned to 200 juveniles per tank. Fish were reared at a constant temperature of approximately 18°C under a 16L : 8D artificial light cycle.

Common garden experiment

The goal of the first experiment was to test if phenotypic differences between progeny types persisted when reared under similar environmental conditions (referred to below as the 'common garden experiment'). Three replicate aquaria, each containing 25 fish, were prepared for both progeny at 24 days post hatch, and the tanks were systematically interspersed. Progeny were kept in separate aquaria because they could not be identified

or marked at this small size. Both progeny types were fed the same diet throughout the experiment. From day 37 onwards, I supplemented the live *Artemia* diet with chopped frozen bloodworm, and from day 68 onwards with whole frozen bloodworm. The common garden experiment was terminated 197 days post hatch (mean SL = 44.7 mm, SE = 0.38, $N = 127$), when the fish were euthanized in a lethal dose of MS222. After fixing in 10% formalin, fish were rinsed in water, stained with alazarin red in a 1% KOH solution to accentuate lateral plates and fin rays, and preserved in 40% isopropyl alcohol (Lavin & McPhail, 1985).

Foraging experiment

The goal of the second experiment was to test for trade offs in the foraging efficiency of both forms feeding on different prey. I anticipated that my ability to compare trade offs would be limited by the marginal divergence between open- and shallow-water progeny due purely to heritable variation. Morphological differences between more divergent species of sticklebacks is due to a combination of heritable differences and phenotypic plasticity in response to diet (Day *et al.*, 1994), and it is likely that similar plastic responses contribute to the morphological variation observed in the natural Cranby lake population. Therefore, I attempted to amplify phenotypic differences between the two phenotypes by differentiating shallow- and open-water diets in the stock tanks following Day *et al.* (1994). The shallow-water progeny diet was supplemented with chopped frozen bloodworm (a benthic prey type) beginning at 37 days post hatch, and their diet switched completely to chopped bloodworm at 42 days. Feeding with whole bloodworm commenced on day 68. Bloodworms delivered in the water column rapidly sank to the bottom of the aquarium. Open-water progeny were reared exclusively on live *Artemia* nauplii (a pelagic prey type) that was kept suspended in the water by increasing the rate of aeration in the tanks during feeding.

Behavioral tests

Foraging success of individual fish was assessed in two artificial habitats, pelagic and benthos, presented separately in two aquaria (described below). An experimental trial consisted of releasing a single fish into the test aquarium and observing it for a period of time after foraging began (pelagic habitat = 10 min, benthos = 15 min). A stickleback was taken sequentially from either an open- or shallow-water stock tank, placed into a test aquarium illuminated from above, and observed from a distance of 1.5 m. Fish usually began feeding within five minutes, and fish not feeding after 10 minutes were rejected. Onset of feeding signaled the start of the foraging trial. I recorded time to onset of feeding (latency), the number of strikes at prey made in the water column, and at the tank bottom. Fish were then removed from the tank, euthanized, weighed, individually identified, and preserved as described above for morphological measurement and analysis of stomach contents.

The total number of prey items eaten by each fish was determined by dissecting out the stomach and counting prey under a dissecting microscope. This data was converted into two measures of foraging success: intake rate (number of prey items consumed per minute), and capture effort (mean number of bites per prey item). Both measures will influence handling time, which is widely regarded as an important element of foraging costs (Stephens & Krebs, 1986). One additional measure of foraging behavior measured in the benthic trials was the length of the largest amphipod consumed by each fish. This allowed a test of differences between types in the selection of maximum prey size. The relationships between morphology and foraging success were analyzed using ANCOVA, with size as covariate, and type as an independent factor.

Pelagic environment

The experimental pelagic habitat was a featureless 18 l tank filled with clean water and a slowly bubbling airstone stocked with three live *Artemia* nauplii per litre ($N = 54$ nauplii). New *Artemia* were counted into the cleaned and refilled aquaria using a small glass capillary tube and a dissecting microscope for each feeding trial. Sixty-nine individual feeding trials (35 open and 34 shallow types) were performed between September 9-30 (98-119 days post hatch) when the mean SL of open- and shallow-water forms were respectively 24.3 mm (SD = 1.8) and 23.0 mm (SD = 1.7; two-sided t -test = 3.23, $df = 67$, $p < 0.002$).

Benthic environment

The experimental benthic habitat was a 102 l aquarium (outside dimensions $1 \times w \times d$ in cm: $76 \times 31 \times 46$) with coarse gravel and sand to a depth of 2.5 cm at the bottom, and a third of the bottom area (2355 cm^2) covered with 5 cm deep patches of filamentous algae. The benthic aquarium was stocked with at least 250 live amphipods (*Hyallela* spp.) of all sizes collected regularly from a local pond. The experiment was purposefully designed to provide fish with a higher density of amphipods than they would normally experience in the wild, because both progeny had never experienced amphipods, which could limit feeding. Amphipods are fast moving arthropods with hard exoskeletons that forage on detritus on the bottom. High densities were maintained by adding approximately 25 amphipods from a stock tank to the benthic tank after every 5 trials. The tendency for amphipods to hide over successive trials was reduced by the addition of the naïve amphipods and by tapping the tank just before adding each trial stickleback. Fifty-nine individual feeding trials (31 open and 28 shallow progeny) were performed between November 19-December 5 (169-185 days post hatch) when the mean SL of open- and shallow-water forms were respectively 30.7 mm (SD = 3.1) and 30.1 mm (SD = 4.5, 2-sided $t = 0.66$, $df = 59$, $p = 0.52$).

