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ECOLOGICAL CHARACTER DISPLACEMENT AND SPECIATION IN STICKLEBACKS

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Abstract.—We present evidence of ecological character displacement among species of three-spined sticklebacks that inhabit small lakes of coastal British Columbia. Geological data suggest that the populations resulted from multiple divergence and speciation events over the past 13,000 yr. In lakes with two species, one is invariably "limnetic" in morphology and habitat, and the other is "benthic." Other lakes contain a single form morphologically intermediate between sympatric species and exploiting both habitats. Within solitary populations individuals exploit one habitat or the other according to their morphology, which underscores the divergent selection pressures operating on either side of the habitat boundary. Our results satisfy at least four of the six major criteria for demonstrating the occurrence of character displacement: (1) a statistical null model of no displacement is easily rejected; (2) variation between and within populations is genetically based; (3) differences in sympatry reflect evolutionary shifts, not merely the biased extinction of similar forms; and (4) morphology is closely linked to resource use. Minimal resource differences between one- and two-species lakes and the presence of competition between similar phenotypes are still to be established. Our data suggest that competition for food has played a critical role in the divergence between species. We consider the possibility that it also helped in species formation, which would expand its potential role in adaptive radiation.

Knowledge of the ecological forces shaping diversification is essential to understand adaptive radiation. One force with large potential impact is competition for food between newly formed species (Lack 1947; Schluter and Grant 1984; Taper and Case 1985; P. R. Grant 1986; Schluter 1988*a*, 1988*b*). For example, Lack's (1947) scenario for the origin of the Galápagos finches included competition-induced character divergence as the final stage in the cycle of events producing two coexisting species from a single ancestor (see P. R. Grant 1981).

In general, however, the importance of competition during adaptive radiation is not clear. Evidence that the process occurs comes from a growing number of examples of ecological character displacement between closely related species (Brown and Wilson 1956; P. R. Grant 1972; Arthur 1982; Taper and Case 1992). The evidence includes greater morphological and ecological differences between species in sympatry than in allopatry (Schoener 1970; Huey and Pianka 1974; Fenchel 1975; Case 1979; Dunham et al. 1979; Fjeldsa 1983; Malmquist 1985; Schluter et al. 1985; Diamond et al. 1989; Losos 1990); nonrandom character distributions in coexisting sets of related species (Schluter and Grant 1984;

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Schoener 1984; Dayan et al. 1989, 1990; Schluter 1990); and exaggerated levels of divergence between new species formed in isolation from competing taxa, such as on remote archipelagoes (Schluter 1988*a*).

In this article we describe a new example of possible character displacement involving the three-spined sticklebacks of small coastal lakes in southwestern British Columbia (B.C.). The case has several unique aspects that make it interesting for study. First, pairs of species with large and parallel character differences have apparently evolved independently in several lakes. The evolutionary sequence leading to modern forms may thus be repeatable. Second, the species are very young, all having originated in the past 13,000 yr. Third, it is conceivable that competition for food has aided the actual formation of the stickleback species. This latter possibility, if correct, would push back the start of competition's role during adaptive radiation to a point well before the final stage of the speciation cycle envisioned by Lack (1947).

P. R. Grant (1972), Arthur (1982), and others suggested a variety of tests and criteria for character displacement to be applied to any potential case of exaggerated morphological (or other phenotypic) differences between competing species. These include the following criteria:

1. Chance should be ruled out as an explanation for the pattern.
2. The phenotypic differences between populations in sympatry and allopatry should have a genetic basis.
3. Enhanced differences between sympatric species should be the outcome of evolutionary shifts, not simply of the inability of similar-sized species to coexist (e.g., because of competitive exclusion or introgression).
4. Morphological (or other phenotypic) differences should reflect differences in resource use.
5. Sites of sympatry and allopatry should not differ greatly in food, climate, or other environmental features affecting the phenotype; this includes P. R. Grant's (1975) criterion that differences in the zone of sympatry should not be predictable from geographical variation outside the zone.
6. Independent evidence should be gained that similar phenotypes actually compete for food.

We assemble the statistical and evolutionary evidence (criteria 1 and 3) and document diet and habitat consequences of morphological differences (4). We also summarize other work showing a genetic basis to morphological diversity (2). We do not yet have the data to satisfy the remaining two criteria, although evidence will be presented that the most critical resources are present in all lakes (5).

HISTORICAL BACKGROUND

Marine three-spined sticklebacks (*Gasterosteus aculeatus*) occur throughout much of the Northern Hemisphere, where they breed along coastlines in estuaries and mouths of rivers and streams (Wootton 1976). This marine form has also given rise to permanent freshwater populations in most coastal drainages (Münz-

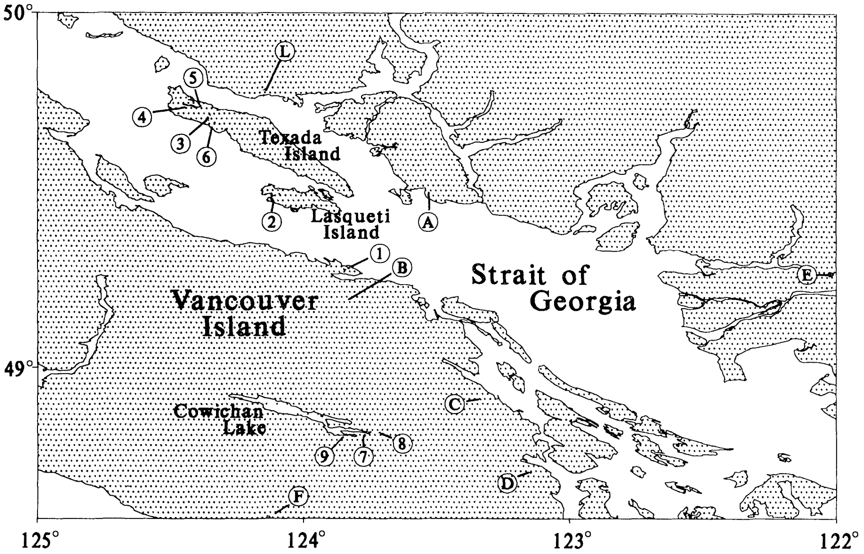

FIG. 1.—Map of the study area. Labels 1–5 indicate lakes containing two species of three-spined sticklebacks, whereas 6–9 and *A*–*F* contain one species each. The lakes are (1) Enos, (2) Hadley, (3) Paxton, (4) Priest, (5) Emily, (6) Cranby, (7) Beaver, (8) Kwassin, (9) Bear, (*A*) Trout, (*B*) Blackjack, (*C*) Chemainus, (*D*) Dougan, (*E*) Erroch, (*F*) Fairy. Marine (anadromous) sticklebacks were collected at Lang Creek (*L*).

ing 1963; McPhail and Lindsey 1970; Bell 1976). Lake and river populations in southwestern B.C. (fig. 1) were established following deglaciation in the late Pleistocene. Most small lakes with sticklebacks were initially below sea level and hence were colonized from the sea as the land uplifted rapidly to near-present levels about 12,500 yr ago (Mathews et al. 1970; Clague et al. 1982; Clague 1983). Most lakes are presently inaccessible from the sea and have been isolated since the final drop in sea level. None of the freshwater populations in this study presently encounters the marine form.

