



Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape

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Threespine sticklebacks, small fish with a circumglobal distribution in coastal marine and freshwater of the northern hemisphere, present a remarkable scope of variation in body and fin shape among populations. The repeated evolution of divergent body shapes in a radiation of stickleback from Cook Inlet, Alaska suggests that diversification has proceeded by extensive parallel selection. To explore this hypothesis, hydromechanical equations of fish propulsion and descriptions of stickleback foraging and anti-predator behaviours were used to develop a series of hypotheses that predicted the evolutionary effects of native predatory fishes (NPF) and relative littoral area (RLA) on body shape. Body shape was measured using Cartesian coordinates of anatomical landmarks transformed by the generalized resistant fit superimposition. In general, the results were consistent with the hypotheses that (1) RLA has a direct effect on selection for foraging behaviour and morphology, (2) RLA has an indirect effect on selection for morphology employed in predator evasion, (3) presence of NPF has a direct effect on selection for evasive morphology, and (4) presence of NPF has an indirect effect on selection for foraging behaviour and morphology. The magnitude of the divergence of body shapes present in the Cook Inlet system suggests that extreme phenotypes have evolved by opportunistic expansion into new habitat relatively free of interspecific competition.

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ADDITIONAL KEY WORDS:—locomotion – biomechanics – size and shape – parallel evolution – adaptation – geometric morphometrics – randomization tests – bootstrap – comparative method – interaction.

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INTRODUCTION

The threespine stickleback is a small fish with a circumglobal distribution in coastal marine and freshwater of the northern hemisphere (Bell & Foster, 1994a). Throughout its range, the anadromous life-history form is known to rapidly found freshwater populations (Francis, Havens & Bell, 1985; Klepaker, 1993; M.A. Bell, unpublished data). Thousands of lakes in the Cook inlet region of Alaska were colonized by threespine stickleback (hereafter, stickleback) following the retreat of the Cordilleran ice sheet beginning 16 500 years ago (Reger & Pinney, 1995). This freshwater radiation presents a large scope of interlake variation in trophic, body shape, and defensive armour traits (Bell, Francis & Havens, 1985; Francis *et al.*, 1986; Bell *et al.*, 1993; Bourgeois, Blouw & Bell, 1994; Bell & Ortí, 1994; Walker, 1996). The geographic distribution of these traits is consistent with the hypothesis that derived states have independently evolved multiple times (Bell, 1988; Bell & Foster, 1994b; Bell & Ortí, 1994). The repeated evolution of derived body shapes suggests that diversification has proceeded by extensive parallel selection (Endler, 1986).

In the traditional comparative research programme, correlations between organismal design and environmental variation are used to investigate adaptation and infer historical patterns of natural selection (Harvey & Mace, 1982; Harvey & Pagel, 1991; Ridley, 1983; Endler, 1986; Brooks & McLennan, 1991). *Post hoc* functional explanations are frequently created to explain observed associations within an adaptationist framework. When treated as hypotheses for further investigation, *post hoc* qualitative functional explanations form a legitimate step in the comparative method (Mayr, 1981; Endler, 1986). Often, *post hoc* functional explanations are never tested experimentally but, nevertheless, attain a nearly dogmatic status. Not surprisingly, *post hoc* functional explanations have been criticized as ‘Just So Stories’ (Gould & Lewontin, 1979). Biomechanical models based on first principles, however, can be used to generate *a priori* hypotheses of expected ecomorphological relationships that can be tested with comparative data (Webb, 1984a,b, 1988; Webb & Weihs, 1986; Endler, 1986; Wainwright, 1987, 1988; Losos, 1990; Emerson, 1991; Williams,

1992). To explore the hypothesis of parallel evolution of stickleback body shape, I use hydromechanical equations of fish propulsion and descriptions of stickleback foraging and anti-predator behaviours to develop a series of predictions on the evolutionary effects of native predatory fishes (NPF) and relative littoral area (RLA) on stickleback body shape. I then compare the observed and predicted effects as a preliminary test of the parallel selection model.

Ecomorphological models of locomotor behaviours

Anti-predator behaviour

Of the many anti-predatory behaviours (Huntingford, Wright & Tierney, 1994) and potential predators (Reimchen, 1994), I focus on the functional consequences of evasion from piscivorous fishes, although the model should also be applicable to evasion from birds. Several factors can contribute to the efficacy of an evasion response, including response latency, maximum acceleration and manoeuvrability (Howland, 1974; Weihs & Webb, 1984), but there are no empirical data to rank the importance of these components. For this study, I assume that the probability of successful evasion for interactions with all predatory fishes is proportional to the maximum acceleration achieved during an evasive response.

Models of the expected morphologies for optimal acceleration performance are critically dependent on the kinematics of the evasion response. Many fish, including stickleback (Taylor & McPhail, 1986), utilize a highly stereotyped C-start to rapidly accelerate in response to threat of predation (Weihs, 1973; Webb, 1975a, 1978, 1984a, 1986; Eaton, Bombardieri & Meyer, 1977; Taylor & McPhail, 1985; Harper & Blake, 1990; Domenici & Blake, 1991; Jayne & Lauder, 1993). In the first stage of a C-start, axial flexion bends the fish into a 'C' shape. Stickleback employ the C-start for two distinct anti-predator behaviours: jumps and bursts into cover. A jump is a rapid acceleration and powered turn followed by a stop. A burst is a rapid acceleration followed by a sprint into nearby cover, such as vegetation, fallen trees or branches, or the open bottom. Rapid accelerations are also employed in tortuous, or protean, flights (Driver & Humphries, 1988), which are prolonged, high velocity escape responses with frequent and sharp changes in direction.

Both acceleration reaction forces (Daniel, 1984) and lift contribute to thrust in a C-start (Weihs, 1972, 1973, 1989; Frith & Blake, 1991). The acceleration reaction is a result of the caudal body and tail sweeping through the water, accelerating a mass of water behind the fish. The water, in turn, exerts a reaction force in the opposite direction, which propels the fish forward. Lighthill (1970, 1971, 1975) modelled the acceleration reaction by partitioning the length of the body into a series of transverse sections, or propulsive segments of length, da . During the propulsive stroke, each propulsive segment accelerates a mass of water with a force (Weihs, 1973)

$$F_a = \frac{d}{dt}(m_a w da) \quad (1)$$

Where m_a is the mass of the water *per unit length* of fish and w is the velocity of the segment normal to the longitudinal midline at that segment. The mass of accelerated

water is called the added mass because the propulsive force accelerates both the body mass and a mass of surrounding water. The total thrust due to acceleration reaction, T_a , is the sum of the thrust components for each propulsive segment, or for segments of infinitely small length (Weihs, 1972, 1973; Frith & Blake, 1991),

$$T_a = \frac{d}{dt} \int_0^1 m_a w \sin \theta da \quad (2)$$

where θ is the angle between the tangent of the midline at the segment and the forward direction of the fish.

The mass of water accelerated by a propulsive segment is proportional to the depth of the segment. Lighthill (1970, 1971) has expressed this as

$$m_a = \frac{\pi}{4} \rho d^2 \beta \quad (3)$$

where ρ is the density of the water, d is the depth of the segment, and β is a coefficient that is a function of the shape of the propulsive segment. Equations 2 and 3 indicate that thrust is a function of the velocity of the laterally moving segment, the orientation of the segment relative to the direction of movement of the fish and the depth of the segment, which may include a contribution from both the body and fins. Based on kinematic comparisons, Webb (1977, 1978, 1982b, Webb & Blake, 1985) has emphasized that thrust is maximized when the greatest depth is distributed in the caudal region. This follows from the observation that not all propulsive segments contribute equally to thrust. The normal velocity component, w , of a propulsive segment increases posteriorly due to the larger displacement of more caudal segments. In addition, the direction of the resultant force is aligned more in the direction of the forward motion of the fish for the caudal segments. Experimental evidence is consistent with the hypothesis that the caudal segments contribute a larger proportion to thrust (Webb, 1977; Frith & Blake, 1991).

Caudal depth may be increased by increasing body depth caudally, by moving the median fins caudally, or, if the median fins are in a caudal position, by increasing median fin area. The consequences of increasing caudal depth by increasing body depth or by increasing dorsal and anal fin area are not functionally equivalent. Because inertial resistance to acceleration is proportional to body mass, selection should favor profiles with large caudal depth but little body mass. Weihs (1989) demonstrates this point simply but elegantly by modelling the energy required to move a fish as

$$E = E_f + E_a = \frac{1}{2} M_f U^2 + \frac{1}{2} M_a U^2 \quad (4)$$

where E_f is the energy to move the mass of fish, E_a is the energy to move the total added mass of water, and U is the velocity of the fish. A fish works to move both its own mass, M_f , and the added mass of water summed for all segments, M_a , but the energy transferred to move the fish is proportional only to the summed added mass of water. The hydrodynamic (Froude) efficiency, η , is

$$\eta = \frac{E_a}{E} = \frac{E_a}{E_f + E_a} \quad (5)$$

The contribution to hydrodynamic efficiency for any segment will be

$$\eta = \frac{ma}{m_f + m_a} \quad (6)$$

The mass of an elliptical segment of fish is

$$m_f = \frac{\pi}{2} \rho p d da \quad (7)$$

where ρ is the density of the segment, which is equal to the density of water for a neutrally buoyant fish, and d and b are the depth and breadth of the segment. Body mass is proportional to both depth and breadth (eq. 7) but thrust is proportional only to depth (eq. 3). Hydrodynamic efficiency, therefore, is proportional to d/b . Because d/b for a segment of fin is greater than d/b for a segment of the body, increasing caudal depth by moving median fins into a caudal position or by increasing the length and depth of the median fins results in greater hydrodynamic efficiency than increasing caudal body depth. Given this model, stickleback that forage in habitats with high risk of predation from vertebrate piscivores are expected to have longer and more caudally positioned median fins than those foraging in lower risk habitats.

Foraging behaviour

In general, stickleback are generalized carnivores that prey on both limnetic and littoral invertebrates (Hart & Gill, 1994). Individual populations fall on a continuum of specialization for prey type (Rogers, 1968; Lavin & McPhail, 1986; Gross & Anderson, 1984; Foster, Baker & Bell, 1992). Among lake populations, this specialization reaches an extreme in the pairs of sympatric populations found within six lakes in southwestern British Columbia (Larson, 1976; Larson & McIntire, 1993; Bentzen & McPhail, 1984; McPhail, 1984, 1992, 1993, 1994; Schluter & McPhail, 1992; Schluter, 1993). In each lake, one population feeds almost exclusively on littoral prey while the second population feeds almost exclusively, except during the breeding season, on open water prey (Schluter & McPhail, 1992). I use benthic to refer to littoral foraging behaviours and morphologies and limnetic to describe open water foraging behaviours and morphologies (Larson, 1976; McPhail, 1984).