I was concerned that sticklebacks fed only benthic or planktonic prey prior to the foraging trials would result in differences in foraging success that was primarily due to experience rather than morphological differences. I attempted to minimize differences in experience in two ways. First, I fed shallow forms exclusively with *Artemia* nauplii, and open forms with frozen blood worm for five of the six days prior to the foraging experiments to acquaint them with the prey (fish were not fed for the 24 hours immediately preceding foraging trials). I assumed that a 5-day diet switch was sufficient to remove much of the short term learned foraging differences between types, as suggested elsewhere (e.g. Ware, 1971; Mittelbach, 1981; Ehlinger & Wilson, 1988; Kieffer & Colgan, 1991; Schluter, 1993; Skulason *et al.*, 1993). Second, in the benthic foraging trials, both types foraged on a novel live benthic prey (live amphipods). In the pelagic trials, I also assumed that behavioral differences due to experience were reduced because shallow-water forms had had 39 days of prior experience feeding on *Artemia* nauplii during their early development.

Analysis of size and shape

To assess differences in body shape between progeny reared in the common garden experiment, I measured 15 features on each fish (Table 1) using an ocular micrometer on a dissecting microscope following Lavin & McPhail (1985). To test relationships between morphology and foraging efficiency in fish from the feeding experiments, I measured only 4 traits (Table 2), all known to be strongly related to feeding behaviour from previous studies (Lavin & McPhail, 1985; Schluter, 1993).

TABLE 1. *Body shape variation between open- and shallow-water progeny in the common garden experiment*

	Multivariate canonical correlation	Univariate means			
		Shallow		Open	
Traits:					
Standard length	0.30	43.60	(0.49)	46.10*	(0.55)
Body depth	-0.35	9.06	(0.05)	8.77*	(0.05)
Head length	-0.12	8.76	(0.05)	8.64	(0.06)
Eye diameter	-0.18	4.30	(0.02)	4.23	(0.02)
Pectoral fin length	0.04	6.48	(0.04)	6.50	(0.04)
Gill raker number	0.41	13.0	(0.09)	13.7*	(0.11)
Gill raker length	0.17	1.12	(0.011)	1.15	(0.012)
Mouth width	-0.50	4.35	(0.031)	4.10*	(0.034)
Jaw length	-0.09	3.38	(0.04)	3.32	(0.04)
Snout length	-0.03	2.92	(0.03)	2.90	(0.04)
Dorsal spine number	-0.27	3.0	(0.048)	2.8*	(0.043)
Dorsal spine length	0.05	3.10	(0.036)	3.13	(0.040)
Pelvic spine length	0.16	4.21	(0.053)	4.37	(0.059)
Lateral plate number	-0.04	5.6	(0.09)	5.5	(0.10)
Pectoral girdle length	0.20	6.76	(0.065)	6.99	(0.072)

The effect of progeny type on shape was evaluated using two methods: canonical discriminant function analysis (DFA) of the 15 traits combined, and by univariate analyses of each trait. The canonical correlation represents the correlation (contribution) of each trait to the discriminant function. Individual analyses of standard length, and the numbers of gill rakers, dorsal spines, and lateral plates were performed using ANOVA, while the remaining traits were tested using ANCOVA with standard length as covariate. Trait means (mm) and standard errors are provided for each type, and are adjusted to an average standard length of 45 mm for those traits related to size. Significance levels for the univariate results were adjusted using the sequential Bonferroni method to preserve a table-wide α -level of 0.05 at $*p < 0.003$ (Rice, 1989).

Variation in body shape between progeny types in the common garden experiment was analyzed by two methods, multivariate canonical discriminant function analysis (DFA) of all 15 traits, and by separate univariate analyses of each trait. All morphological traits except the numbers of dorsal spines, lateral plates, and gill raker number were positively related to standard length. I statistically removed this size effect by first regressing each of the remaining 11 traits against standard length and calculating residual variation with both types combined. This method assumes that shallow- and open-water progeny had similar allometric relationships for each trait (Reist, 1985). Patterns of allometry were not significantly different between forms for any of the 11 traits that covaried with size (homogeneity of slopes test using ANCOVA with independent factors, progeny type and standard length as covariate, were not significant; e.g. Fig. 1). The size-free residual variation in shape was then analyzed using a DFA of the 15 traits (11 size-adjusted traits, 3 unadjusted traits, and standard length)

TABLE 2. *Body shape variation between open- and shallow-water forms used in the foraging experiments*

Traits:	Univariate means			
	Shallow		Open	
Standard length	26.50	(0.37)	27.50*	(0.36)
Gill raker number	9.7	(0.20)	10.2	(0.20)
Gill raker length	0.57	(0.01)	0.63*	(0.01)
Mouth width	1.80	(0.03)	1.90*	(0.03)

The effect of phenotype was evaluated for only four traits with ANOVA (for standard length and the number of gill rakers), or ANCOVA with standard length as covariate (for gill raker length and mouth width). Trait means (mm) and standard errors are provided for each type, and are adjusted to an average standard length of 27 mm for gill raker length and mouth width. Significance levels were adjusted using the sequential Bonferroni method to preserve a table-wide α -level of 0.05 at $*p < 0.0125$ (Rice, 1989).

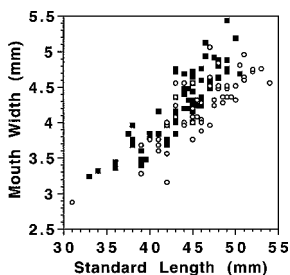


Fig. 1. Relationship between standard length (mm) and lower mouth width (mm) in the progeny of open-water (open circles) and shallow-water sticklebacks (solid squares) reared under common laboratory conditions.

with replicate tanks combined and progeny type as the independent factor. I used DFA because it is sensitive to group differences on several variables simultaneously, and can identify the dimensions along which groups differ. A one factor ANOVA of the discriminant scores was used to test whether replicate variation (nested within treatments) explained significant differences in body shape. I also tested for an effect of progeny type on raw shape data with separate ANCOVA analyses of the 11 traits that covaried with standard length, and ANOVA analyses of the remaining four traits. An alpha level of 0.05 was maintained among univariate tests by employing a sequential Bonferroni correction factor (Rice, 1989). Group differences with respect to the four body traits measured in the foraging experiment were separately analyzed using ANCOVA and ANOVA models as described above.