Most lakes contain only one species of three-spined stickleback, but coexisting pairs of species have recently been found in four drainages on three islands in the Strait of Georgia (Texada, Lasqueti, and Vancouver; fig. 1). Morphological and genetic evidence has been presented (McPhail 1984, 1992*a*) to refute the possibility that the two sympatric forms merely represent a single-species polymorphism. The species have not been formally described, and we refer to them as "benthic" and "limnetic" on the basis of preferred foraging habitat (Larson 1976; Bentzen and McPhail 1984; see below). This is merely a convenience and is not meant to imply that the different populations of limnetics (or benthics) are monophyletic. Indeed, their distributions suggest that species pairs evolved several times (McPhail 1992*b*), although a conclusive test awaits a good phylogeny of stickleback populations. Single populations are referred to as "solitary."

The precise origin of each species pair is unknown, but two alternative sce-

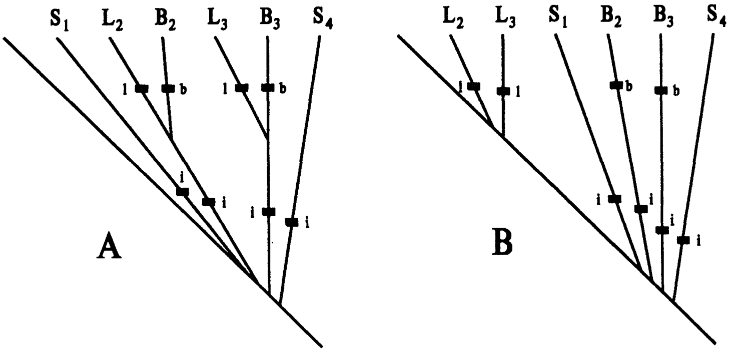

FIG. 2.—Alternative origins of solitary (*S*), limnetic (*L*), and benthic (*B*) populations in small lakes of southwestern B.C. from a marine ancestor. Subscripts refer to individual lakes (e.g., L_2 and B_2 are sympatric). Hypothesized morphological shifts are indicated along the branches: (*i*) intermediate morphotype, (*l*) limnetic morphotype, and (*b*) benthic morphotype. The sequence assumes that the ancestor to all freshwater populations resembled the present marine form and that no morphological transitions occurred prior to the invasion of freshwater. Scenario *A*, species pairs arose by sympatric speciation; *B*, species pairs resulted from separate invasions by the marine form.

narios are consistent with the geological history of the region. The first possibility (fig. 2*A*) is that each lake was colonized once by the marine form following deglaciation and that pairs of species evolved within the lakes by sympatric speciation. This hypothesis is not entirely unreasonable because, as we show below, the ecological preconditions for sympatric speciation as summarized by Wilson (1989) are present in these lakes. However, the genetic preconditions for sympatric speciation may be difficult to meet (Felsenstein 1981). The hypothesis also does not easily explain why pairs of species should occur in only a few lakes, whereas the majority of ecologically similar lakes possess only one species.

The second alternative (suggested by McPhail [1992*b*]) is that the marine form invaded several lakes a second time (fig. 2*B*). In this scenario at least partial reproductive isolation between the marine and lake forms had evolved in the years between invasions, which permitted their coexistence. This double-invasion hypothesis is supported by the geological record: By dating sediments overlying post-Pleistocene terrestrial material, Mathews et al. (1970) concluded that sea levels in the Strait of Georgia rose a second time about 11,500 yr ago. The degree of submergence was less than that immediately following deglaciation and would have provided the marine form with temporary access to lakes just above the sea's margin. All lakes presently containing two species (fig. 1) are about 50–90 m in elevation, slightly above the sea level of 50 m estimated by Mathews et al. (1970) for the second submergence in the same vicinity. The sea receded again to near-present levels about 11,000 yr ago. These dates suggest that the second invasion would have taken place about 1,500–2,000 yr after the first.

Figure 2*B* illustrates this double-invasion model, assuming in addition that each benthic species is derived from the first invasion. This assumption is based on laboratory experiments showing that eggs of the limnetic species are more tolerant of brackish and salt water than are eggs of benthics (J. D. McPhail, unpublished data). Such a difference would be expected if freshwater populations giving rise to benthics preceded the limnetics and if saltwater tolerance decays with time after initial colonization of fresh water. Our tests of character displacement do not require that the actual order of invasions is known, but for simplicity we will use the model shown in figure 2*B*.

Our double-invasion scenario (figure 2*B*) is oversimplified, and in reality small lakes may presently contain solitary populations established during the first wave of colonization; pairs of species resulting from separate marine invasions 1,500 yr apart; solitary forms established in the second wave of colonization, in low-elevation lakes inundated by the second marine incursion; or solitary forms resulting from pairs of species in which one form has gone extinct through chance, competitive exclusion, or hybridization. The geological record is not detailed enough to allow identification of all these types. Efforts to further illuminate the origin of populations using independent means (e.g., DNA sequences) are planned.

DEFINITION

The term ''ecological character displacement'' is used in different ways by different authors, and to avoid confusion we define it here: Character displacement is the influence of one species on the evolution of resource use in another species as a consequence of resource competition (Schluter et al. 1985; Schluter 1988). Divergence between similar species and the maintenance of differences between already distinct forms are both instances of character displacement. This definition underscores the contemporary nature of character displacement; it is not merely a ''ghost of competition past'' but a process that may continue to affect populations today. Convergence resulting from competition is also a theoretical possibility (Abrams 1986), but good examples are lacking.

MATERIALS AND METHODS

Lakes and Collection Methods

We examined the morphology and diet of paired species from the four drainages in which they have been discovered (fig. 1): Enos Lake on Vancouver Island, Hadley Lake on Lasqueti Island, and Paxton, Priest, and Emily lakes on Texada Island. Emily is a short distance downstream from Priest; both are in a separate drainage from Paxton. The lakes are relatively small: Priest is 44 ha, and the others are between 5 and 20 ha. Morphology was also measured in a selection of 10 solitary populations from the same region (fig. 1), from lakes similar in size to those in which species pairs are found. One other fish species is present in these lakes, the indigenous cutthroat trout (*Salmo clarki*), which preys on the sticklebacks. For comparison with the freshwater forms, marine sticklebacks were collected from the mouth of Lang Creek on the mainland north of Texada Island (fig. 1).