The predation cycle can be divided into search, pursuit, attack, and capture components (O'Brien, 1979). In this study, I focus on the mechanical consequences of variation in searching behaviour, which is an important component of the predation cycle because of both the difficulty in locating prey (O'Brien, 1979) and the energetic costs of this component relative to other components (Drost & van den Boogaart, 1986). A detailed description of searching behaviour in stickleback is not available in the literature. The following description is based on laboratory and field observations by myself and others (Hart & Gill, 1994).

Variation in searching behaviour between open water and vegetated bottom is largely a function of differences in structural complexity. The benthic environment

is characterized by moderate to dense vegetation, sunken logs and branches, leaf litter and, in some lakes, gravel, cobbles and boulders. Near shore, overhanging shrubs add to structural complexity. Common benthic prey, including chironomid larvae and amphipods (Rogers, 1968; Manzer, 1976; Lavin & McPhail, 1986; Hart & Gill, 1994), prefer habitats with a high density of aquatic vegetation (Beattie, 1982; Dvorak & Best, 1982; Gregg & Rose, 1985; Cyr & Downing, 1988; Downing, 1991). It has been repeatedly demonstrated in fishes that increased structural complexity reduces foraging performance (Crowder & Cooper, 1982; Savino & Stein, 1982, 1989a,b; Stoner, 1982; Werner *et al.*, 1983 a,b; Gilinsky, 1984; Ryer, 1988; Diehl, 1988; Gotceitas & Colgan, 1989; Dionne & Folt, 1991; Heck & Crowder, 1991). Populations of stickleback colonizing lakes with extensive littoral habitat should evolve behaviours and morphologies that would increase foraging performance in structurally complex environments.

Increased manoeuvrability provides one potential mechanism to increase littoral foraging performance. Manoeuvrability is the ability to rapidly and precisely modify steady, forward locomotion and includes accelerating, braking, turning, rising, falling, and hovering behaviours (Breder, 1926). I use this more general definition rather than the more restricted definition that limits manoeuvrability to the ability to turn in confined spaces (Norberg & Rayner, 1987; Webb, 1994). In this study, I specifically focus on the functional morphology of turning manoeuvres. During routine turns, a stickleback, as do many fish, bends the body with the head oriented in the direction of the turn. Both pectoral fins are used to generate turning moments (Walker, unpublished data). With both blades broadside to the flow of water, the fin on the side of the turn is abducted, as in braking (Breder, 1926), while the contralateral fin is adducted, as in the power stroke during drag-based labriform propulsion (Blake, 1979). Clearly, the position and shape of the pectoral fins should have a great influence on turning performance.

Nevertheless, there is also good reason to expect body shape to influence turning performance. A turn is composed of both the centre of mass of the fish moving along the arc of a circle with radius, R , and the body of the fish rotating around the centre of mass. Turning performance should be inversely proportional to both R and the resistance to rotation of the body. Turning radius is a function of many parameters, including axial flexibility, turning kinematics, and body shape. The relationship between turning radius and body shape was modeled by Webb (1983). Instead of turning radius, I will use turning curvature, κ , which is the inverse of turning radius and, therefore, directly proportional to manoeuvrability. For any turn with constant radius, the centripetal force is equal to the force available for the turn.

$$m_v a_c = \frac{1}{2} \rho_w S U^2 C_T \quad (8)$$

where m_v is the virtual mass, which is the sum of the body mass plus the mass of entrained water, ρ_w is the density of water, S is the wetted surface area of the fish, U is the velocity of the moving fish, and C_T is the thrust coefficient. The mass of the body and entrained water is

$$m_v = \rho_f V_f + \rho_w V_w = \rho V \quad (9)$$

since stickleback are neutrally buoyant (i.e. $\rho_f = \rho_w = \rho$) and the virtual volume, V , is $V_f + V_w$. a_c is the centripetal acceleration of the centre of mass,

$$ac = \frac{U^2}{R} = \kappa U^2 \quad (10)$$

where R is the radius of the turn. Substituting equations 9 and 10 into 8, we have

$$\rho V \kappa U^2 = \frac{1}{2} \rho S U^2 C_T \quad (11)$$

Solving for turning curvature,

$$\kappa = \frac{1}{2} \frac{S}{V} C_T \quad (12)$$

Turning curvature is proportional to the ratio of surface area to body (and entrained water) volume, S/V . For equal size fish, S/V , and thus, κ , is proportional to d/b . Fish with deep, laterally compressed bodies (highly elliptic in transverse section) and long median fins should have greater turning curvature, and, thus, manoeuvrability, than fish with shallow, broad bodies (circular transverse sections) with short median fins.

Both viscous (Alexander, 1967a) and inertial forces resist the rotation of the body during a turn. Because viscous forces are proportional to the velocity squared, inertial forces may be more important during foraging-related turns because of the low average velocities. The inertial resistance is

$$\Gamma = I\alpha \quad (13)$$

where I , the moment of inertia about the rotational axis, is

$$I = \Sigma(mr^2) \quad (14)$$

m is the mass of a small volume of the fish body (and entrained water) and r is the distance of the volume of mass to the axis of rotation. Inertial resistance to rotation is, therefore, a function of the distribution of virtual mass around the rotational axis. Keeping mass constant, I , inertial resistance to rotation, increases from fish with short, deep bodies to fish with elongated, shallow bodies. Given equations 12–14, stickleback with truncated, deep bodies are expected to have greater manoeuvrability, and, thus, littoral foraging performance, than those with elongate, shallow bodies.

The limnetic zone presents a very different searching environment than the benthic zone. The open water of the limnetic zone is largely free of structure, although some aquatic plants consist of columnar stems that extend through the limnetic zone. Near shore, large fallen trees can create complex but ephemeral structure. Wind, predation, and other agents produce a spatially heterogeneous distribution of zooplankton (Colebrook, 1959; George & Edwards, 1976; Kerfoot, 1980; Jakobsen & Johnsen, 1987; Pinel-Alloul *et al.*, 1988; Downing, 1991; Folt & Schultze, 1993), the preferred prey in open water (Hynes, 1950; Rogers, 1968; Manzer, 1976; Campbell, 1991). For this study, I assume that stickleback foraging in the open water swim at steady velocities, or cruise, for much longer periods of time than those foraging in the littoral zone. This would occur, for example, if

stickleback swim long distances in search of profitable patches of prey. Qualitative field observations (pers. observ.) are consistent with this assumption.

Flume studies (Taylor & McPhail, 1986; Whoriskey & Wootton, 1987; Stevens, 1993) and observations in the wild (pers. observ.) indicate that stickleback employ a pectoral fin, or labriform (Breder, 1926), propulsive mechanism for cruising in the open water. The body and caudal fin remain rigid. The median fins and, on occasion, the caudal fin, are collapsed (pers. observ.). Thrust is generated by the synchronous rowing of the pectoral fins. Both pressure and skin-friction drag resist motion and the magnitude of this resistance is highly dependent on body shape (Webb, 1975b; Blake, 1983; Vogel, 1994). A flat, circular body is referred to as a bluff body while a body characterized by an anteriorly positioned maximum depth, or shoulder, and an elongated, tapering caudal region is referred to as a streamlined body (von Mises, 1945) (Fig. 1). Water flowing around a fish cannot follow the contour of the body precisely but, instead, separates from the body creating a pressure difference between the anterior and posterior regions of the fish. In bluff bodies, the point of separation is relatively anterior, leaving a large region of low pressure. In contrast, the point of separation in streamlined bodies is relatively posterior, resulting in only a small region of low pressure.

Skin friction drag results from water sticking to the moving fish. Quantitatively, this is expressed by (Vogel, 1994),

$$D = \frac{1}{2} \rho S U^2 C_d \quad (15)$$

where S is the wetted surface area of the fish body and fins (which will depend on the degree of erection of the fins) and C_d is a drag coefficient. For constant length and volume, a shallow fish with a round cross section will incur less frictional drag during steady labriform propulsion than a deep fish with a highly elliptic cross section. Minimization of pressure and skin-friction drag leads to the expectation that limnetic foraging stickleback should have more elongate, shallow, and streamlined bodies than benthic foraging stickleback (Fig. 1).

Ecomorphological model

Two environmental variables, Predator State (PS) and Relative Littoral Area (RLA) are modelled to have effects on the evolutionary history of evasive and foraging morphology in stickleback (Fig. 2). PS, which is based on the presence or absence of predatory fishes, should have a direct effect on evasive morphology if predatory fish have higher capture success when striking fish with less evasive body shapes and an indirect effect on foraging morphology if the presence of predatory fish causes a shift in foraging-habitat use. RLA should have a direct effect on foraging morphology if the distribution of prey types is associated with lake habitat and stickleback prefer the most available prey type. Additionally, RLA might have an indirect effect on evasive morphology if different foraging habitats within a lake are associated with different risks of predation from predatory fish.

METHODS

Samples and measurements

Stickleback samples were collected from 40 lakes in the Mat-Su Valley and the Kenai Peninsula, Alaska between 1990 and 1994 (Table 1). Collections were made

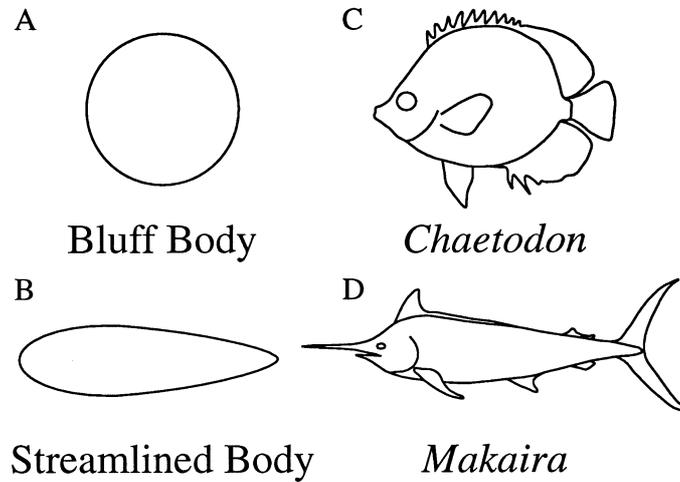


Figure 1. Shape of idealized (A) bluff body and (B) streamlined profiles. Natural analogues of engineering shapes: (C) *Chaetodon*, with a bluff body profile and (D) *Makaira*, with a streamlined profile.

during the breeding season, when reproductive males nest near shore, using both minnow traps and dip nets. Minnow traps were either baited with Cheddar cheese (1990) or unbaited (1992–1994) and placed on the bottom 1–3 m off shore at depths of 0.5–2 m. Dip nets were used while diving. Fish were anaesthetized in ms-222, fixed in buffered 10% formalin, stained in Alizarin Red-S, and stored in 50% isopropyl alcohol. Samples were sorted by sex and a rough estimate (by eye) of length and only the largest, sexually mature males in each sample were measured. This removed variation due to sex and reduced variation due to ontogeny. Minimizing ontogenetic variation by measuring only a common ontogenetic stage among groups imposes a non-statistical method to control ontogenetic variation. Regardless, body shape allometry is small following sexual maturity (Walker, 1993) and not expected to effect the results of this study. Sample sizes vary among lakes (Table 1) and a total of 870 fish was measured.