Results

Body shape divergence

Differences in body shape between shallow- and open-water progeny suggest that the two types differed with respect to morphology despite being reared in a common laboratory environment. The DFA successfully categorized 87% of the 127 fish to the correct progeny type (Fig. 2; Wilks' lambda = 0.49, $F_{15,111} = 7.7$, $p < 0.0001$). A single factor ANOVA of the canonical body shape scores estimated by the DFA found no significant differences in body shape between replicate tanks nested in progeny type, justifying the pooling of replicate tanks in this analysis of body shape (replicate $F_{4,121} = 1.25$, $p = 0.29$). Five traits contributed most to the differences in body shapes between shallow- and open-water progeny (Table 1). Shallow-water progeny had on average shorter body lengths, more dorsal spines, fewer gill rakers, a deeper body, and wider mouths (Fig. 1) than did open-water progeny.

Most of these differences in body shape were maintained between the forms used in the foraging experiments, although there was also evidence of morphological plasticity in response to diet (Table 2). Differences between forms in standard length, and gill raker number, did not change in response to diet indicating that they were generally not labile (Fig. 3a, b). Gill raker length was slightly plastic because the open-water types had longer gill rakers than shallow-water forms in the foraging experiment but not in the common garden experiment (Fig. 3c, and compare Tables 1 and 2). Mouth

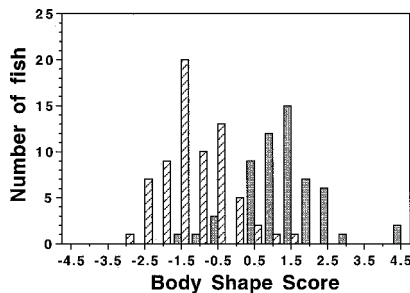


Fig. 2. Distribution of body shape scores for the progeny of open- and shallow-water threespine sticklebacks from Cranby Lake estimated by the discriminant function analysis of size-adjusted body measurements, with progeny type as the independent factor (see Table 1). Shallow water forms (hatched) had negative body shape scores corresponding to generally shorter, deeper bodies, fewer gill rakers, and wider mouths compared to open-water forms (grey bars and positive scores).

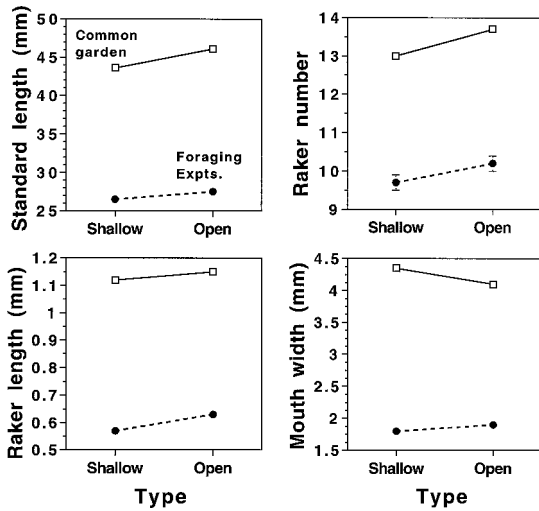


Fig. 3. Mean values of four traits for shallow- and open-water forms in the common garden (squares, solid line) compared to the foraging experiments (circles, broken line). The morphological difference between types was maintained between the two experiments for all traits except mouth width where phenotype order was reversed (see also Tables 1 and 2).

width unexpectedly responded the most to diet. The open-water fish reared on *Artemia* had mouths that were, on average 5.5% wider than the shallow-water fish reared on bloodworm for the foraging experiments, contrary to the results of the common garden results above (Fig. 3d).

Foraging behavior

The order of foraging success reversed between benthic and pelagic foraging trials, indicating that both types experienced trade offs in intake rate and capture effort (Fig. 4a, b). In pelagic foraging trials, the open-water types were the most successful at foraging on live *Artemia*. Body size, measured as standard length, had no influence on intake rate (prey/min) or capture effort (bites/prey) in the pelagic trials (Table 3). Open-water forms consumed more *Artemia* per minute than did shallow-water sticklebacks (Fig. 4a, ANOVA: $F_{1,67} = 8.43$, $p = 0.005$, $R^2 = 0.11$, means: 2.9 vs 2.1 prey/min). Open-water sticklebacks also required half as many bites to consume each *Artemia* compared to shallow-water fish (Fig. 4b, ANOVA of natural log transformed bites/prey: $F_{1,66} = 7.21$, $p = 0.009$, $R^2 = 0.10$, means: 3.1 vs 6.2 bites/prey). These effects were not a result of minor differences

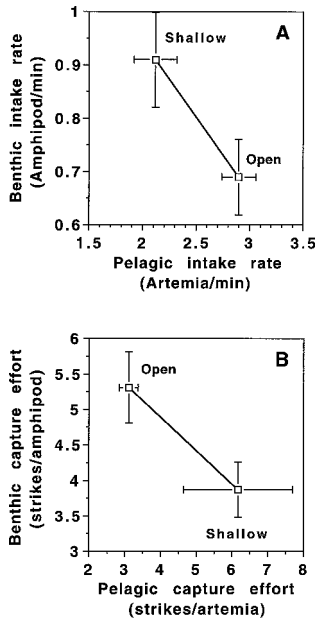


Fig. 4. Mean foraging efficiency (and standard errors) of open- and shallow-water forms in pelagic (*Artemia nauplii*) and benthic (amphipods) feeding trials. Two components of foraging efficiency were estimated: (A) intake rate (prey/min) and (B) capture effort (strikes/prey). The two forms were tested in benthic and pelagic environments simulated in lab aquaria. The negative slope of the line connecting the performance of each form indicates that a trade off exists in foraging efficiency between the two environments.

in standard length between forms, because limiting the analysis to the size range of complete overlap (SL: 22.0-25.5 mm) did not significantly change the results (prey/min $p = 0.004$, bites/prey $p = 0.002$).