Sticklebacks were collected using minnow traps and seines. At least 40 fish were kept and measured per population per collection. For diet analysis, collections from the paired populations and four solitary populations (Cranby, Beaver, Kwassin, and Bear) were obtained in spring (May–June) and autumn (September) of 1988. Collecting traps were checked at hourly intervals to minimize digestion of prey. Captured fish were immediately anesthetized with MS-222 and then placed in 10% formalin for at least one week. Fish were stained using alizarin red (as described in Lavin and McPhail 1985) and finally stored in 37% isopropyl alcohol.

Morphological Measurements

Five external traits were measured on the left side of individual fish: body length, body depth, gape width, gill raker length (all in mm), and number of gill rakers. (Measurement techniques are described in Lavin and McPhail 1985.) Gill raker length was measured on the third most anterior raker on the first gill arch, typically the longest raker. This raker was highly reduced in many individuals from Cranby Lake, and for this population we used the longest of the first five rakers instead. The five traits were selected because they are highly divergent among populations and were considered a priori to be among the most strongly related to foraging efficiency, diet, and habitat use (Hagen and Gilbertson 1972; Larson 1976; Hyatt 1979; Bentzen and McPhail 1984; Gross and Anderson 1984; Lavin and McPhail 1985, 1986). All traits were ln-transformed prior to analysis.

Individuals in each two-species lake were classified to species using the above morphological dimensions. In such lakes two distinct modes were evident in frequency distributions of gill raker number and in other traits, such as gill raker length after adjusting for size (fig. 3; see below for method). This contrasts with a single mode observed in all solitary populations (fig. 3). Similarly, two distinct multivariate clusters were seen in scatterplots of measurements from two-species lakes, but only a single cluster was present in one-species lakes. To classify fish in lakes with two species, individuals were first assigned to one of the two clusters (species) by eye. The discriminant function separating these two clusters was then computed and used to reclassify all individuals. Any fish whose posterior probability of belonging to one or the other species was less than 0.98 was considered to be a possible hybrid and deleted from the analysis. This affected only about 1% of individual fish.

Individuals within each population differed substantially in overall body size, a pattern largely attributable to differences in growth. We attempted to correct for size when comparing different populations by calculating a composite "size" variable (first principal component, PC1) from the pooled variances and covariances of the five ln-transformed traits. Each population and sex was treated as a separate group in this analysis. By "pooled" we mean that measurements within each group were converted to deviations from the group mean prior to combining observations and calculating variances and covariances. Therefore, PC1 represents size variation among individuals within groups and incorporates no variation between group means. Pooling was preferable to a separate analysis for each group, because the latter would have prevented us from comparing size across

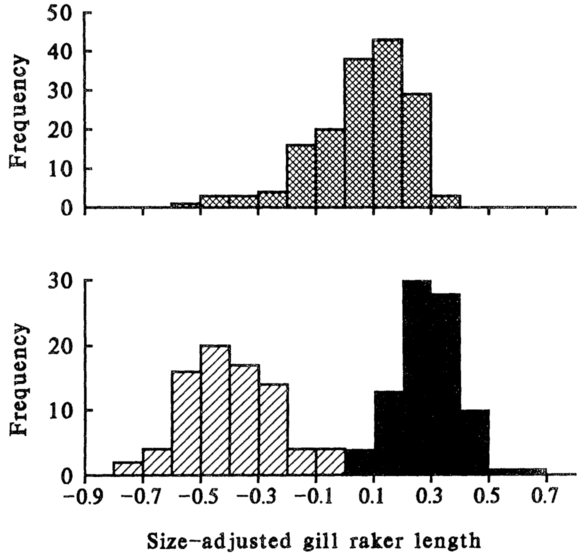

FIG. 3.—Frequency distributions of size-adjusted gill raker length in lakes with one species (Cranby; *upper graph*) and two species (Paxton; *lower graph*). *Shading* in lower figure indicates benthic (*hatched*) and limnetic (*solid*) forms. Gill raker distributions in other one-species lakes were similar to Cranby's, and distributions in other two-species lakes were similar to Paxton's.

groups. However, PC1 is meaningful only if it is approximately parallel to the axis of size variation within each group separately (see below). The first principal component accounted for 75% of the pooled variance among individuals.

To correct for size we regressed each trait separately against PC1 (e.g., fig. 4) and then calculated for each group the predicted value of Y corresponding to $X = 3.73$, the overall mean size. This was done in two ways: first, we assumed that the slopes of the regressions were identical for all groups; second, we used a separate slope for every group. Results were similar, and we present only those from the first correction. Regressions from different groups were approximately parallel (fig. 4); this implies in turn that PC1 is a reasonable measure of size in most populations. Gill raker length in the Cranby Lake population was a conspicuous exception (fig. 4), although this made little difference to the size-corrected value near $X = 3.73$; slopes for other traits were more similar than for gill raker length. A second potential problem was that the marine population did not overlap the value $X = 3.73$, and adjusting for size involved a considerable extrapolation (fig. 4). Mean length of gill rakers (size adjusted) is thus somewhat uncertain in the marine population, although it is certainly large. Gill raker number was uncorrelated with size within populations, and we did not adjust this trait. Population means for size-adjusted traits and gill raker number are provided in the Appendix.

We carried out one further analysis to illustrate differences between populations in dimensions other than body size. The means of size-adjusted traits and

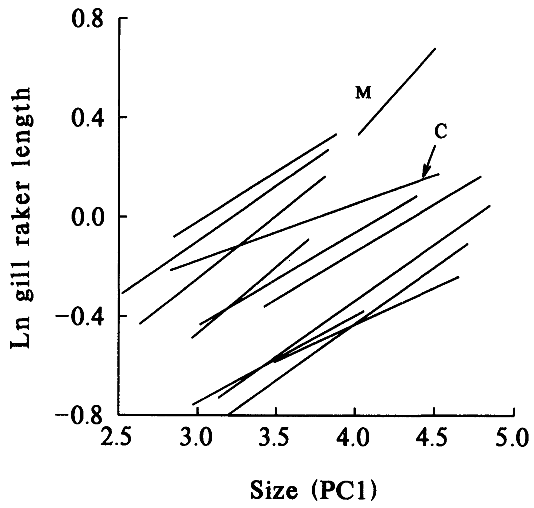

FIG. 4.—Regressions of gill raker length on body size in females. The first principal component (PC1) represents size variation among individuals within populations. Each line is based on a different population; only those for which $N \geq 30$ are illustrated. The letters *M* and *C* refer to the lines for the Marine and Cranby Lake populations. The pattern in males was similar.

ln gill raker number were used to calculate a first principal component from the variances and covariances between groups (sexes and populations). This composite dimension represents the major axis of variation between populations in size-corrected traits. Gill raker length predominated (component coefficient = −0.86), followed by gape width (0.37), gill raker number (−0.28), body depth (0.21), and body length (0.03). This axis thus separates populations by shape: those having relatively long, numerous gill rakers, narrow gapes, and slender bodies from those having fewer short rakers, deeper bodies, and wider gapes.