The lakes sampled were chosen to maximize variation in RLA and PS. In addition, to minimize potentially confounding, historical effects, including common ancestry and geneflow, on body shape, stickleback from lakes with similar environmental characteristics were sampled from separate drainages.

RLA is a measure of the proportion of littoral foraging habitat within a lake and

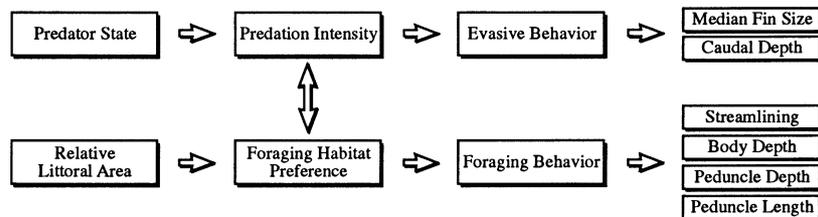


Figure 2. Path model of expected relationships between Predator State and Relative Littoral Area on foraging and evasive behaviour and body shape traits.

TABLE 1. Lake data. Kenai = Kenai Peninsula, Mat-Su = Matanuska-Susitna valley, NPF = native predatory fish, RLA = relative littoral area, Rakers = mean gill raker count

Lake	<i>n</i>	Region	NPF	RLA	Rakers
Hidden	20	Kenai	present	14.996	20.55
Weed	18	Kenai	present	20.347	20.39
Lower Ohmer	50	Kenai	present	23.371	21.56
Price	20	Kenai	present	23.855	20.65
Beck	20	Kenai	present	29.797	20.00
Stormy	20	Kenai	present	32.737	20.35
Watson	20	Kenai	present	47.091	19.75
Parsons	20	Kenai	present	80.282	19.25
Engineer	20	Kenai	present	90.649	20.25
Duck	20	Kenai	present	100	18.55
Headquarters	20	Kenai	present	100	21.15
Upper Cohoe	20	Kenai	present	100	20.05
Music	20	Kenai	absent	24.203	19.60
Nowack	15	Kenai	absent	26.084	19.80
Bruce	20	Kenai	absent	74.553	19.40
Douglas	20	Kenai	absent	91.04	21.10
Arness	22	Kenai	absent	92.066	18.77
Denise	16	Kenai	absent	95.967	20.56
Bottenintnin	20	Kenai	absent	96.489	20.30
Kalifonsky	20	Kenai	absent	100	20.75
Suneva	10	Kenai	absent	100	19.00
Whisper	20	Kenai	absent	100	19.50
Beaverhouse	20	Mat-Su	present	15.623	21.30
Lynda	20	Mat-Su	present	24.172	20.70
Long	20	Mat-Su	present	30.211	21.90
Wasilla	20	Mat-Su	present	32.551	19.90
Lazy	20	Mat-Su	present	43.609	21.55
Corcoran	20	Mat-Su	present	100	20.45
Kashwitna	20	Mat-Su	present	100	20.85
Mud	60	Mat-Su	present	100	17.97
Little Beaver	10	Mat-Su	absent	24.147	21.50
Vera	10	Mat-Su	absent	46.609	21.40
Kalmbach	20	Mat-Su	absent	48.047	21.70
Zero	20	Mat-Su	absent	51	22.60
Farmer	20	Mat-Su	absent	69.706	21.80
Lorraine	20	Mat-Su	absent	85.223	22.35
Visnaw	54	Mat-Su	absent	95.215	23.20
Diamond	20	Mat-Su	absent	96.831	21.30
Sharon	20	Mat-Su	absent	100	20.40
Weinee	25	Mat-Su	absent	100	18.20

is estimated as the percentage of lake surface area in which the depth of the bottom is less than the euphotic zone depth (EZD). EZD was estimated from the linear regression of EZD on lake water colour reported by Koenings *et al.* (1987). Lake perimeters and approximate contours of estimated euphotic zone depth were digitized from bathymetric maps (obtained from the Sport Fish Division of the Alaska Department of Fish and Game) using MorphoSys (Meacham & Duncan, 1990). This measure assumes that the relative proportion of habitat with complex structure is associated with the proportion of lake area above EZD. I use *shallow* to refer to lakes with high RLA and *deep* to refer to lakes with low RLA.

PS is a measure of variation in the intensity of predation from gape-limited predators and is estimated simply as the presence or absence of predatory fishes that are native to the lake (Bell *et al.*, 1993). These data were obtained from the

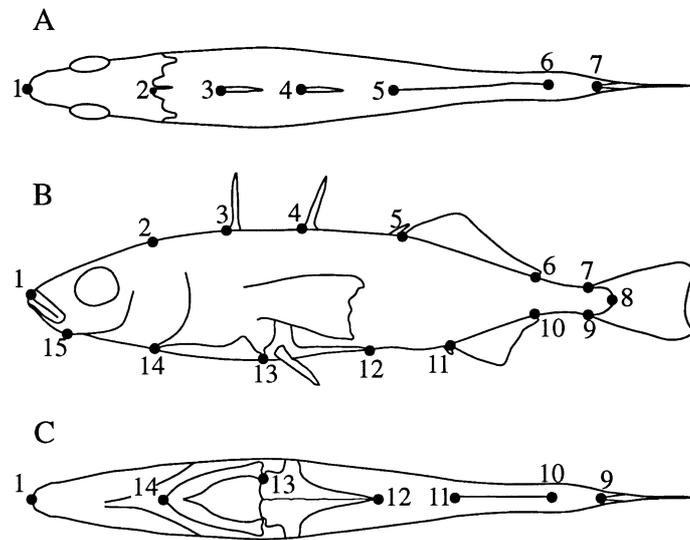


Figure 3. Location of 15 anatomical landmarks in (A) dorsal view, (B) lateral view and (C) ventral view.

Sport Fish Division of the Alaska Department of Fish and Game. As a measure of predation regime, PS ignores variation in the density and taxonomic diversity of native predatory fishes (NPF). It also ignores avian piscivores altogether, which can be a highly significant component of predation on threespine stickleback (Reimchen, 1980, 1994). Use of PS assumes that the evolution of evasive performance is largely a function of differences in the long term risk of predation among lakes and only marginally a function of differences in the taxonomic diversity of predators among lakes. The many studies that have found differences in anti-predator behaviours among stickleback sampled from high predation risk sites and low predation risk sites, regardless of taxonomic differences among the predators, support this assumption (Huntingford, 1982; Huntingford & Giles, 1987; Huntingford *et al.*, 1994; Giles, 1984; Giles & Huntingford, 1984; Tulley & Huntingford, 1987a,b).

Fifteen landmarks that describe the shape of the stickleback in left lateral view were digitized in two dimensions using a video camera and MorphoSys software (Meacham & Duncan, 1990). The landmarks digitized are (Fig. 3): (1) anterior tip of upper lip; (2) supraoccipital notch immediately lateral to the dorsal midline (DML); (3) anterior junction of first dorsal spine with the DML; (4) anterior junction of the second dorsal spine with the DML; (5) base of the first dorsal fin ray at the DML; (6) insertion of the dorsal fin membrane on the DML; (7) origin of caudal fin membrane on the DML; (8) caudal border of hypural plate at lateral midline; (9) origin of caudal fin membrane on ventral midline (VML); (10) insertion of anal fin membrane on VML; (11) base of first anal fin ray on VML; (12) caudal tip of posterior process of pelvic girdle on VML; (13) posterior tip of ectocoracoid; (14) anterior border of ectocoracoid on VML and (15) posterior edge of angular. In addition to the morphometric landmarks, the number of gill rakers on the first right branchial arch were counted.

Following Goodall (1991), I refer to the configuration of landmarks for a specimen

as a figure. Figures were superimposed within samples using a slight modification of the generalized orthogonal resistant fit superimposition (Rohlf & Slice, 1990; see also Siegel, 1982; Siegel & Benson, 1982; Olshan, Siegel & Swindler, 1982). A superimposition analysis estimates and removes both non-biological variation due to the arbitrary placement and orientation of the specimens in the video field and geometric size variation. In my modified version, I used the mean and not the median figure to estimate the consensus because exploration of the scatter of transformed coordinate values did not reveal outliers and distributions were approximately normal.

Some of the figures had missing data due to either the absence of the first dorsal spine or the pelvis. For these figures, the superimposition parameters were estimated only from the set of landmarks present. The set of 40 sample mean figures, computed from the mean coordinates within samples, were superimposed using the generalized orthogonal resistant fit. For convenience, the superimposed sample mean figures were rotated by the angle that aligned landmarks 1 and 8 of the grand mean figure in a horizontal orientation. This final rotation did not modify the orientation of the sample mean figures relative to each other. The 30 coordinates (one x and y pair for each of the 15 landmarks) transformed by this nested superimposition procedure are the shape variables for this study.

Methods using the decomposition of the thin-plate spline were not used because these require separate analyses of affine and non-affine shape variation (see Walker, 1996). Superimposition methods have been criticized on the grounds that many criteria of fit are available (Lele, 1991). While the different methods can produce uncomfortably different results when figures have few landmarks (Siegel & Benson, 1982; Rohlf & Slice, 1990), results become increasingly similar with more landmarks (Slice, 1993). In an exploratory analysis of a subset of these data, results obtained by different superimposition methods were remarkably similar (Walker, 1996).

Effects of size

Correlations between size and shape among samples may reflect mechanical or physiological constraints (e.g. McMahan, 1975; Schmidt-Nielson, 1984; Calder, 1984) or a common environmental factor (Calder, 1984). I use least squares regression to investigate the relationship between sample mean size and shape (Walker, 1993) using median size (Rohlf & Slice, 1990) as the estimate of geometric size. Centroid size (Bookstein *et al.*, 1985; Bookstein, 1991) could not be compared among figures because this estimate is a function of the number of landmarks and three of the samples had figures with a single missing landmark. For these data, the choice of size measure is less important than the method of scaling (isometrically or allometrically): for the 818 figures without missing landmarks, the correlation between median size and both centroid size and standard length is 0.99.

Univariate effects of predator state, relative littoral area and their interaction

Both parametric and non-parametric tests were performed to estimate the effects of PS, RLA and their interaction, on sample mean shapes (i.e. configurations of transformed coordinates), gill raker count, and median size. For the parametric

analysis, I used ANCOVA (Sokal & Rohlf, 1994), with PS as a fixed effect and RLA as a covariate.