The order of foraging success was reversed in the benthic foraging trials on amphipods. Both measures of foraging success on amphipods were related to mouth width and standard length (Table 3). Shallow-water sticklebacks consumed more amphipods per minute than did open-water forms after controlling for differences in mouth width (Fig. 4a, ANCOVA of ln-transformed prey/min with mouth width as covariate — MW: $F_{1,54} = 22.5$, $p < 0.0001$; Fish type: $F_{1,54} = 4.0$, $p = 0.05$; MW \times FT: $p = 0.96$; $R^2 = 0.31$, adjusted means 0.91 vs 0.69 prey/min). Shallow-water sticklebacks also required on average one less strike per amphipod during handling than the open-water fish (Fig. 4b, ANCOVA of ln-transformed bites/prey with mouth width as covariate — MW: $F_{1,55} = 20.3$, $p < 0.0001$;

TABLE 3. *Pearson correlation coefficients between morphology and foraging efficiency in threespine sticklebacks feeding in simulated pelagic (N = 65) and benthic (N = 58) habitats*

Trait:	Pelagic trials		Benthic trials	
	<i>Artemia</i> per min	Bites per <i>Artemia</i>	Amphipods per min	Bites per Amphipod
Gill raker number	0.47*	-0.31	0.04	-0.15
Gill raker length	0.41*	-0.32	0.29	-0.30
Mouth width	0.15	-0.04	0.51*	-0.48*
Standard length	0.20	-0.05	0.59*	-0.64*

Shallow- and open-water forms were combined for analysis in each habitat. Gill raker length, and both measures of foraging efficiency in the benthic trials were transformed to their natural logarithms for analysis. Significance levels were adjusted using the sequential Bonferroni method to preserve a table-wide α -level of 0.05 at $*p < 0.006$ for each experimental habitat (Rice, 1989).

Fish type: $F_{1,55} = 5.2$, $p = 0.026$; MW \times Type: $p = 0.63$; $R^2 = 0.30$, adjusted means 3.9 vs 5.3 bites/prey). Finally, there was a clear difference in the maximum size of the amphipods eaten by the two types because the length of the largest amphipod consumed was positively related to standard length in shallow- but not open-water forms (Fig. 5, ANCOVA of amphipod length with standard length as covariate — SL: $F_{1,51} = 18.3$, $p = 0.0001$; Fish type: $F_{1,51} = 12.1$, $p = 0.001$; SL \times Type: $F_{1,52} = 14.5$, $p = 0.0004$; $R^2 = 0.50$). This indicated that open-water forms either did not select, or could not consume, larger amphipods with increasing standard length.

Factors related to foraging success

I tested if foraging efficiency was related to morphology by the significance of their correlation. However, if additional factors influenced foraging, then foraging success would still vary between forms having the same trait value. In the pelagic foraging trials, the number of gill rakers and gill raker length were both positively related to intake rate, and weekly negatively related with capture effort, while standard length and mouth width were not related to either estimate of foraging efficiency (Table 3). No additional variation in intake rate was explained by type after accounting for raker length. However, open-water forms had significantly higher intake rate than shallow-water forms with the same raker number (Fig. 6; ANCOVA of *Artemia*/min, with

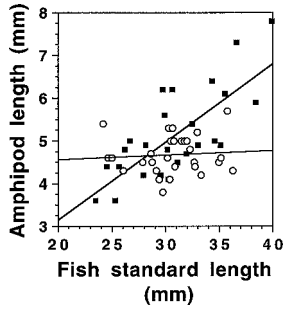


Fig. 5. Relationship between fish size (standard length) and the length of the largest amphipod recovered from the stomachs of shallow-water (solid squares) and open-water (open circles) forms in the benthic feeding trials.

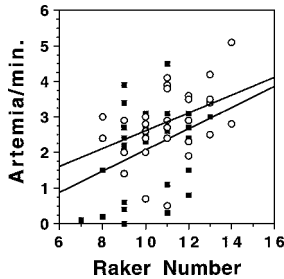


Fig. 6. Relationship between the number of gill rakers on the posterior element of the first gill arch and the intake rate of *Artemia* by shallow-water (solid squares) and open-water (open circles) sticklebacks in the pelagic feeding trials.

raker number as covariate — Raker number: $F_{1,66} = 12.4$, $p = 0.0008$; Fish type: $F_{1,66} = 4.7$, $p = 0.04$; $RN \times Type$: $p = 0.77$; $R^2 = 0.25$). This indicated that additional factors besides raker number influenced *Artemia* intake rate. No additional variation in capture effort on *Artemia* was explained by type after accounting for raker number or length.

Contrary to the relatively weak effects of additional factors in the pelagic trials, additional factors regularly influenced benthic foraging efficiency. Standard length and mouth width were both positively correlated with intake rate and negatively correlated with capture effort of amphipods as expected (Table 3). The number of gill rakers and raker length were unrelated to either estimate of foraging efficiency. However, open-water forms required more bites to consume each amphipod compared with shallow-water forms having the same mouth widths (Fig. 7, ANCOVA results presented above), and consumed fewer amphipods per minute when having equal mouth width

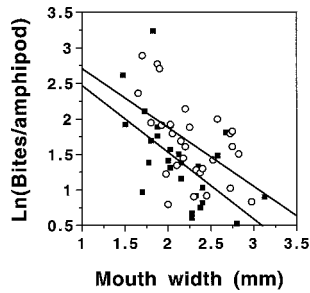


Fig. 7. Relationship between lower mouth width and capture effort for amphipods by shallow-water (solid squares) and open-water (open circles) sticklebacks in the benthic feeding trials.