Population means in both the size and shape dimensions are illustrated in figure 5. The *X* variable is the projection of each group mean on the composite size axis (based on the pooled, within-population variances and covariances). The *Y* variable is the projection of each mean on the composite shape axis (based on differences among population means in size-corrected measurements).

Diet and Habitat Use

We inferred the habitat use of sticklebacks from the contents of their diet. We identified animal prey to order and occasionally to family using the keys in Pennak (1978). Prey were then classified into one of three groups on the basis of the habitat in which they most commonly occur. "Benthos" includes items typically found in or on the lake sediment or attached to vegetation, such as ostracods, annelids, amphipods, gastropods, pelycepods, most insect larvae and pupae, harpactacoid copepods, and chydorid cladocerans. "Plankton" refers to prey inhabiting the water column and includes *Chaoborus*, calanoid copepods, rotifers, and most cladocerans (except Chydoridae). Prey occurring in neither habitat (stickleback eggs) or in both habitats (cyclopoid copepods, chironomid pupae, young sticklebacks) were classified as "other." Length and width of items were measured using an ocular micrometer attached to a dissecting microscope.

The diet proportions consisting of benthos, plankton, and other items were calculated for each individual fish. Population diet proportions are unweighted means of individual fractions. Similarly, mean prey size (length and width) was calculated for each fish, and population means are unweighted averages of individual values.

Differential passage rates of prey unavoidably affect estimates of diet made from items in the gut. We attempted to minimize bias by examining only the contents of the stomach and not the intestine. Remaining biases should be common to all populations and should not therefore unduly affect estimates of diet differences. Another possible bias in the spring collections is an exaggerated frequency of stickleback eggs in the diet, because of enhanced predation of nests near traps following the initial capture of attending males.

Plant material was common in the diet of some populations in autumn. Items included mainly diatoms and filamentous algae obtained from the lake bottom and other substrates. Quantifying amounts in the gut proved difficult, and we only recorded presence or absence. Diet fractions presented here refer only to the animal component.

Morphology-Ecology Relations

We examined the relationship between morphology, habitat, and prey size using regression. To simplify the analyses we included only two morphological traits (gill raker length and body size) because they were the most variable among populations. Other traits were excluded because most were too highly correlated with gill raker length among populations even after correcting for size (e.g., the correlation between size-adjusted gill raker length and gape width, within the same sex and season, was 0.89). One should therefore keep in mind that our regression coefficients for body size and gill raker length may measure the direct importance of these two variables or alternatively the effect of other characters correlated with them.

The X variables body size and gill raker length were standardized in regressions so that their coefficients indicate changes in Y per change in standard deviation of X. Sex and season were included in the regressions as indicator X variables (male = 0, female = 1; spring = 0, fall = 1) so that their coefficients indicate the magnitude of the differences between sexes and seasons in Y when the morphological variables are also taken into account. Our sample sizes were restricted, so we did not test for possible interactions between variables.

A problem with comparisons of populations in mean diet and morphology is that each population was represented up to four times (once for each sex and season), and lakes were represented even more frequently, such that observations may not be independent. A solution is to include "population" and "lake" as variables in the regressions, but this would leave too few degrees of freedom to test for effects of morphology. Another solution is to restrict analysis to indepen-

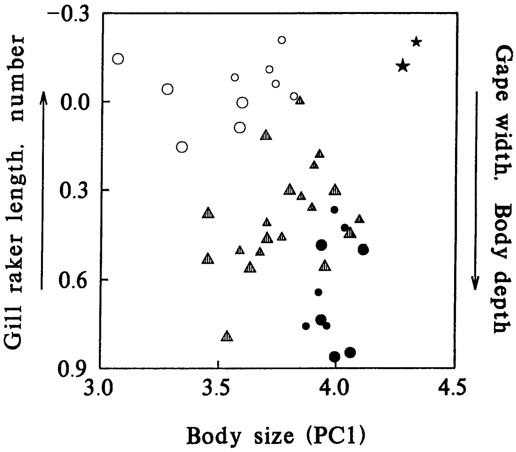

FIG. 5.—Mean size and shape of stickleback populations. Body size is essentially mean position along the common, within-population growth trajectory. The Y-axis is the major axis of variation among means of size-corrected measurements. See Methods for details of calculation. The Y dimension indicates that populations differ primarily in the number and length of gill rakers relative to gape width and body depth once size differences are removed. *Circles* indicate paired species: limnetic (*open*) and benthic (*solid*). *Triangles* indicate solitary populations. Values for the marine species (*star*) are also shown for comparison. Large points refer to females, small ones to males. Data are from specimens obtained in the breeding season and exclude young of the year.

dent subsets of data. For example, we compared diet with morphology separately for each sex and season, after randomly deleting the data of one species from lakes possessing two. Such analyses yielded coefficients and significance levels not greatly different from those presented herein. The present results are therefore fairly robust.

RESULTS

Statistical Evidence for Character Displacement

In all five lakes containing two species, striking morphological differences were seen between them (fig. 5; Appendix). One species (limnetics) tended to be smaller in size (PC1) than the other species (benthics), although they overlapped in this dimension. There was no overlap in the means of other traits (size corrected) except body length: limnetics have longer and more numerous gill rakers, smaller mouths (narrower gapes), and more slender bodies than sympatric benthics. Solitary populations were intermediate overall (fig. 5).

Are the differences between coexisting populations greater than chance alone would dictate? The usual test of character displacement is to compare sympatric and allopatric populations of the same two species. However, if lakes contain phylogenetically distinct freshwater lineages (fig. 2), then each population is es-

TABLE 1

STATISTICAL TESTS OF CHARACTER DISPLACEMENT

TRAIT	MALES		FEMALES	
	Observed	Expected	Observed	Expected
Body size	.29	.15	.68**	.24
Length	.01	.03	.01	.04
Depth	.17**	.06	.13	.05
Gape width	.22	.09	.25*	.09
Gill raker length	.56**	.15	.53**	.18
Gill raker number	.24**	.07	.21**	.08

NOTE.—Observed values are the absolute differences between coexisting limnetics and benthics, averaged over four lakes (Emily excluded). Expected values are the mean absolute differences between all possible pairs of solitary populations. Values are based on ln-transformed data. Traits other than size and gill raker number are size corrected.