For the non-parametric analysis, least squares regressions of the transformed coordinates on RLA were computed for each level of PS separately. Although a reduced major axis regression may have been warranted given the error in RLA (Ricker, 1984; Rayner, 1985; McArdle, 1988; Sokal & Rohlf, 1994), a least squares regression was used because this model provides the best estimate of the expected coordinate value for a given RLA. The slope of the regression line reflects an RLA effect while the differences in elevation, or expected \mathcal{Y} , reflects a PS effect. The effect of RLA was investigated using a nested bootstrap (described below) to calculate 95% confidence intervals of the the correlation coefficient. With a significant interaction effect, the effects of PS will depend on the level of RLA. To investigate the effects of PS at extreme levels of RLA, I computed the expected value of the transformed coordinates at $RLA=0$ and $RLA=100$ for both levels of PS based on the least squares regression and used the difference between these expected values, $\hat{Y}_{NPF \text{ absent}} - \hat{Y}_{NPF \text{ present}}$, as the test statistic. The nested bootstrap was used to estimate the 95% confidence intervals of this statistic.

Multivariate effects of predator state

Both parametric and permutation tests were used to estimate the statistical significance of multivariate shape differences between the two levels of PS. Goodall (1991) developed a two-sample test based on Procrustes distance, D_p ,

$$D_p = [(\mathbf{y}_1 - \bar{\mathbf{y}}_2)(\mathbf{y}_1 - \bar{\mathbf{y}}_2)]^{1/2} \quad (16)$$

where \mathbf{y}_j is a vector of length pk of the coordinates of the mean shape for the j th group, p is the number of landmarks and k is the number of dimensions. Procrustes distance between group mean shapes is equivalent to the Euclidean distance between the group centroids in a pk dimensional space and therefore, both homogenous and uncorrelated variation among the coordinates within groups are assumptions of Goodall's two-sample test (Goodall, 1991). Because variation among the coordinates is neither homogenous nor uncorrelated within groups, an F statistic based on the generalized Mahalanobis distance, D_g , was used in place of the F statistic based on Procrustes distance

$$F_{[k(p-2), n_1 + n_2 - k(p-2) - 1]} = \left\{ \frac{n_1 + n_2 - k(p-2)}{(n_1 + n_2 - 2)k(p-2)} \right\} T_g^2 \quad (17)$$

where

$$T_g^2 = \left(\frac{n_1 n_2}{n_1 + n_2} \right) D_g^2 \quad (18)$$

and n_1 and n_2 are the number of mean figures in groups 1 and 2, respectively. The computation of the F statistic and the numerator and denominator degrees of

freedom are adjusted for the degrees of freedom lost due to the translation, rotation, and scaling, of the original figures (i.e. there are $k \times 2$ fewer degrees of freedom of shape variation than number of shape variables).

The traditional Mahalanobis distance, D , computed using the inverse of the pooled within group covariance matrix, \mathbf{W}^{-1} ,

$$D = [(\mathbf{y}_1 - \mathbf{y}_2)^t \mathbf{W}^{-1} (\mathbf{y}_1 - \mathbf{y}_2)]^{1/2} \quad (19)$$

is simply the Euclidean distance between the group centroids in a space that has deformed the within group variation to have homogenous and uncorrelated variation among the variables. The generalized Mahalanobis distance, D_g , was employed to avoid potential complications of a singular within group covariance matrix due to the reduced degrees of shape variation relative to number of shape variables. D_g is the simple absolute difference between sample mean shapes in the subspace defined by the first canonical vector computed using a two-stage principal component analysis (Rempe & Weber, 1972; Campbell & Atchley, 1981).

For the permutation tests, the Procrustes distance between group mean shape was used as the test statistic. To estimate the significance of D_p , group membership between the two groups was randomly permuted 99 999 times, each time recalculating a new Procrustes distance, D_p^* from the pseudosample. The probability for this test is calculated as $(k + 1) \div (100\ 000)$, where k is the number of D_p^* greater than or equal to D_p . This test compares the Procrustes distance resulting from the observed assignment of figures to the two groups with the distribution of distances resulting from a random assignment of figures to the two groups.

To infer the pattern of shape differences between stickleback inhabiting lakes with and without native predatory fish, the raw canonical coefficients from the computation of D_g were rescaled to equal the correlation between the first canonical vector scores and the original coordinates for the 40 cases (the total variation structure coefficients). Ninety percent confidence intervals for the structure coefficients were computed using the nested bootstrap procedure described below.

Nested bootstrap procedure

In this analysis of sample means, sampling error is a function of both the individuals measured within samples and the lakes sampled from the Cook Inlet region. To include both these sources of error in the estimate of confidence intervals, both lakes and individual figures were resampled in a nested fashion. This procedure involved (1) randomly sampling, with replacement, one of the lakes from one level of PS; (2) randomly sampling, with replacement, n individual figures from this lake, where n is the original sample size of the lake; (3) repeating steps 1 and 2 until N_j pseudosamples were generated, where N_j is the number of samples in the j th level of PS, and (4) repeating steps 1 through 3 for the second level of PS. This nested bootstrap maintained the original number of samples within both levels of PS ($n = 20$) and the original number of specimens within samples (Table 1) but the total number of figures differed from iteration to iteration.

Figures in each pseudosample were superimposed with the generalized orthogonal resistant fit. The two sets of pseudosample mean figures were computed, combined into a single data set superimposed using the generalized orthogonal resistant fit

and rotated into a horizontal orientation as per the original data set. The desired tests statistic(s) were computed on this new set of data. The nested resampling scheme was repeated 999 times, which, including the original analysis, resulted in 1000 estimates of each statistic. Confidence intervals were estimated using the appropriate percentiles of the generated distribution.

Effects of history

If both morphometric and environmental variation are correlated with geography (spatial autocorrelation), then correlations between shape and environment may reflect history and not independent adaptation. Spatial autocorrelation is common in ecological data sets (Sokal & Oden, 1978a, b; Legendre, 1993) and could arise in the morphometric data as a result of an isolation-by-distance process of population differentiation or increased geneflow among neighbouring populations. I attempted to minimize spurious effects of history by sampling lakes that have similar environments from geographically distinct regions. Nevertheless, to remove the influence of phylogeny on the correlations between morphometric and environmental variation, I used the Smouse-Long-Sokal test (Smouse, Long & Sokal, 1986).

For the relationship between body shape and PS, scores from the CVA were used to construct an anti-predator morphological distance matrix, M_{pred} with each element equal to the absolute value of the difference between the corresponding CVA scores. For the relationship between body shape and RLA, I used only the cases within the subset of lakes with NPF, since there was no effect of RLA on body shape among lakes without NPF. I used principal component analysis of the 24 coordinates with significant RLA effects to construct a single variable, the first principal component, that has a high correlation with RLA. With this variable, I constructed a foraging morphological distance matrix, M_{for} , with each element equal to the absolute value of the difference between the corresponding PC I scores.

Two environmental (E) and two geographic (G) distance matrices were constructed. E_{PS} was constructed by assigning 0 to elements in which PS was the same for the corresponding lakes and 1 to elements in which PS differs between the corresponding lakes. E_{RLA} was constructed by assigning each element the absolute value of the difference between RLA for the corresponding lakes. G_{birds} , the ‘as a bird flies’ matrix, was based on the great circle distances between lakes. G_{fish} , the ‘as a fish swims’ matrix, was based on the shortest distance along drainages between lakes. The matrix correlation between M and E reflects ecomorphological associations and that between M and G reflects the effects of geography on morphological similarity. To partial out the effects of G on the matrix correlation between M and E, I used the Smouse-Long-Sokal statistic (Smouse et al., 1986), which is simply the partial correlation between M and E holding G constant.

I used both Mantel’s (Mantel, 1967) asymptotic approximation test and matrix permutation tests (Mantel, 1967; Sokal, 1979; Douglas & Endler, 1983; Dietz, 1983; Manly, 1986; Cheverud, Wagner & Dow, 1989) to compute the significance of the observed matrix correlations. Right-tailed probabilities were computed because only positive correlations were expected. For the comparison between M_{pred} and E_{PS} , permuting either matrix would result in nearly 50% of the permuted matrix correlations with the same value as the observed correlation because of the binary coding of E_{PS} . For each permutation, therefore, I randomly permuted the assignment

of each case to PS and recomputed E_{PS} instead of permuting M_{pred} or E_{PS} directly. For the comparisons with foraging morphology, I randomly permuted M_{RLA} . Matrices were permuted 9999 times. The distribution of 10 000 correlations was used to compute the righthailed probability as $(k + 1) \div (10\ 000)$, where k is the number of permutation correlations greater than or equal to the observed correlation.

Graphical display of ecomorphological variation

The statistical tests produced many coefficients. In addition to reporting these in tables, I illustrate the patterns of shape change graphically. Following superimposition of multiple figures, each landmark consists of a scatter of points around a bivariate mean. Patterns of covariation between coordinates among landmarks or between coordinates and external variables (e.g. RLA) cannot be readily determined from these scatters. One of the admirable features of geometric morphometrics is that these patterns of shape variation can be illustrated using the coefficients from traditional statistical analyses. This is possible because the coefficients from both the regression and canonical variates analyses retain the geometric properties of the transformed coordinates.

The bivariate mean described previously is the expected location of the landmark in the absence of any effect. The expected location of a landmark will change, however, given different values of an effect (e.g. RLA or PS). For the regression analysis, the expected location of a landmark at a given value of some external variable, X , is found by

$$\begin{aligned}\hat{x} &= a_x + b_x X \\ \hat{y} &= a_y + b_y X\end{aligned}\tag{20}$$

(Walker, 1993). In this study, the parameters of the regression equations were found by least squares. An arrow from the expected location of a landmark at the minimum value of X to the maximum value of X reflects the path of shape change as a function of change in X (Walker, 1993). I refer to these paths from the regression analyses as regression vectors. To facilitate the interpretation of the vectors, I used the thin-plate spline (Bookstein, 1989b, 1991) to deform an outline of a stickleback to match the configuration of the landmarks of the hypothetical figure at both the minimum and maximum value of X . Both median size and RLA were used as independent variables. In the analyses with RLA as the independent variable, separate regressions were fit for both levels of PS and four hypothetical figures were generated. Differences between hypothetical figures within levels of PS but between levels of RLA reflect effects of RLA and those between levels of PS but within levels of RLA reflect effects of PS.