(ANCOVA results presented above). Additional variation in capture effort also existed between open and shallow forms having the same standard length (ANCOVA of strikes per amphipod with standard length as covariate — Standard length: $F_{1,55} = 41$, $p < 0.0001$; Fish type: $F_{1,55} = 3.7$, $p = 0.05$; SL \times Type: $p = 0.39$; $R^2 = 0.45$). Finally, recall that variation in the maximum size of amphipods eaten was also influenced by type after accounting for the effects of body size (Fig. 5, ANCOVA results presented above). All this suggests that additional factors besides morphology contributed more significantly to foraging success in the benthic compared to pelagic foraging trials.

Discussion

Previous studies of divergent species of sticklebacks in British Columbian lakes suggested that alternative selection pressures in the open- and shallow-water environments have directed morphological transitions in this rapidly radiating group. While these studies strongly indicate that alternative selection pressures are currently maintaining morphological divergence, they cannot address whether the same selective forces could have directed divergence before speciation when forms were considerably more similar. I have demonstrated statistically significant trade offs in foraging efficiency in only slightly divergent open- and shallow-water forms from a single population feeding on planktonic and benthic prey. I also found evidence of heritable variation in body form in the population. Morphological variation had important consequences for foraging efficiency because they were predictably

correlated, and because significant trade offs in foraging efficiency occurred when the two forms fed on different prey. This suggests that single populations may experience divergent resource-based selection, and is consistent with the hypothesis that the rapid morphological divergence of sticklebacks colonizing freshwater habitats may have been originally directed by alternative selective pressures between environments.

Three components of my results provide indirect evidence that functional links exist between morphology and foraging performance here, as in other studies of sticklebacks. First, the predicted correlations between body form and foraging efficiency were confirmed, along with the prediction that these correlations would change depending on prey type. Foraging performance on planktonic prey was related to the number of gill rakers and raker length, but was unrelated to body size or mouth width. In the benthic foraging trials, standard length and mouth width were related to foraging efficiency, while gill raker features were not. These correlations parallel similar relationships found in studies of threespine sticklebacks, and other fish taxa (Bentzen & McPhail, 1984; Lavin & McPhail, 1986; Schluter & McPhail, 1992; Schluter, 1993; Robinson & Wilson, 1994; Robinson & Schluter, 2000).

Second, I found that the differences in body shape between open- and shallow-water forms were also related to habitat-use efficiency as predicted. The foraging success of shallow-water forms was superior to open-water forms on benthic prey, while conversely, open-water forms were superior foragers on plankton. Trade offs in foraging efficiency were detected even though forms differed with respect to morphology by, on average only 4-10%, depending on the trait. Schluter (1993) found similar, but stronger effects of morphology on foraging efficiency in his study of the more divergent benthic and limnetic stickleback species. The greater morphological differences observed between species resulted in larger shifts in resource use efficiency than those reported here. This is consistent with an evolutionary model of divergence driven by resource-based natural selection, because we expect the strength of the relationships between phenotype and resource use to increase with greater divergence.

Third, there was some indication that the shallow-water form experienced somewhat greater trade offs in foraging efficiency compared to the open-water form with respect to capture effort. This is consistent with findings from the pairs of stickleback species (Schluter, 1993). The capture effort of open-water forms feeding on plankton here was on average half that

of shallow-water forms (ratio of open:shallow = 3.1:6.2 bites per prey), while the capture effort of shallow-water forms was two thirds that of open-water forms on the benthic prey (ratio of shallow:open = 3.9:5.3 bites per prey). Intake rates were more similar between prey types (on plankton: shallow form was 72% that of the open form; on amphipods, open form was 76% that of the shallow form). This suggests that shallow-water forms may be somewhat more ecologically specialized because open-water forms may not face as steep a trade off in foraging efficiency as shallow water forms when foraging in the alternate environment. Robinson *et al.* (1996) found a similar asymmetry in polymorphic sunfish. Schluter (1993) found a more pronounced asymmetry between stickleback species in his tank foraging trials, with Limnetics having similar foraging success between habitats, while the foraging success (measured as energy intake) of benthics was dramatically superior in the benthos compared to the pelagic trials. These preliminary results suggests that asymmetric trade offs can evolve in a single polymorphic population, with some forms being more specialized than others, much as is found between the species pairs.

I have argued above that morphological variation between open- and shallow-water forms influenced their habitat use efficiency. However, it is difficult to distinguish which of the wide array of possible traits (morphological or behavioural) primarily influence foraging efficiency (*e.g.* Schluter, 1993). Two results suggested that foraging efficiency was influenced by additional factors. First, mouth width of shallow-water forms was unexpectedly narrower than open-water forms, yet shallow-water forms included larger amphipods in their diet. Mouth width is widely believed to constrain maximum prey size (Werner, 1977; Bentzen & McPhail, 1984; Lavin & McPhail, 1986; Wainwright, 1988; Norton, 1991; Schluter, 1993), although foraging efficiency often declines in fish when the ratio of prey width to mouth width is greater than 0.6 (Gill & Hart, 1994). Large mouths of the Benthic compared to Limnetic species was thought to contribute significantly to a greater foraging success on benthos (Schluter, 1993). Conversely, a smaller mouth may improve foraging efficiency on plankton by improving suction (*e.g.* Werner, 1977). My contrary results imply that the functional link between mouth width and foraging efficiency may not be so clear cut, at least between forms from a single population. Open-water forms could not, or chose not to, consume larger amphipods despite their slightly wider mouths, perhaps because of their prior experience with only planktonic *Artemia* during