* $P < .05$.

** $P < .02$.

sentially a unique species whose traits are acquired separately. For this reason we compared sympatric species pairs to the pool of solitary populations: In the absence of character displacement, sympatric species should be no more different than two solitary forms picked at random.

Sympatric species tend to be more divergent than randomly paired solitary populations in every trait except size-corrected body length (table 1). Displacement in gill raker length and number is significant in both sexes. Differences in body size and size-corrected body depth and gape width are significant in one sex, and the trend is the same in the other sex. Statistical significance was judged by comparing the estimate of the variance (= mean squared difference) between sympatric species, pooled over all pairs (s^2_{pairs}), to an estimate of the variance between solitary populations (s^2_{solitary}); this latter quantity also estimates the variance (= mean squared difference) between any two randomly selected solitary forms. Under the null hypothesis of no displacement the ratio $F = s^2_{\text{pairs}}/s^2_{\text{solitary}}$ will have an F distribution with df = 4,9. This test assumes that each species pair is independent (for this reason Emily Lake, downstream from Priest Lake, was excluded from the analysis). If the pairs are not independent (e.g., because they are all descended from a single ancestral pair), then the test statistic F will have df = 1,9. The differences in table 1 remain significant in this case ($P < .05$) except gape width in females ($P = .09$).

The above tests do not require that the immediate ancestor to both limnetic and benthic forms resemble the present-day solitary form. Rather, we assume that the distribution of morphologies, under the null hypothesis of no coevolution between sympatric species, is best represented by the solitary forms (since by definition the solitary sticklebacks are not coevolving with any others). An estimate of the actual sequence of morphological changes from ancestors to descendants requires further assumptions about the adaptive significance of these changes. Hence, we first describe the ecological relevance of morphological variation and postpone the estimation of historical shifts until the Discussion.

TABLE 2

DIETS OF LIMNETIC, BENTHIC, AND SOLITARY POPULATIONS IN SPRING AND FALL

	MAY–JUNE (BREEDING)				SEPTEMBER (NONBREEDING)			
POPULATION	*N*	Plankton	Benthos	Other	*N*	Plankton	Benthos	Other
Limnetic:								
Enos	30	**.70**	.13	.17	33	**.83**	.02	.14
Hadley	. . .	. . .	. . .	. . .	33	**.73**	.09	.18
Paxton	39	.25	.20	**.56**	32	**.75**	.13	.12
Priest	35	.19	**.59**	.21	29	**.52**	.16	.32
Emily	37	**.63**	.24	.13	. . .	. . .	. . .	. . .
Benthic:								
Enos	31	.06	**.54**	.40	21	.04	**.90**	.05
Hadley	. . .	. . .	. . .	. . .	36	.04	**.83**	.14
Paxton	33	.00	**.79**	.21	32	.10	**.84**	.06
Priest	37	.00	**.88**	.12	24	.09	**.83**	.08
Emily	36	.10	**.71**	.19	. . .	. . .	. . .	. . .
Solitary:								
Cranby	60	.10	**.70**	.20	74	**.62**	.26	.12
Beaver	34	.17	**.43**	.40	26	.27	**.67**	.06
Kwassin	39	.21	**.52**	.26	27	.09	**.86**	.05
Bear	30	.03	**.53**	.44	. . .	. . .	. . .	. . .

NOTE.—Proportions are means of values in *N* individuals having at least five items in the stomach. "Benthos" refers to items found on the lake bottom or attached to vegetation, and "plankton" includes prey found in the water column. Prey exploiting neither or both of the two habitats were placed in the third category. The predominant fraction is given in boldface.

Morphology and Resource Use among Populations

A requirement for any putative case of character displacement is that morphological differences reflect variation in resource use. Here we demonstrate the link between morphology, habitat use, and prey size across populations. In the subsequent section we show that similar patterns hold also among individuals within populations.

The differences between sympatric species in diet and habitat use were clearest in the nonbreeding season (table 2). The benthic forms in all lakes obtained the majority of their prey from substrates, whereas the limnetics took mainly plankton. Habitat use by benthics was usually unchanged in the breeding season, but limnetic populations exploited benthos to a greater degree in May–June than in September. This opportunistic use of benthos by limnetics in spring probably reflects the greater profitability of the habitat at this time (see, e.g., Werner et al. 1983), but it may also be linked to the requirements of breeding: males build and defend nests on the sediment in the littoral zone, and gravid females seek them out. Accordingly, the plankton fraction of the spring diet in Paxton and Enos lakes was 0.29 lower in male limnetics than in females ($P < .05$); the difference was smaller in Priest and Emily lakes (0.20 and 0.03; $P > .05$).

Solitary populations tended to exploit both habitats (table 2). The mean plankton fraction of solitary populations in September was greater than that for benthics but less than that for limnetics (Tukey pairwise comparisons on arcsine

TABLE 3

RELATIONSHIP BETWEEN MORPHOLOGY AND DIET ACROSS POPULATIONS

	REGRESSION COEFFICIENTS	
VARIABLE	Plankton Fraction	ln Prey Width
Body size (PC1)	−.21**	.25**
Gill raker length	.25**	−.15**
Sex	−.02	−.13
Season	.01	−.40**
N	46	46
R^2	.72	.78

NOTE.—Significance levels in the first column are based on a logistic transformation of Y—that is, $Y' = \ln(Y/(1 - Y))$—but for simplicity coefficients refer to the untransformed data.

** $P < .01$.

square-root-transformed data, all $P < .01$, $N = 11$ populations). As expected, use of benthos by solitary populations was also intermediate (all $P < .01$). Benthos predominated in the diet in the breeding season, but plankton was also used. These results establish that the two main habitats partitioned by species in sympatry (water column and benthos) are also present in lakes containing only one species.

The differences among populations in foraging habitat were summarized as a function of size and gill raker number. We expressed the number of items of plankton in the diet as a fraction of the total number of items of plankton and benthos and regressed it on morphology, sex, and season (table 3). A subset of the pattern is illustrated in figure 6, which plots September plankton fraction against an index of gill raker length relative to body size. The most planktivorous populations had long gill rakers and small body size (limnetics), whereas populations consuming benthos were larger with relatively short gill rakers. Solitary populations exploited both plankton and benthos, the degree depending on their morphology (fig. 6).

Stickleback eggs comprised the majority of items in the "other" fraction in May–June (table 2). In fall, items in this category were mainly chironomid pupae and cyclopoid copepods, foods whose source habitat could not be identified unambiguously. (Additional accounts of diet in several of these populations are given in Larson [1976], Bentzen and McPhail [1984], and Lavin and McPhail [1986].)