I also used vectors to illustrate the pattern of variation described by the structure coefficients from the canonical variates analysis, which I will refer to as CVA vectors. The raw canonical coefficients were rescaled to equal the covariance between the first canonical vector and the original coordinates. With this scaling, the coefficients corresponding to the x and y coordinates of a single landmark are the components of a resultant vector that reflects the direction and magnitude of shape difference at the landmark relative to the within sample variation of all landmarks simultaneously. The tips of the CVA vectors describe a configuration reflecting an

TABLE 2. Effects of predator state, relative littoral area and size on mean gill raker count

(a) ANCOVA						
	Effect	<i>MS</i>	<i>F</i>	<i>P</i>		
	PS	0.1258	0.0946	0.760		
	RLA	4.3868	3.2995	0.078		
	PS × RLA	0.1360	0.1023	0.751		
(b) Effect of relative littoral area						
Predator state	<i>n</i>	Slope	SE	<i>r</i>	<i>F</i>	<i>P</i>
NPF +	20	−0.013	0.006	0.461	4.8538	0.041
NPF −	20	−0.009	0.011	0.188	0.6572	0.428
(c) Effect of size						
	<i>n</i>	Slope	SE	<i>r</i>	<i>F</i>	<i>P</i>
	40	0.211	0.1027	0.3161	4.219	0.0469

extreme hypothetical shape at one pole of the canonical vector. By multiplying each coefficient by -1 , the tips of the CVA vectors describe the geometrically opposite shape.

Miscellany

The great number of statistical tests and computations of confidence intervals substantially increase type I error rates. The traditional remedy for this situation is to apply a Bonferroni adjustment to the observed probabilities to reflect the number of tests (Sokal & Rohlf, 1994; Rice, 1989). I have chosen not to adjust the P values for two reasons. First, what is the proper divisor for the adjustment, the number of tests in a single table, or, the number of tests in the paper, or, the number of tests that I used to explore the data, some of which are reported in other manuscripts? Second, Bonferroni adjustments are appropriate for multiple independent tests. The shape changes observed here are highly correlated and, as a consequence, even sequential Bonferroni methods are too conservative.

Finally, the superimposition, regression, canonical variates, Mantel and principal component analyses were performed on a Sun SPARCserver 1000. I used JMP 3.1 (SAS, inc.) to compute the ANOVAs and ANCOVAs.

RESULTS

There is moderate variation in size among the samples in this study, sample mean standard length (SL) ranges from 42.4 to 64.6 mm. RLA has no effect on median size (NPF present: slope = -0.0126 , $F=0.9494$, $P=0.3428$, NPF absent: slope = -0.001814 , $F=0.0273$, $P=0.8706$). Stickleback in lakes with NPF are, on average, slightly larger than those from lakes without NPF ($F=4.2786$, $P=0.0454$): the average median size of fish in the largest size class is 19.7 for lakes with NPF and 18.6 for lakes without NPF, corresponding to 52.65 mm and 49.43 mm SL, respectively.

An ANOVA with mean gill raker count as the response variable and PS and RLA as the main effects suggests a RLA effect but no PS effect (Table 2). The separate regressions of mean gill raker count on RLA within each level of PS, however, indicates the RLA effect is present only in the subset of lakes with NPF (Table 2). The interaction term of the two-way ANOVA is not significant, indicating

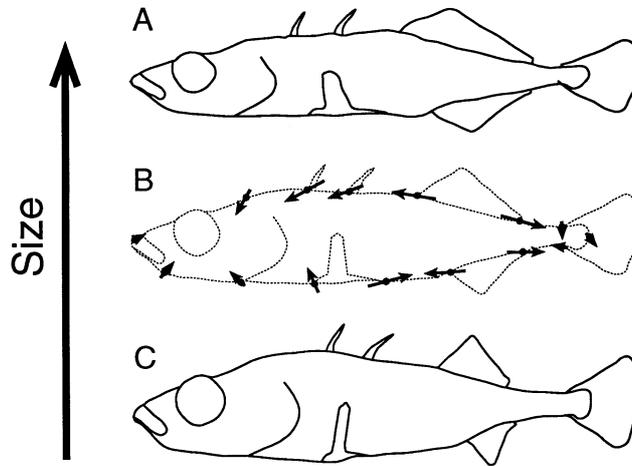


Figure 4. Regression vectors based on least squares regression of transformed coordinates on median size. The magnitude of the vectors in (B) has been increased four-fold. The bottom panel (C) illustrates the expected shape of a small fish while the top panel (A) illustrates the expected shape of a large fish.

that the slopes of the separate regression may not differ, but the error of the slope estimate in the subset of lakes without NPF is nearly twice the error in the subset with NPF (Table 2). This suggests that similarity of slopes may simply be a sampling artifact.

Interpopulation allometry is present among the Cook Inlet samples. Mean gill raker count is positively correlated with body size among samples (Table 2). The direction of shape change with increasing size is indicated by the arrows in Figure 4. The dorsal spines (x3, x4) are more anterior and both the dorsal (X5, X6) and anal fins (X10, X11) are longer in larger fish (Fig. 4, Table 3).

The scatterplots of the transformed coordinate values on RLA illustrate effects of RLA, effects of PS and interaction effects (Fig. 5). The ANCOVAs (Table 4) indicate effects of RLA on body shape but the confidence intervals of the correlation coefficients (Table 5) indicate that this effect occurs only among stickleback from lakes with NPF. In the subset of lakes without NPF, confidence intervals bound zero for each coordinate of every landmark. The many significant interaction effects between PS and RLA on body shape (Table 4, 5) reflect this lack of association between RLA and body shape in lakes without NPF. The ANCOVAs (Table 4), univariate distance statistics (Table 5), Hotelling's T^2 tests ($D_g = 7.526$, $T^2 = 566.407$, $F = 7.4527$, $P = 0.00025$) and non-parametric multivariate tests ($k = 0$, $P \leq 0.00001$) indicate effects of PS on body shape. Consistent results were obtained between univariate and multivariate tests and between parametric and non-parametric tests.

The pattern of regression vectors for both levels of PS are illustrated in Figure 6. The direction of the arrows indicates shape differences that occur with increasing RLA. Confidence intervals of the correlation coefficients between all transformed coordinates and RLA cover zero for the subset of lakes without NPF (Table 5) and the pattern of the vectors will not be discussed. The multiple effects of RLA on head, body, and fin shape among the lakes with NPF are highlighted with hypothetical extreme figures (Fig. 6b) based on the univariate regression coefficients.

The relative position of the tip of the snout (X1) is relatively invariant, but the

TABLE 3. Regression statistics and 95% bootstrap confidence intervals for regression analyses of coordinates on median size

	n	F	P	Pearson's ρ		n	F	P	Pearson's ρ
x1	40	0.15	0.442 0.7005 -0.334	0.063	x9	40	0.05	0.287 0.8311 -0.339	-0.035
y1	40	0.07	0.359 0.7883 -0.231	0.044	y9	40	0.11	0.293 0.7443 -0.278	-0.053
x2	40	2.70	0.058 0.1087 -0.511	-0.257	x10	40	22.20	0.757 0.0000 0.368	0.607
y2	40	4.98	0.002 0.0316 -0.556	-0.340	y10	40	0.00	0.414 0.9835 -0.279	0.003
x3	39	3.58	0.031 0.0667 -0.586	-0.301	x11	40	6.23	-0.138 0.0170 -0.583	-0.375
y3	39	2.99	-0.003 0.0923 -0.517	-0.277	y11	40	0.12	0.300 0.7364 -0.336	-0.055
x4	40	5.83	-0.028 0.0207 -0.615	-0.365	x12	39	1.30	0.484 0.2607 -0.149	0.185
y4	40	0.74	0.109 0.3936 -0.428	-0.139	y12	39	0.68	0.412 0.4153 -0.121	0.134
x5	40	8.76	-0.184 0.0053 -0.626	-0.433	x13	39	1.54	0.165 0.2219 -0.499	-0.197
y5	40	0.39	0.344 0.5361 -0.164	0.101	y13	39	3.51	0.553 0.0687 0.008	0.291
x6	40	20.48	0.764 0.0001 0.348	0.592	x14	40	0.86	0.225 0.3604 -0.444	-0.149
y6	40	8.07	-0.079 0.0072 -0.600	-0.418	y14	40	1.97	0.510 0.1686 -0.108	0.222
x7	40	0.01	0.323 0.9405 -0.292	0.012	x15	40	0.53	0.461 0.4691 -0.275	0.118
y7	40	5.39	-0.026 0.0258 -0.546	-0.352	y15	40	1.37	0.493 0.2498 -0.125	0.186
x8	40	0.24	0.401 0.6277 -0.224	0.079					
y8	40	3.45	0.022 0.0708 -0.484	-0.289					