rearing. Second, significant additional differences between forms influenced foraging efficiency after accounting for variation in specific morphological traits. This occurred with respect to intake rate of *Artemia*, but more so for intake rate and capture effort of amphipods, and for the maximum size of amphipods consumed. This is clear evidence that additional unknown morphological or behavioral factors influenced foraging efficiency, particularly in the benthos. Theory suggests that correlations among traits are important in determining the nature and magnitude of natural selection on individual traits (Lande & Arnold, 1983; Price & Langden, 1992). If it is the case that more traits are involved in specialization on benthic compared to planktonic prey, and those traits are correlated, then it will likely be more difficult to determine how selection is manipulating traits in fish from the shallow littoral compared to open pelagic environment.

Two confounding factors, prior experience and body size variation, may have contributed to the observed variation in foraging efficiency. I cannot rule out the possibility that different diets experienced during rearing influenced my foraging results. Prior experience can have permanent or transient effects. First, the diets may have induced permanent modifications to sensory or mechanical features, such as neural pathways, connections, musculature, and bone structure, during development (Smith-Gill, 1983; Colgan *et al.*, 1986; Marcotte & Browman, 1986; Wainwright *et al.*, 1991; Day & McPhail, 1996). Second, the diets may have caused transient modifications that reflect learning, and influenced the effectiveness of search images, attack, and handling strategies (Ehlinger, 1989; Magurran, 1990; Croy & Hughes, 1991; Kieffer & Colgan, 1991; Skulason *et al.*, 1993). I attempted to reduce transient modifications by providing experience with the prey for five days prior to a feeding trial, and by providing a prey novel to both forms in the benthic habitat. Five days of foraging experience with a new prey type may be enough to optimize foraging efficiency because this appears to be the norm for a variety of fishes. For example, Schluter (1993) found no significant differences in capture success by sticklebacks in similar foraging trials with fish given either a two or seven day acclimation period with a novel prey. Skulason *et al.* (1993) have demonstrated that the change in time to notice prey stabilized by day six in juvenile arctic char. Ehlinger & Wilson (1988) have shown that bluegill sunfish required 3-5 days to reach the maximum asymptote in capture efficiency in longer foraging trials like these here, although Mittelbach (1981) found that foraging rate continued to

improve over seven days in very brief trials (0.5-3 min in duration). These similar rates of learning to forage on novel prey are consistent with several other studies (Kieffer & Colgan, 1991), although they need to be empirically verified here.

Diet switching prior to feeding trials is unlikely to reduce the effects of more permanent modifications due to diet because the switch period was likely too short, or because the influence of diet on phenotype only occurs during specific developmental windows (*e.g.* Meyer, 1990; Wimberger, 1992). It is possible that the early experience that both forms had with *Artemia* may have reduced plastic responses to diet that could have affected foraging efficiency in the pelagic trials. I do not know if foraging efficiency on a novel benthic prey (live amphipods) could have been differentially influenced by a prior diet on another benthic prey (dead bloodworm). At this point, I cannot rule out the possibility that irreversible plastic responses to diet may have produced some of the differences in foraging efficiency detected between forms in these experiments.

Small differences in body size can also influence foraging efficiency in sticklebacks, with smaller fish having relatively greater handling costs than larger fish (Gill & Hart, 1996). This raises the possibility that variation in foraging efficiency between forms could have been due to body size differences. This is unlikely in the benthic foraging trials because the greater costs experienced by the open-water fish came despite having a slightly larger standard length on average than shallow-water fish. In my pelagic trials, however, shallow-water forms were slightly smaller than open-water forms and also experienced greater foraging costs. Gill & Hart's (1996) conclusion is based on foraging trials with large benthic prey above the critical threshold prey width to mouth width ratio (PW:MW) of 0.6. In the pelagic trials with first instar *Artemia* nauplii here, this ratio was approximately 0.4, and the effects of body size seem unlikely to be strong enough to account for all of the observed differences in foraging efficiency between forms. Nonetheless, body-size variation may play a significant role in foraging efficiency and the trophic divergence of sticklebacks in natural lakes (McPhail, 1994; Gill & Hart, 1996).

Divergent environmentally-based selection in lakes

The trade offs in foraging performance demonstrated here are consistent with the hypothesis that selection is divergent between open- and shallow-water

environments in Cranby, and perhaps other lakes. Selection is only divergent, however, if individuals with intermediate phenotypes have lowered fitness relative to more specialized morphs in each environment. Levins (1962) termed this a 'concave fitness' set because the fitness of intermediates averaged over the two environments is less than that of the more specialized forms (*e.g.* the performance of intermediates falls below the straight line representing the trade offs in performance of the specialized forms in each environment). The foraging performance of intermediate relative to open- or shallow-water forms remains to be tested in this population, and so I cannot definitively conclude that selection is divergent here. Other prerequisites for divergent selection include stable resources, and effective habitat selection by the forms (*e.g.* Wilson & Yoshimura, 1994). While these are rarely tested, evidence from other studies suggests that selection is often divergent between these two lake environments. For example, the relative fitness of intermediate forms from a polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*) were inferior to more extreme forms in the open-water, but not reduced enough in the shallow-water environment to be statistically significant (Robinson *et al.*, 1996). Nonetheless, the shape of that fitness landscape appeared weakly disruptive. Results from a reciprocal transplant experiment in Cranby Lake with stickleback forms similar to those used here along with an intermediate form, indicate that intermediates are inferior in the open-water but not the shallow-water environment (Robinson, unpubl. data). Benthic and limnetic species of sticklebacks also have higher growth rates in enclosures placed in their respective habitats compared to F1 hybrids having intermediate phenotypes (Schluter, 1995). Direct evidence of divergent selection acting between lake environments on sticklebacks and other lake fishes is obviously preliminary, and more studies, especially including intermediate forms, are required. Nonetheless, an increasing body of indirect evidence supports this view (reviewed in Robinson & Wilson, 1994; Schluter, 1996; Bernatchez & Wilson, 1998; Robinson & Schluter, 2000).