Morphology also affected prey size (table 3). The largest prey were consumed by large-bodied populations having relatively short gill rakers (benthics). Limnetics had the smallest bodies and longest gill rakers and took the smallest prey on average. Solitary populations were intermediate in both morphology and prey size. Prey size is partly related to habitat, since large food items are absent from the water column. The mean size of consumed prey declined from spring to fall independently of seasonal differences in mean morphology of populations (table 3).

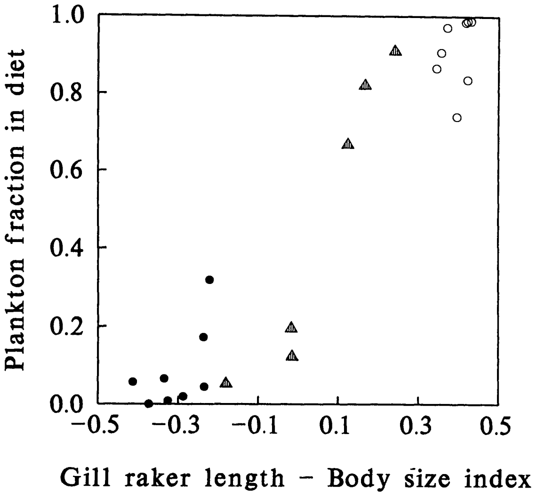

FIG. 6.—Foraging habitat and morphology among limnetic (*open circles*), benthic (*solid circles*), and solitary populations (*triangles*) in September. The Y-axis is observed fraction of the diet consisting of plankton from the water column. The X-axis is an index representing decreasing body size (PC1) and increasing gill raker length. The index is based on the multiple regression of diet fraction on standardized morphological measurements (table 3): X = 0.25(gill raker length) − 0.21(body size).

Within-Population Variation

An analysis of individual variation in morphology and resource use is the first step to understanding the selection pressures working on populations. If morphology is molded by habitat, then the utility of alternative habitats should be related to the morphology of population members. We examined variation in solitary populations because they are intermediate between limnetic and benthic species in both diet and body form (fig. 5). We focused on Cranby Lake, which contains one species and lies adjacent to (but in a different drainage from) Paxton Lake containing two species (fig. 1). The Cranby population is morphologically intermediate between the Paxton limnetic and benthic species (Appendix) and overlaps them in distribution (fig. 7).

Of Cranby fish collected 80% had either mostly plankton (≥90% of items) or mostly benthos in their stomachs, which indicated that individuals concentrated in one habitat or the other, at least over the short term. Choice of habitat depended strongly on the morphology of the individual. Those taking prey from the water column had longer gill rakers and were smaller than fish foraging on benthos (table 4, fig. 7). This pattern is strikingly similar to the pattern of habitat and morphology seen between sympatric species (table 3, fig. 6). Indeed, degree of resemblance of Cranby individuals to each Paxton species was a good predictor of habitat use in September (fig. 7).

Similar patterns of morphology-dependent habitat use were found within the two other solitary populations sampled in spring and fall (Beaver and Kwassin

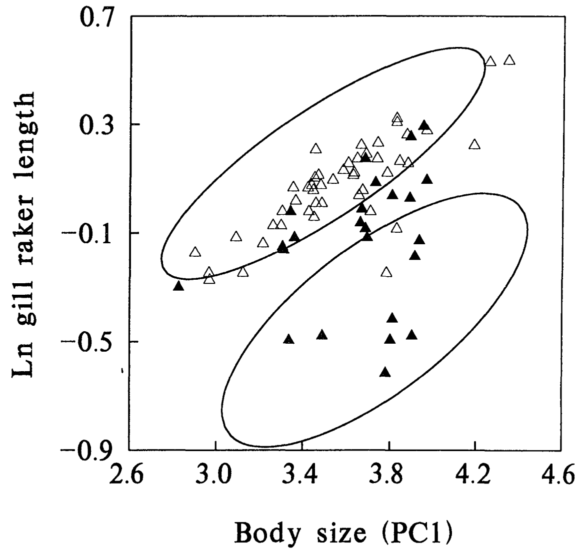

FIG. 7.—Morphology and habitat use in the solitary population of Cranby Lake in September. Symbols distinguish individuals whose diet was mainly (>50%) plankton from the water column (*open*) from those whose items were obtained mainly from the benthos (*solid*). Individuals having fewer than five items in the stomach were excluded. Ellipses enclose approximately 90% of the measurements of limnetics (*upper ellipse*) and benthics (*lower ellipse*) from nearby Paxton Lake.

lakes; table 4), but sample sizes were smaller and few effects were significant. Habitat use also varied seasonally (table 4). Use of plankton increased from spring to fall in Cranby Lake but declined in the other two lakes (significant in Kwassin only), when morphology is also accounted for. This suggests that individual habitat choice is contingent not only on body form but on food availability and/or other factors varying seasonally.

Finally, prey size and morphology were associated among individuals (table 5) in much the way that they were associated among populations (table 3). Similar effects of body size were found within benthic, limnetic, and solitary forms. The effect of gill raker length on prey size was strongest in solitary populations and weakest in benthic populations, with limnetics intermediate. This pattern in solitary populations probably results indirectly from an effect of gill raker length on habitat (table 4, fig. 7); the relation between gill raker length and prey size within habitats was weaker and not significant ($P > .05$).

DISCUSSION

Character Displacement and Alternatives

The adaptive radiation of sticklebacks in small coastal lakes has produced a variety of forms in a brief time span. We investigated the possibility that ecologi-

TABLE 4

Predictors of Variation among Individuals within Solitary Populations in the Fraction of the Diet Consisting of Plankton

Variable	Regression Coefficients Cranby	 Beaver	 Kwassin
Body size (PC1)	−.19**	−.22*	−.11
Gill raker length	1.16**	.17	.11
Sex	.02	.07	−.05
Season	.40**	−.14	−.26*
N	133	59	66
R^2	.54	.15	.22

Note.—Significance levels are based on logistic regressions, but for simplicity coefficients are calculated using the actual fractions.
* $P < .05$.
** $P < .01$.

TABLE 5

Predictors of Within-Population Variation in Prey Width

Variable	Regression Coefficients Solitary	 Limnetic	 Benthic
Body size (PC1)	.29**	.30**	.19**
Gill raker length	−.15**	−.10	−.01
Sex	−.01	−.22**	−.01
Season	−.25**	−.54**	−.24**
Lake	**	**	**
N	290	259	242
R^2	.39	.53	.30

Note.—Continuous independent variables were ln transformed and standardized.
** $P < .01$.

cal character displacement has played a role in the origin of this diversity. Though still incomplete, our results suggest that character displacement has indeed occurred, probably on multiple occasions. Our evidence is fourfold.