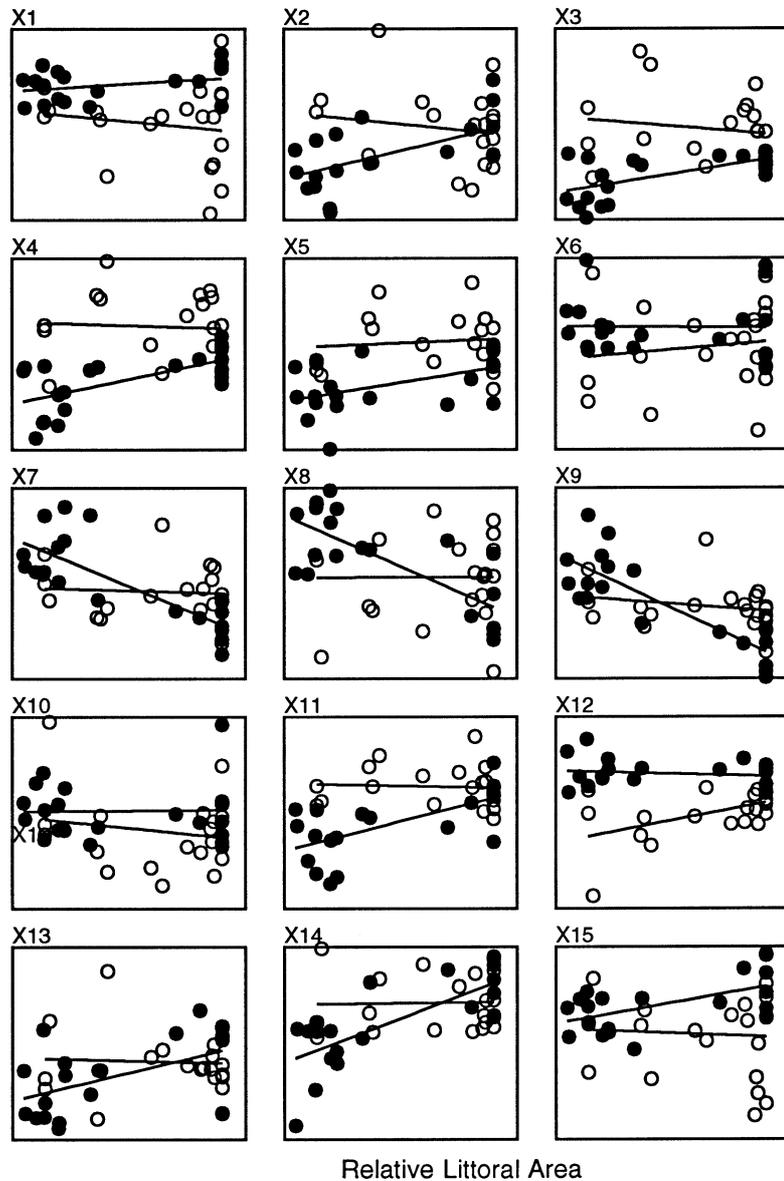
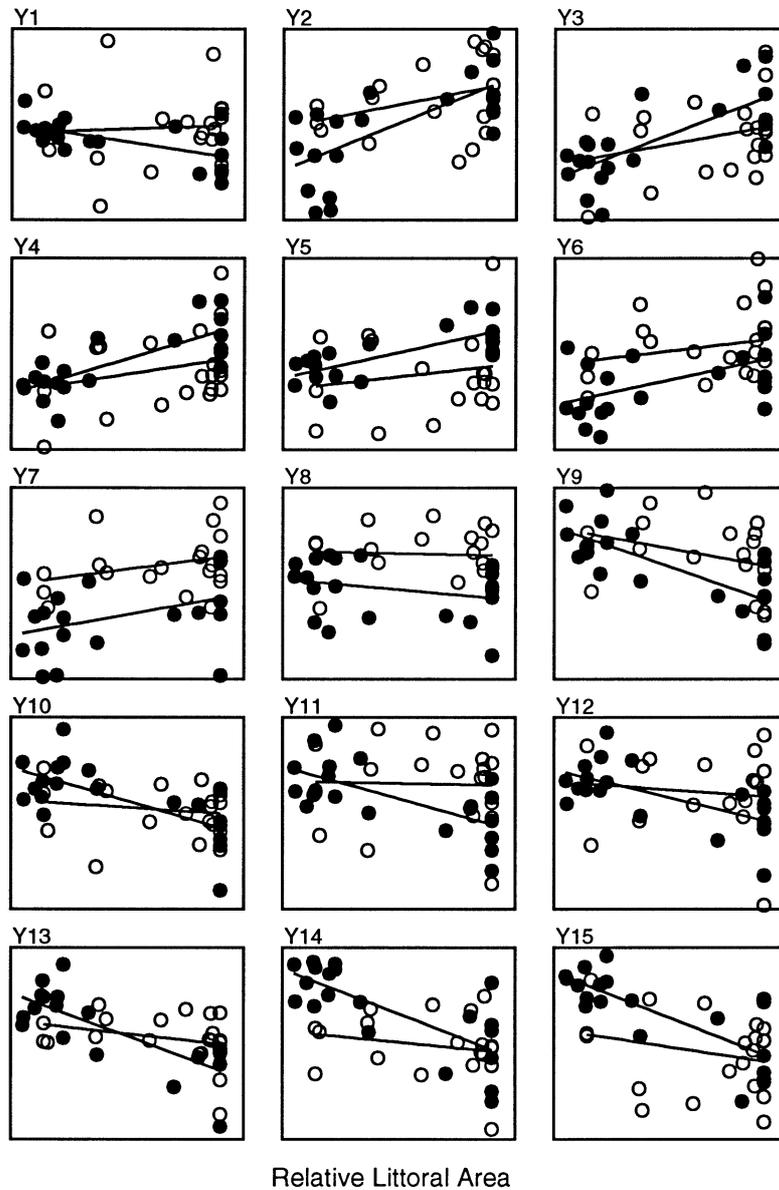


Figure 5. Scatterplots and least squares regressions of x (this page) and y (facing page) coordinates for the 15 landmarks on RLA. The scatter is grouped by PS. Native predatory fish present (●), absent (○).

position of the angular (X15) moves posteriorly with increasing RLA, indicating longer jaws in shallow lakes. The dominant pattern of the regression vectors indicates that depth increases along the length of the head and body (Y5, Y6, Y9, Y10, Y11) with increasing RLA. In addition, the body shortens with increasing RLA due to the relative contraction of the caudal peduncle. This contrast between short, deep body profiles in lakes with high RLA and elongate, shallow profiles in lakes with low RLA is consistent with the expected pattern given foraging habitat variation.

Figure 5.—*contd*

Contrary to expectations, depth increases uniformly along the length of the body with increasing RLA. This indicates that stickleback in lakes with low RLA do not have a more anteriorly positioned shoulder (point of maximum depth). Finally, the entire ectocoracoid (X13, X14) shifts posteriorly with increasing RLA but the anterior end shifts at a greater rate, which indicates that this bone is shortening with increasing RLA.

In addition to body shape changes, the dorsal spines (X3, X4) are positioned more

TABLE 4. Parametric statistics for ANCOVAs with RLA as covariate

	<i>n</i>	Predator state		RLA		Interaction	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
x1	40	0.43	0.5171	0.07	0.7970	1.22	0.2768
y1	40	0.30	0.5852	0.78	0.3818	1.91	0.1750
x2	40	7.80	0.0083	0.80	0.3774	4.97	0.0321
y2	40	2.86	0.0994	13.99	0.0006	1.69	0.2019
x3	39	10.83	0.0023	1.00	0.3236	2.62	0.1147
y3	39	0.88	0.3548	12.80	0.0011	2.08	0.1583
x4	40	15.29	0.0004	1.94	0.1722	3.52	0.0687
y4	40	0.04	0.8414	10.50	0.0026	1.09	0.3041
x5	40	7.05	0.0117	2.76	0.1052	0.96	0.3347
y5	40	0.14	0.7126	5.65	0.0229	0.61	0.4396
x6	40	1.42	0.2407	0.22	0.6454	0.29	0.5960
y6	40	2.58	0.1168	4.95	0.0324	0.41	0.5256
x7	40	8.03	0.0075	14.07	0.0006	10.68	0.0024
y7	40	4.44	0.042	4.74	0.0362	0.13	0.7210
x8	40	5.28	0.0275	5.88	0.0205	5.94	0.0199
y8	40	1.52	0.2256	0.80	0.3765	0.32	0.5772
x9	40	7.16	0.0112	25.77	0.0000	13.33	0.0008
y9	40	0.03	0.8561	14.09	0.0006	1.34	0.2542
x10	40	0.01	0.9358	0.37	0.5485	0.49	0.4882
y10	40	3.30	0.0774	8.83	0.0053	3.54	0.0682
x11	40	16.20	0.0003	4.94	0.0327	6.77	0.0134
y11	40	0.53	0.4696	3.37	0.0745	2.56	0.1184
x12	39	23.41	0.0000	3.13	0.0855	5.70	0.0225
y12	39	0.09	0.7627	5.11	0.0302	0.80	0.3760
x13	40	3.69	0.0628	2.11	0.1553	3.25	0.0800
y13	40	2.99	0.0921	18.33	0.0001	5.33	0.0269
x14	40	8.35	0.0065	8.75	0.0054	7.71	0.0087
y14	40	8.43	0.0063	12.57	0.0011	4.55	0.0398
x15	40	0.00	0.9903	0.78	0.3821	1.94	0.1717
y15	40	5.67	0.0227	13.05	0.0009	2.54	0.1194

posteriorly and the median fins (X5, X11) are shortened in lakes with high RLA, Median fin length was expected to have an association with predation regime. The observed association between median fin length and RLA in lakes with NPF suggests that RLA indirectly effects predation regime. This would occur if stickleback foraging in the open water face higher risk of predation from vertebrate piscivores than those foraging in the vegetated littoral zone (Reimchen, 1980; Bell & Foster, 1994b).

Effects of PS on body shape can be inferred from the expected distance statistics at $RLA = 0$ and $RLA = 100$ (Table 5), the multivariate canonical structure coefficients (Table 6) and the corresponding scatterplots (Fig. 5), regression vectors (Fig. 6) and CVA vectors (Fig. 7). The direction of the arrows in Figure 7 indicates the shape expected in lakes without NPF. Figure 7A is the expected shape of a stickleback in a lake with NPF and Figure 7C is the expected shape of a stickleback in a lake without NPF. The snout (X1, X15) is anteriorly extended and head depth (Y2, Y14) is greater in stickleback from lakes without NPF. Relative to stickleback in lakes with NPF, those from lakes without NPF have more posteriorly positioned dorsal spines (X3, X4), a more anteriorly positioned tip of the posterior pelvic process (X12), and shorter median fins (X5, X11). The absence of an effect on the position of the posterior end of the ectocoracoid (X13) indicates no effect on the position of the pelvis as a whole but, instead, an effect on the length of the posterior process.

TABLE 5. Regression statistics, with 95% bootstrapped confidence intervals, for regression analyses of coordinates on RLA. Pearson's ρ is the product moment correlation between the coordinate and RLA among lakes with (NPF+) or without (NPF-) NPF. The Expected difference is the difference between the expected coordinate value when RLA is 0 and when RLA is 100 based on a least squares regression