Any of my conclusions are subject to the criticism that the differences in foraging efficiency measured here were artifacts of performing the experiment in the lab. However, preliminary evidence from field experiments do not support this view. Trade offs in growth rate (an important component of fitness in fishes) have been found between environments for both forms of sticklebacks here (Robinson, unpubl. data). Schluter (1995) has also demonstrated stronger trade offs in growth rate between environments in the same

way using two species of sticklebacks. The consistency of these laboratory and field results suggests that morphological differences can influence fitness in these environments whether below or above the species threshold, and that divergence is related to alternative selection pressures involving habitat use efficiency.

Freshwater threespine sticklebacks and other northern lake fishes appear ideal for studying the ecological factors directing recent adaptive radiation (Robinson & Wilson, 1994; Schluter, 1996; Bernatchez & Wilson, 1998; Robinson & Schluter, 2000). Using stickleback forms from a single population, I have demonstrated that morphology is related to foraging efficiency in predictable ways, and that trade offs that influence efficient foraging on resources can occur even when divergence is much less than that observed between species. That similar functional trade offs occur below as well as above the species threshold across similar lake habitats, suggests that the ecologically important trade offs observed in recently diverged stickleback species are more likely a cause rather than a consequence of divergence. Preliminary evidence also suggests that similar patterns occur in other post-glacial fishes and perhaps elsewhere. Taken together, these findings highlight how the ecological consequences of intraspecific variation can provide valuable insights into how selection pressures may have molded certain rapidly radiating species.

References

- Andersson, M. (1994). Sexual selection. — Princeton University Press, Princeton.
- Bell, M.A. & Foster, S.A. (eds) (1994). The evolutionary biology of the threespine stickleback. — Oxford University Press, Oxford.
- Bentzen, P. & McPhail, J.D. (1984). Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): specialization for alternative trophic niches in the Enos Lake species pair. — *Can. J. Zool.* 62, p. 2280-2286.
- Bernatchez, L. & Wilson, C.C. (1998). Comparative phylogeography of nearctic and palearctic fishes. — *Molec. Ecol.* 7, p. 431-452.
- Colgan, P.W., Brown, J.A. & Orsatti, S.D. (1986). Role of diet and experience in the development of feeding behaviour in largemouth bass, *Micropterus salmoides*. — *J. Fish Biol.* 28, p. 161-170.
- Cresko, W.W. & Baker, J.A. (1996). Two morphotypes of lacustrine threespine stickleback, *Gasterosteus aculeatus*, in Benka Lake, Alaska. — *Env. Biol. Fishes* 45, p. 343-350.
- Croy, M.I. & Hughes, R.N. (1991). The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback *Spinachia spinachia*, L. — *Anim. Behav.* 41, p. 149-159.

- Day, T. & McPhail, J.D. (1996). The effect of behavioral and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). — *Oecologia* 108, p. 380-388.
- —, Pritchard, J. & Schluter, D. (1994). Ecology and genetics of phenotypic plasticity: a comparison of two sticklebacks. — *Evolution* 48, p. 1723-1734.
- Ehlinger, T.J. (1989). Learning and individual variation in bluegill foraging: Habitat-specific techniques. — *Anim. Behav.* 38, p. 643-658.
- — & Wilson, D.S. (1988). Complex foraging polymorphism in bluegill sunfish. — *Proc. Natl Acad. Sci. USA* 85, p. 1878-1882.
- Futuyma, D.J. & Moreno, G. (1988). The evolution of specialization. — *Ann. Rev. Ecol. Syst.* 19, p. 207-233.
- Gill, A.B. & Hart, P.J.B. (1994). Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness. — *Anim. Behav.* 47, p. 921-932.
- — & — — (1996). How feeding performance and energy intake change with a small increase in the body size of the threespine stickleback. — *J. Fish Biol.* 48, p. 878-890.
- Hatfield, T. (1997). Genetic divergence in adaptive characters between sympatric species of stickleback. — *Am. Nat.* 149, p. 1009-1029.
- Kieffer, J.D. & Colgan, P.W. (1991). Individual variation in learning by foraging pumpkinseed sunfish, *Lepomis gibbosus*: The influence of habitat. — *Anim. Behav.* 41, p. 603-611.
- Lande, R. & Arnold, S.J. (1983). The measurement of selection on correlated characters. — *Evolution* 37, p. 292-305.
- Lavin, P.A. & McPhail, J.D. (1985). The evolution of freshwater diversity in the threespine stickleback (*Gasterosteus aculeatus*): site-specific differentiation of trophic morphology. — *Can. J. Zool.* 63, p. 2632-2638.
- — & — — (1986). Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). — *Can. J. Fish. Aqua. Sci.* 43, p. 2455-2463.
- Levins, R. (1962). Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. — *Am. Nat.* 96, p. 361-373.
- Liou, L.W. & Price, T.D. (1994). Speciation by reinforcement of premating isolation. — *Evolution* 48, p. 1451-1459.
- Magurran, A.E. (1990). The inheritance and development of minnow anti-predator behavior. — *Anim. Behav.* 39, p. 828-834.
- Marcotte, B.M. & Browman, H.I. (1986). Foraging behaviour in fishes: perspectives on variance. — *Env. Biol. Fishes* 16, p. 25-33.
- McPhail, J.D. (1992). Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): evidence for a species pair in Paxton Lake, Texada Island, British Columbia. — *Can. J. Zool.* 70, p. 361-369.
- — (1993). Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. — *Can. J. Zool.* 71, p. 515-523.
- — (1994). Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. — In: *Evolutionary biology of the threespine stickleback* (M.A. Bell & S. Foster, eds). Oxford University Press, Oxford, p. 399-437.
- Meyer, A. (1987). Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. — *Evolution* 41, p. 1357-1369.