First, sympatric species of sticklebacks are more different than expected under the null hypothesis of no character displacement. The enhanced morphological differences are repeated in several lakes and involve similar traits on each occasion. Solitary populations are morphologically intermediate between sympatric species, which suggests that the displacement is approximately symmetrical around the value otherwise expected.

Second, evidence suggests that the morphological displacement represents true coevolution between sympatric species. An alternative hypothesis is that the enhanced differences are the result of colonization and biased extinction without coevolution, as follows. A number of lakes were colonized in the past by two stickleback species; the colonists to some lakes were very different morphologically, whereas the colonists to other lakes were more similar. One of the two species went extinct in lakes in which the colonists were too similar as a result of competitive exclusion or introgression, and only morphologically different colonists now persist. However, although biased extinction may have played a role in the history of stickleback populations, the evidence suggests that it is not sufficient on its own to account for the differences between sympatric species. For example, the range of mean morphologies of limnetic and benthic species extends well beyond that observed for solitary populations in lakes of comparable size (fig. 5). The biased extinction hypothesis also assumes that a large range of morphologically different source populations (including limnetics and benthics) was available to colonize lakes. While the history of lake invasions cannot be known with certainty, the geological record along with present stickleback distributions suggest limited opportunities for colonization and a limited diversity of colonists to these small lakes.

Third, morphology of populations is closely linked to resource use. Sympatric species exploit different habitats within a lake, whereas solitary populations are morphologically intermediate and tend to exploit both habitats. Within solitary populations individuals exploit habitats according to morphology: those tending to resemble limnetic species in body form consume plankton, whereas the more benthiclike individuals take food mainly from substrates. Such results highlight the contrasting selection pressures at work on opposite sides of the habitat boundary. Conceivably, selection in solitary species is disruptive and favors alternative extreme phenotypes in the different habitats (see also B. R. Grant 1985; Ehlinger and Wilson 1988; Smith 1990).

Fourth, while fish morphology can be remarkably plastic and can vary with diet (Meyer 1987; Wimberger 1991), the morphological differences between stickleback populations are mainly genetically based. Fish from several of these populations were raised on the same food in the laboratory, including limnetic, benthic, and solitary forms, and it was shown that natural differences in mean size and shape persist (McPhail, 1984, 1992*a;* Lavin and McPhail 1987). We note that within-population variation in morphology also has a strong heritable component (Hagen 1973; Bell 1984; Baumgartner 1986; Lavin and McPhail 1987; D. Schluter, unpublished data). For example, comparison of wild-caught limnetic parents from Enos Lake with their offspring raised in the lab yielded an estimate of $h^2 = 0.45$ in size-adjusted gill raker length (D. Schluter, unpublished data). Traits within populations are therefore expected to respond quickly to changing selection pressures.

In all, these results satisfy four of the six commonly listed criteria for ecological character displacement. They therefore support the hypothesis over several alternative explanations (i.e., chance, nongenetic morphological shifts, biased extinctions, and absence of a link to resource use). What other mechanisms might account for the pattern?

First, it is conceivable that one- and two-species lakes differ in resource availability. For example, certain lakes might possess only one habitat whereas others possess two. Such a resource effect has been observed in at least one study of coevolution: Differences between Galápagos Islands in the number of finch species and their mean beak sizes partly reflect differences in the number and location of fitness "peaks" present, a function of seed availability (Schluter and Grant 1984). Resource differences between lakes would not rule out character displacement (e.g., it may still be responsible for differences in sympatry), but the full impact of the process would not be certain until the differences are controlled for. Possible ways to accomplish this control include a comparison of adaptive surfaces (Schluter and Grant 1984; Schluter et al. 1985), multiple regression (Dunham et al. 1979), or (best of all) experimental manipulations of species occurrences. However, results thus far indicate that resource differences are unlikely to explain the stickleback patterns. The exploitation of both water column and benthos by solitary species confirms that both habitats are present in sympatry as well as allopatry.

A second possibility is that coevolution has indeed taken place, but its mechanism is not competition. For example, selection against interspecific hybrids might give extreme phenotypes a reproductive advantage if they are less likely to mate with the opposite species. Divergence would then be favored by reproductive rather than ecological character displacement. This mechanism is unlikely here because the largest differences between sympatric species include length and number of gill rakers, which are internal and not used in mate choice (although conceivably they may be highly genetically correlated with external traits and so would not evolve independently of them). Uncertainty over mechanism nevertheless remains, which warrants a direct test of competition between similar phenotypes (criterion 6).

Evolutionary Events

We have ventured to trace in a general way the history of morphological changes in the lineage since lakes were colonized, using the alternative phylogenies suggested in figure 2. The estimated sequence of shifts follows from two assumptions. First, we assume that the present-day marine form approximates the ancestor to all freshwater populations. This is not unreasonable, because the marine form today is not highly differentiated throughout its holarctic range regardless of latitude (Bell 1976). The species is adapted to an ocean pelagic, planktivorous existence (e.g., it has long, numerous gill rakers; fig. 5), and this was probably true also in the late Pleistocene. Indeed, even marine sticklebacks from the middle Miocene are not markedly different from the modern marine form (Bell 1977; Sychevskaya and Grechina 1981). Second, we assume that by itself a stickleback species in a small lake evolves to an intermediate morphology. This assumption is really an observation: solitary populations in small lakes are morphologically intermediate between benthics and limnetics and tend to exploit both major habitats.

The estimates (fig. 2) are simplified—for example they do not identify the individual characters involved in transitions, nor do they recognize morphological differences among populations of the same morphotype. Nevertheless, they illustrate the shifts thought to have occurred since lakes were colonized. They also emphasize that two character displacement "events" have occurred in each unique species pair. If pairs evolved sympatrically, then speciation was accompanied by two approximately symmetric morphological shifts to either side of the previous mean (fig. 2*A*). These changes mainly involved shape but also size in females (fig. 5; table 1). If the double-invasion model is correct instead (fig. 2*B*), then the implied events following the second invasion include a displacement of morphology (primarily shape) in the first species from a solitary morphotype to a benthic morphotype (see fig. 5), a reduction in size in the second invader, and the absence of a shift toward an intermediate shape in the second invader.

It may seem unnecessary in the double-invasion scenario to consider the absence of shape shift (second invader) as significant an event in evolution as the presence of one (first invader). However, this view is accurate in recognizing that the first colonist to a lake altered the course of evolution in the second; this is our definition of character displacement. It also emphasizes that character displacement is not merely a historical phenomenon. Rather, the persistent large differences between sympatric species in highly heritable traits imply that natural selection continues to hold the species apart. In principle, it should be possible to measure these selection pressures directly.