	Pearson's ρ		Expected difference			Pearson's ρ		Expected difference	
	NPF+	NPF-	RLA 0	RLA 100		NPF+	NPF-	RLA 0	RLA 100
x1	0.641	0.290	0.006	-0.009	y8	0.348	0.394	0.014	0.011
	0.282	-0.156	-0.008	-0.027		-0.250	-0.054	0.004	0.007
	-0.338	-0.488	-0.043	-0.043		-0.571	-0.604	-0.001	0.002
y1	0.057	0.519	0.018	0.018	x9	-0.656	0.216	-0.003	0.021
	-0.588	0.058	-0.004	0.010		-0.840	-0.224	-0.016	0.013
	-0.742	-0.438	-0.028	-0.0005		-0.903	-0.584	-0.030	0.006
x2	0.742	0.335	0.027	0.007	y9	-0.353	0.045	0.010	0.008
	0.582	-0.173	0.018	-0.001		-0.710	-0.342	-0.001	0.004
	0.129	-0.456	0.000	-0.007		-0.858	-0.691	-0.005	-0.001
y2	0.857	0.581	0.027	0.007	x10	0.428	0.435	0.021	0.002
	0.680	0.354	0.012	-0.0003		0.021	-0.172	-0.001	-0.010
	0.500	-0.003	0.003	-0.010		-0.536	-0.576	-0.029	-0.022
x3	0.835	0.526	0.097	0.038	y10	-0.362	0.355	0.003	0.007
	0.601	-0.076	0.059	0.021		-0.668	-0.166	-0.008	0.003
	0.240	-0.519	0.007	0.005		-0.831	-0.641	-0.018	-0.003
y3	0.887	0.665	0.036	0.001	x11	0.831	0.354	0.078	0.025
	0.742	0.287	0.011	-0.011		0.639	-0.064	0.054	0.007
	0.578	-0.267	-0.018	-0.026		0.308	-0.475	0.029	-0.007
x4	0.797	0.417	0.068	0.025	y11	-0.349	0.434	0.019	0.025
	0.612	-0.062	0.041	0.015		-0.633	-0.031	-0.007	0.014
	0.250	-0.534	0.013	0.005		-0.819	-0.491	-0.028	0.002
y4	0.890	0.625	0.034	-0.003	x12	0.404	0.852	-0.049	-0.025
	0.766	0.258	0.003	-0.015		-0.156	0.467	-0.137	-0.048
	0.601	-0.333	-0.028	-0.031		-0.574	-0.158	-0.263	-0.075
x5	0.753	0.528	0.066	0.034	y12	-0.353	0.373	0.027	0.030
	0.478	0.095	0.035	0.018		-0.625	-0.171	-0.004	0.012
	0.017	-0.388	0.010	0.004		-0.778	-0.605	-0.033	-0.006
y5	0.844	0.539	0.027	-0.005	x13	0.813	0.517	0.034	0.006
	0.728	0.182	-0.005	-0.018		0.501	-0.056	0.015	-0.004
	0.508	-0.367	-0.034	-0.033		0.007	-0.539	-0.005	-0.013
x6	0.466	0.640	0.017	0.010	y13	-0.616	0.093	0.002	0.026
	-0.016	0.131	-0.015	-0.006		-0.777	-0.287	-0.016	0.012
	-0.546	-0.432	-0.045	-0.021		-0.864	-0.578	-0.030	0.000
y6	0.822	0.518	0.017	0.008	x14	0.836	0.556	0.047	0.003
	0.507	0.217	0.007	0.003		0.728	0.028	0.027	-0.008
	0.197	-0.343	0.0004	-0.004		0.500	-0.404	0.003	-0.016
x7	-0.590	0.370	-0.006	0.021	y14	-0.382	0.260	-0.004	0.008
	-0.794	-0.074	-0.022	0.012		-0.733	-0.208	-0.016	0.000
	-0.886	-0.469	-0.041	0.002		-0.886	-0.566	-0.026	-0.010
y7	0.812	0.632	0.015	0.009	x15	0.761	0.451	0.019	-0.005
	0.395	0.299	0.007	0.005		0.585	-0.060	0.000	-0.021
	-0.003	-0.275	0.002	0.0005		0.080	-0.437	-0.031	-0.034
x8	-0.372	0.530	0.003	0.017	y15	-0.403	0.320	0.001	0.007
	-0.756	0.002	-0.019	0.008		-0.761	-0.258	-0.016	-0.002
	-0.853	-0.521	-0.044	-0.003		-0.884	-0.633	-0.036	-0.012

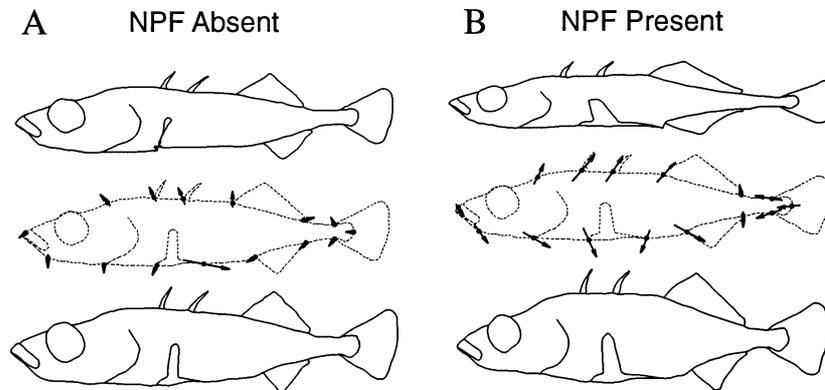


Figure 6. Regression vectors based on least squares regression of transformed coordinates on RLA. The vectors reflect the direction and relative magnitude of change in the location of the landmarks for a unit change in RLA. The vectors have been magnified five-fold to magnify the effects of RLA on body shape. (A) Native predatory fish absent. (B) Native predatory fish present. Outlines of the extreme hypothetical figures have been fit to the origins and tips of the vectors within each level of PS. The shapes of these figures represent the expected body shape for stickleback from deep lakes without native predatory fishes (A, top panel), shallow lakes without native predatory fishes (A, bottom panel), deep lakes with native predatory fishes (B, top panel) and shallow lakes with native predatory fishes (B, bottom panel).

The shorter median fins in stickleback from lakes without NPF is consistent with the ecomorphological model. Note, however, that (i) the median fins are not more caudally positioned and (ii) mid-body and caudal body depth are not greater in lakes with NPF. The effects of PS on dorsal spine and pelvic landmarks indicates an effect of predation regime on armour structure in addition to locomotor morphology.

The distance statistics in Table 5 and the corresponding regression vectors in Figure 6 also highlight interaction effects. Positive distance statistics for the x and y coordinates indicate that the expected position of the landmark is more posterior and more dorsal, respectively, in lakes without NPF. Thus, in shallow but not deep lakes, stickleback in lakes without NPF have shallower body profiles (Y4, Y5, Y11, Y13) and longer caudal peduncles (X7, X9) compared to those in lakes with NPF. In deep lakes, all stickleback have shallow, elongate profiles (Fig. 5).

Finally, the correlation between morphological and geographic distance matrices are extremely low (Table 7) and the Smouse-Long-Sokal tests indicate that spatial autocorrelation due to common ancestry or geneflow cannot account for the effects of PS and RLA on body shape (Table 7).

DISCUSSION

Isometric scaling

Size and shape are the two components of form (Bookstein, 1991; Goodall, 1991). Size refers to the scale of a figure and shape refers to the geometry of a figure that is invariant to translations, rotations, and scaling (Bookstein, 1991; Goodall, 1991). These definitions derive from our common, everyday use of size and shape. The

TABLE 6. CVA structure coefficients (c_i) with 90% confidence intervals

	c_i		c_i		c_i
x1	-0.353	x6	-0.037	x11	0.710
	-0.507		-0.221		0.555
	-0.712		-0.506		0.370
y1	0.437	y6	0.611	y11	0.446
	0.109		0.462		0.097
	-0.098		0.184		-0.121
x2	0.524	x7	0.091	x12	-0.577
	0.240		-0.123		-0.662
	0.026		-0.404		-0.802
y2	0.537	y7	0.746	y12	0.315
	0.309		0.646		-0.007
	0.097		0.423		-0.235
x3	0.752	x8	0.074	x13	0.405
	0.627		-0.196		0.081
	0.465		-0.412		-0.125
y3	0.268	y8	0.696	y13	0.191
	0.033		0.581		-0.093
	-0.272		0.327		-0.380
x4	0.775	x9	0.172	x14	0.458
	0.645		-0.027		0.234
	0.491		-0.329		0.002
y4	0.169	y9	0.383	y14	-0.194
	-0.059		0.081		-0.417
	-0.357		-0.201		-0.679
x5	0.733	x10	-0.074	x15	-0.146
	0.579		-0.287		-0.361
	0.406		-0.562		-0.597
y5	0.008	y10	0.113	y15	-0.190
	-0.208		-0.225		-0.488
	-0.525		-0.472		-0.640

shape of a photocopied image does not change if we rotate the image, or move the image around on the glass, or when we zoom in or out. I refer to this intuitive definition of size as geometric size. The resistant fit procedure used in this study scales figures with a size estimate called median size, which is the repeated-median interlandmark distance (Rohlf & Slice, 1990). Median size, like centroid size or the geometric mean (Mosimann, 1970; Darroch & Mosimann, 1985; Sampson & Siegel, 1985; Bookstein, 1989a), is a function of the measurements of an individual specimen and is an estimate of geometric size. Geometric size differs from general size, which is the factor that explains the largest portion of covariation among the variables (Wright, 1918, 1932; Bookstein *et al.*, 1985; Bookstein, 1989a). General size may have little to do with geometric size if most of the covariation is the consequence of shape differences due to sexual dimorphism, geographic variation, or any number of other factors.

The figures in this study were scaled isometrically, which, like the reduction or magnification of the photocopy machine, does not distort shape (Bookstein, 1989a). In most morphometric analyses, traits are scaled allometrically, that is, some estimate of size-correlated shape variation is removed to produce 'size-free' shape variables.

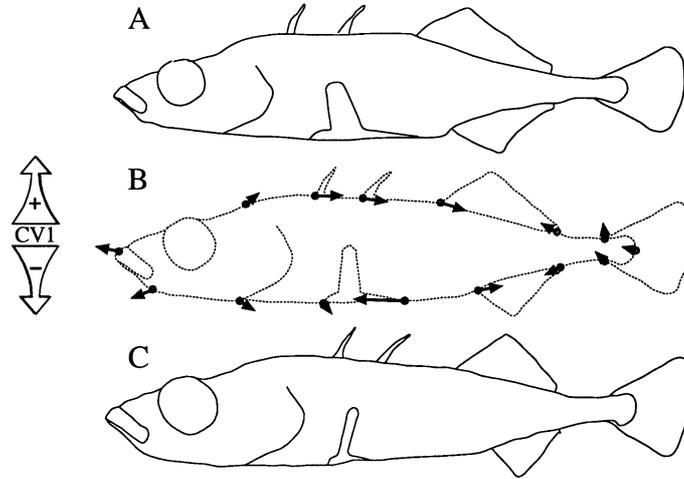


Figure 7. Hypothetical shapes based on CVA vectors. These shapes reflect the direction and relative magnitude of shape difference between stickleback from lakes with (top panel) and without (bottom panel) native predatory fishes. The vectors have been magnified five-fold.

TABLE 7. Matrix correlations and associated right-tail probabilities

	Matrix correlation	Asymptotic P	Permutation P
M_{Pred} vs.			
E_{PS}	0.320	<0.0001	<0.0001
G_{Bird}	-0.020	0.6880	0.6326
$E_{\text{PS}}, G_{\text{Bird}}$	0.320	<0.0001	<0.0001
G_{Fish}	-0.062	0.8757	0.8910
$E_{\text{PS}}, G_{\text{Fish}}$	0.328	<0.0001	<0.0001
M_{For} vs.			
E_{RLA}	0.757	<0.0001	<0.0001
G_{Bird}	0.011	0.4413	0.3462
$E_{\text{RLA}}, G_{\text{Bird}}$	0.757	<0.0001	<0.0001
G_{Fish}	-0.066	0.7965	0.8312
$E_{\text{RLA}}, G_{\text{Fish}}$	0.756	<0.0001	<0.0001

(Reist, 1985, 1986; Bookstein *et al.*, 1985). But why should size-correlated shape variation be statistically separated from ‘size-free’ shape variation? A common argument is that only residual deviation from a regression is adaptive, the regression itself reflects the passive by-product of selection for geometric size (Huxley, 1932; Gould & Lewontin, 1979; Strauss, 1984, 1990). This argument is quite paradoxical. On the one hand, quantitative genetic models indicate that a long term correlated response occurs only if the correlated trait is selectively neutral (Lande, 1979, 1986; Zeng, 1988). On the other hand, residuals from the regression line are supposed to represent adaptive variation. But if the trait is selectively neutral, the residual cannot be adaptive.