- (1989). Cost of morphological specialization: Feeding performance of the two morphs in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*. — *Oecologia* 80, p. 431-436.
- (1990). Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: Alternative adaptations and ontogenetic changes in shape. — *J. Zool.*, London 221, p. 237-260.
- Mittelbach, G.G. (1981). Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. — *Ecology* 62, p. 1370-1386.
- Norton, S.F. (1991). Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. — *Ecology* 72, p. 1807-1819.
- Price, T. & Langdon, T. (1992). Evolution of correlated characters. — *Trends Ecol. Evol.* 7, p. 307-310.
- Reist, J.D. (1985). An empirical evaluation of several univariate methods to adjust for size-variation in morphometric data. — *Can. J. Zool.* 63, p. 129-139.
- Rice, W.R. (1989). Analyzing tables of statistical tests. — *Evolution* 43, p. 223-225.
- & Hostert, E.E. (1993). Laboratory experiments on speciation: what have we learned in 40 years? — *Evolution* 47, p. 1637-1653.
- Robinson, B.W. & Schluter, D. (2000). Natural selection and the evolution of adaptive genetic variation in northern freshwater fishes. — In: *Adaptive genetic variation in the wild* (T. Mousseau, B. Sinervo & J. Endler, eds). Oxford University Press, New York, p. 65-94.
- & Wilson, D.S. (1994). Character release and displacement in fishes: A neglected literature. — *Am. Nat.* 144, p. 596-627.
- & — (1996). Genetic variation and phenotypic plasticity in a polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*). — *Evol. Ecol.* 10, p. 631-652.
- & — (1998). Optimal foraging, specialization and a solution to Liem's paradox. — *Am. Nat.* 151, p. 223-235.
- , — & Shea, G.O. (1996). Trade-offs of ecological specialization: An intraspecific comparison of pumpkinseed sunfish phenotypes. — *Ecology* 77, p. 170-178.
- Schluter, D. (1993). Adaptive radiation in sticklebacks: Size, shape, and habitat use efficiency. — *Ecology* 74, p. 699-709.
- (1994). Experimental evidence that competition promotes divergence in adaptive radiation. — *Science* 266, p. 798-801.
- (1995). Adaptive radiation in sticklebacks: Trade-offs in feeding performance and growth. — *Ecology* 76, p. 82-90.
- (1996). Ecological speciation in postglacial fishes. — *Phil. Trans. Royal Soc. London B* 351, p. 807-814.
- (1998). Ecological causes of speciation. — In: *Endless forms, species and speciation* (D.J. Howard & S.H. Berlocher, eds). Oxford University Press, New York, p. 114-129.
- & McPhail, J.D. (1992). Ecological character displacement and speciation in sticklebacks. — *Am. Nat.* 140, p. 85-108.
- & — (1993). Character displacement and replicate adaptive radiation. — *Trends Ecol. Evol.* 8, p. 197-200.
- Seehausen, O., Witte, F., van Alphen, J.J.M. & Bouton, N. (1998). Direct mate choice maintains diversity among sympatric cichlids in Lake Victoria. — *J. Fish Biol.* 53 (Suppl. A), p. 37-55.

- Skulason, S. & Smith, T.B. (1995). Resource polymorphisms in vertebrates. — *Trends Ecol. Evol.* 10, p. 366-370.
- —, Snorrason, S.S., Ota, D. & Noakes, D.L.G. (1993). Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (Pisces: *Salmonidae*). — *Anim. Behav.* 45, p. 1175-1192.
- Smith, T.B. (1990). Natural selection on bill characters in the two bill morphs of the African finch *Pyrenestes ostrinus*. — *Evolution* 44, p. 832-842.
- — & Skulason, S. (1996). Evolutionary significance of resource polymorphisms in fish, amphibians and birds. — *Ann. Rev. Ecol. Syst.* 27, p. 111-133.
- Smith-Gill, S.J. (1983). Developmental plasticity: developmental conversion versus phenotypic modulation. — *Am. Zool.* 23, p. 47-55.
- Stephens, D.W. & Krebs, J.R. (1986). Foraging theory. — Princeton University Press, Princeton, NJ.
- Taylor, E.B. & McPhail, J.D. (1999). Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insights from mtDNA. — *Biol. J. Linn. Soc.* 66, p. 271-291.
- Wainwright, P.C. (1988). Morphology and ecology: Functional basis of feeding constraints in Caribbean Labrid fishes. — *Ecology* 69, p. 635-645.
- —, Osenberg, S.W. & Mittelbach, G. (1991). Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): Effects of environment on ontogeny. — *Funct. Ecol.* 5, p. 40-55.
- Ware, D.M. (1971). Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. — *J. Fish. Res. Bd. Can.* 28, p. 1847-1852.
- Werner, E.E. (1977). Species packing and niche complementarity in three sunfishes. — *Am. Nat.* 111, p. 553-578.
- Wilson, D.S. & Yoshimura, J. (1994). On the coexistence of specialists and generalists. — *Am. Nat.* 144, p. 692-707.
- Wimberger, P. (1991). Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. — *Evolution* 45, p. 1545-1563.
- — (1992). Plasticity of fish body shape: The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae). — *Biol. J. Linn. Soc.* 45, p. 197-218.
-