An intriguing aspect of these patterns is that they may not be unique, at least in fish. A variety of groups shows relatively rapid speciation accompanied by large morphological differences in traits related to foraging, especially in sympatry (e.g., Svärdson 1961; Greenwood 1965; Behnke 1972; Lindsey 1981; Bernatchez and Dodson 1990; Meyer et al. 1990). A common theme in many of these examples, including the sticklebacks, is the prevailing influence of two major habitats (benthos [including sediment and vegetation surfaces] and the water column) on early evolutionary trends. Why should character displacement so often occur along the same resource gradient? The pattern may reflect a constraint of fish design, but a more likely hypothesis is that it reflects consistent patterns of natural selection. In a lake largely devoid of other fish species, an increment of divergence along the benthos–water column habitat gradient may yield the greatest decline in interspecific competition together with the least compromise in resource availability. The question merits more careful documentation and study because it may stand as one of the few instances in which early patterns of adaptive radiation are predictable.

Character Displacement and Speciation

One further question is why there are sympatric species of sticklebacks at all (McPhail 1992*b*). The issue is related to the unsolved problem of population histories (fig. 2), but there are grounds for considering that reproductive isolation and character divergence evolved jointly, whatever the histories. As the point is relevant to the evolution of character displacement, we outline these considerations briefly.

Assume for the moment that lakes were colonized twice from the sea (as we suspect). We must then ask whether the estimated 1,500 yr separating the two events was sufficient to produce complete reproductive isolation. If so, then speciation was entirely allopatric, and the present morphologies evolved secondarily. Alternatively, it is plausible that reproductive isolation was incomplete at the time of reinvasion, and it continued to evolve in sympatry. Reproductive isolation is incomplete even today: current estimates are that roughly 1% of adult fish are hybrids (McPhail 1992*a*), although we lack an estimate of gene flow.

The presence of ecological character displacement between limnetics and benthics implies that competition for food between phenotypically similar individuals has led to natural selection against intermediate phenotypes (Roughgarden 1976; Slatkin 1980; Milligan 1985; Taper and Case 1985). Yet, such selection would also favor divergence between forms only partly isolated reproductively and may even favor the reinforcement of existing reproductive isolation (see Wilson 1989) because hybrids are of intermediate phenotype. Whether reinforcement has ever happened in nature is still debated (Butlin 1987), but at least the ecological preconditions appear to be at work. In this case character displacement and reproductive isolation could have evolved jointly toward completion. The more extreme possibility is that species evolved entirely by sympatric speciation (fig. 2*A*), in which case the same ecological mechanism could be responsible (Wilson 1989). Ehlinger and Wilson (1988) describe a morphological polymorphism in the bluegill sunfish that involves the same lake habitats described here for sticklebacks, in which similar ecological mechanisms may be at work.

The two components of adaptive radiation are speciation and divergence. Results presented here suggest that competition for food played a hand in one of these processes (divergence). The sticklebacks present an opportunity to examine its potential role in speciation also.

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APPENDIX

TABLE A1

Summary of Morphological Differences between Populations

Lake	Morph	Body Size (PC1)	Body Length	Body Depth	Gape Width	Gill Raker Length	Gill Raker Number
Males:							
Lang Creek	M	4.33	3.75	2.26	1.16	.40	22.80
Enos	L	3.76	3.82	2.17	1.20	.39	24.05
Hadley	L	3.56	3.83	2.27	1.20	.25	25.00
Paxton	L	3.71	3.84	2.18	1.23	.31	23.03
Priest	L	3.74	3.83	2.17	1.28	.26	23.21
Emily	L	3.81	3.82	2.16	1.32	.22	23.76
Enos	B	4.03	3.82	2.33	1.42	−.14	19.23
Hadley	B	3.99	3.84	2.37	1.34	−.11	19.90
Paxton	B	3.93	3.84	2.37	1.49	−.32	17.19
Priest	B	3.96	3.86	2.38	1.55	−.45	18.70
Emily	B	3.87	3.82	2.37	1.59	−.44	19.00
Cranby	S	3.93	3.81	2.26	1.34	.08	19.74
Beaver	S	3.85	3.88	2.36	1.30	−.06	18.93
Kwassin	S	3.59	3.85	2.38	1.40	−.20	17.50
Bear	S	3.89	3.81	2.32	1.39	−.07	18.32
Blackjack	S	4.09	3.84	2.41	1.31	−.12	18.00
Chemainus	S	3.67	3.87	2.34	1.41	−.19	16.74
Dougan	S	3.90	3.82	2.26	1.35	.06	19.00
Erroch	S	3.84	3.83	2.38	1.10	.26	17.75
Fairy	S	3.77	3.81	2.36	1.43	−.17	18.88
Trout	S	3.70	3.88	2.28	1.43	−.16	20.85
Females:							
Lang Creek	M	4.27	3.87	2.33	1.07	.30	21.86
Enos	L	3.07	3.88	2.27	1.13	.31	24.55
Hadley	L	3.34	3.89	2.33	1.24	.05	22.00
Paxton	L	3.28	3.87	2.22	1.22	.24	22.42
Priest	L	3.58	3.91	2.24	1.27	.10	23.33
Emily	L	3.59	3.88	2.21	1.26	.19	23.63
Enos	B	3.94	3.88	2.38	1.37	−.21	18.88
Hadley	B	4.11	3.88	2.39	1.38	−.23	19.42
Paxton	B	3.94	3.87	2.39	1.52	−.42	17.79
Priest	B	4.00	3.90	2.41	1.57	−.55	18.71
Emily	B	4.06	3.86	2.42	1.58	−.54	18.92
Cranby	S	3.99	3.86	2.33	1.33	−.05	20.08
Beaver	S	4.06	3.92	2.38	1.33	−.19	19.08
Kwassin	S	3.54	3.93	2.47	1.46	−.49	18.00
Bear	S	3.45	3.84	2.34	1.37	−.09	18.28
Blackjack	S	3.95	3.90	2.48	1.32	−.27	17.87
Chemainus	S	3.45	3.88	2.37	1.40	−.22	16.60
Dougan	S	3.80	3.88	2.34	1.30	−.06	20.36
Erroch	S	3.70	3.89	2.39	1.13	.14	17.54
Fairy	S	3.70	3.83	2.37	1.40	−.17	18.36
Trout	S	3.63	3.91	2.35	1.44	−.30	20.60

Note.—Means are from fish collected in the breeding season and do not include young of the year. Traits other than body size and number of gill rakers are size corrected. Species are marine (M), limnetic (L), benthic (B), and solitary (S). Gill raker number is presented as untransformed counts. Other traits are based on ln-transformed data.

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