More importantly, allometric scaling can be potentially misleading by removing

ecologically important shape differences between samples. To take a hypothetical example, relative body depth and body size may be negatively correlated among fish species because of correlated selection: both a deep profile and small size enhance maneuverability in littoral environments (Webb, 1983) while both a streamlined profile and large size increase velocity and locomotor efficiency in pelagic environments (Hobson, 1991; Videler, 1993). Allometric size adjustment in this scenario would remove the ecologically relevant shape information (i.e. relative body depth).

Evolutionary allometry

Numerous ecological factors may have interacting ontogenetic and evolutionary effects on body size (Wootton, 1976, 1984, 1994; Baker, 1994; Hart, 1994; Peuhkuri *et al.*, 1995) but life history and nutritional differences among populations may confound interpretations of observed body size variation. If maximum life-span varies among populations (e.g. Baker, 1994), size variation could simply be a consequence of sampling different year classes. Size may respond to variation in lake productivity (Giles, 1987; Wootton, 1994), which can differ between benthic and limnetic habitats within a lake as well as between lakes. Nevertheless, size differences among some populations of stickleback do have a genetic component (Snyder & Dingle, 1989; Snyder, 1991; McPhail, 1993; Lavin & McPhail, 1993).

Predation regime could potentially influence body size evolution via several pathways. Two relationships are important for modeling the effects of predators on fast-start morphology. First, body size is proportional to maximum velocity attained in fast-starts (Webb, 1976; Domenici & Blake, 1993). Second, given isometric scaling of body shape and muscle mass, acceleration during fast-starts should decrease with increasing body size since mass increases with the cube of length but thrust should increase with only the square of length. Large body size, therefore, may be associated with habitats where stickleback more frequently employ a prolonged flight response than a short duration jump or sprint. In habitats with high risk of predation from gape-limited predators, size selective predation could result in the evolution of large body size (Moodie, 1972a, b; Reimchen, 1988, 1990, 1991b). On the other hand, small body size may evolve as a response to increased allocation of energy to reproductive growth relative to somatic growth (McPhail, 1977).

Variation in body size may also reflect interacting foraging effects. Small size may increase foraging performance within dense vegetation (e.g. Stoner, 1982). The cost of transport, a dimensionless variable expressing the energetic cost of transporting a unit of mass a unit distance, decreases with increasing size (Videler, 1993). Given either of these foraging effects, limnetic stickleback that swim long distances during the predation cycle should be larger than benthic stickleback that forage in dense vegetation. Alternatively, a smaller upper size limit in zooplanktivorous fish, relative to benthic fish, may reflect constraints due to picking small, individual zooplankters from the water column (for example, there is simply not enough time to search, strike and handle the amount of prey necessary to maintain large body size).

Can we infer sources of selection on body size and allometry from the pattern of body size variation among Cook Inlet stickleback? There is no measured effect of RLA on median size, suggesting a lack of a foraging habitat effect. Similarly, there are no measured effects of size on foraging related body shape traits but a small

effect on mean gill raker count. On the contrary, the positive allometry in mean gill raker count is evidence that planktivorous stickleback reach larger adult body size than benthic stickleback when NPF are present. These results differ from the pattern of body shape variation among the pairs of sympatric species of stickleback from British Columbia. In these populations, the limnetic species is invariably smaller than the sympatric benthic species (Schluter & McPhail, 1992).

In contrast to RLA, PS has an effect on mean size and there occurs significant allometry in the expression of anti-predator traits. Cook Inlet stickleback are larger in lakes with NPF, on average, than without NPF. Average adult male anadromous stickleback from Cook Inlet are larger than all means of freshwater samples in this study (Walker, unpublished data; see also Baker, 1994). The trend of a size decrease from anadromous fish to freshwater fish from lakes with NPF to freshwater fish from lakes without NPF supports a model of selective predation on smaller body size by gape-limited piscine predators (Moodie, 1972a, b; Reimchen, 1988, 1990, 1991b).

Both muscle cross-sectional area and the added mass of water accelerated during a fast start are proportional to the square of body length. Thrust is, therefore, proportional to length squared but body mass is proportional to length cubed, hence given isometric growth, absolute acceleration should decrease with increasing size. Allometry in the position of the dorsal spines and length of the median fins, then, highlights potential problems in allometrically scaling morphometric characters to investigate ecological consequences of shape variation among populations. That is, the correlation between size and shape probably reflects a history of correlated selection rather than developmentally necessary modifications in shape as a consequence of size change. Were the data in this study scaled allometrically, the effect of PS on dorsal spine position and median fin length may have disappeared.

Evolution of anti-predator design in stickleback

Stickleback from lakes with NPF have longer median fins than those from lakes without NPF. Similarly, within the subset of lakes with NPF, stickleback from deep lakes have longer median fins than those from shallow lakes. Longer median fins increase caudal depth, thus this pattern is consistent with the ecomorphological model. The PS effect suggests a direct evolutionary response in evasive morphology to variation in predation regime among lakes. The RLA effect suggests an indirect response due to predation regime differences between benthic and limnetic foraging habitats (Reimchen, 1980, 1994; Larson & McIntire, 1993; Bell & Foster, 1994b).

A comparison of median fin length between freshwater and anadromous samples, the latter representing the ancestral state (Bell, 1988; Bell & Foster, 1994b), indicates that short dorsal and anal fins are the derived states. Long median fins are associated with predatory fish in both the marine and lake habitat, which suggests that stabilizing selection has maintained the ancestral state of long median fins in stickleback from lakes with NPF. In contrast, the loss of the piscine component of predation in lakes without NPF suggests directional selection for reduced dorsal and anal fin length, although no environmental factor to drive this reduction has been identified.

Modeling expected body shapes for optimizing anti-predator performance is difficult because of the non-overlapping sets of expected morphologies for different components of the evasive and escape responses. Successful evasion during a strike

is a function of both large acceleration and high maneuverability (Howland, 1974; Weihs & Webb, 1984). Successful escape during manipulation from gape-limited predators may be a function of mid-body depth (Moody, Helland & Stein, 1983; Hobson, 1991; Bronmark & Miner, 1992), especially in the heavily armoured stickleback (Gross, 1978; Reimchen, 1983, 1988). The relative importance of these components will be dependent on the context of the predator-prey interaction. Large caudal depth is expected of acceleration specialists, large depth along the length of the body is expected of maneuvering specialists, and large mid-body depth is expected of escape specialists.

It is not clear how much a deep body profile from head to tail compromises acceleration performance (this compromise arising from the substantial increase in inertial drag with little increase in total thrust). In general, ambush predators that use high accelerations during feeding have shallow body profiles with caudally positioned median fins. The little comparative acceleration performance data is inconclusive. The highest acceleration rates during a C-start were recorded in the northern pike (*Esox lucius*) (Harper & Blake, 1990), a voracious piscivore with a typical ambush-predator design. On the other hand, the angelfish (*Pterophylum emekei*), a low-velocity maneuvering specialist, has acceleration rates similar to rainbow trout (*Oncorhynchus mykiss*), a locomotor generalist (Domenici & Blake, 1991).

The PS effect on length of median fins but not body depth suggests that large body depth compromises acceleration performance. this compromise arises from the different hydrodynamic efficiencies associated with large median fins and deep caudal bodies. the resistance due to mass (or inertial resistance) is the largest component of drag on an accelerating fish (Webb, 1982a), thus fast-start specialists should evolve a hydrodynamically efficient design for rapid accelerations. Thrust generated in a C-start is proportional to both caudal body depth and median fin length. All else being equal, however, large fins contribute less to inertial resistance than does a deep caudal body.

On the other hand, the PS effect could reflect a functional trade-off that arises from the multiple biological roles (*sensu* Bock & Von Wahlert, 1965) of stickleback locomotion. These data suggest that stickleback from deep lakes with NPF forage in the open water. Were these populations to evolve deep caudal bodies in response to selective predation, this solution would compromise open water foraging performance because of the increased skin-friction drag due to the large surface area. An effective trade-off is the evolution of a shallow body profile in combination with large median fins. Increasing median fin size is not only a hydrodynamically efficient mechanism for increasing thrust, but, because the median fins are collapsed during steady, open water swimming (pers. observ.), this increase does not add significantly to skin friction drag.

In addition to median fin length, both relative length of the posterior process of the pelvis and position of the dorsal spines are associated with PS and with RLA in lakes with NPF. The pelvis and dorsal spines are components of an extensive bony armour complex in stickleback. The major components of the complex form a complete bony ring enveloping the mid-body of the fish (Reimchen, 1983). Although the ring is composed of different bones, adjacent elements interlock, which gives the ring a rigid structure. The middle of three dorsal spines projects from the dorsal surface of this ring and two pelvic spines project laterally from the ventral surface of the ring. Of the dorsal spines, the middle spine is the most robust, while the third spine is smallest, especially in freshwater populations from Cook Inlet. A

locking mechanism keeps both the dorsal and pelvic spines erect without active input from the fish (Hoogland, Morris & Tinbergen, 1957). The posterior process of the pelvis extends posteriorly from the base of the ring and protects much of the ventral abdominal wall.

Length of the posterior process of the pelvis is an indicator of overall pelvic robustness (Banbura, Przybylski & Frankiewicz, 1989), which varies tremendously among populations (Reimchen, 1983, 1994; Bell, 1984, 1987; Bell *et al.*, 1993; Bell & Foster, 1994b). There is extensive direct and indirect evidence for selective predation on stickleback armour phenotypes (Hoogland *et al.*, 1957; Hagen & Gilbertson, 1972, 1973; Moodie, 1972b; Moodie, McPhail & Hagen, 1973; Moodie & Reimchen, 1976; Gross, 1978; Reimchen, 1988, 1992, 1994; Banbura *et al.*, 1989; Bell *et al.*, 1993). The maintenance of robust armour may carry a high metabolic cost. In low calcium lakes bony armour may be selected against because of the increased cost of allocating energy to calcium uptake and transport (Giles, 1983; Bell *et al.*, 1993; Bourgeois *et al.*, 1994). The pattern of pelvic girdle variation described in this study supports the hypothesis that pelvic girdle expression reflects a balance between selective predation from vertebrate piscivores and metabolic demands (Bell *et al.*, 1993).

The anterior position of the dorsal spines in stickleback from lakes with NPF enables the pterygiophore of the second spine to firmly articulate with the lateral plates, which, in turn, firmly articulate with the ascending process of the pelvis (and thus completing the bony ring enveloping the mid-body) (Reimchen, 1983). In weakly-armoured stickleback, this ring can be incomplete, and there is no functional reason for the second dorsal spine to maintain its position above the ascending process. Reimchen's (1991a) observation that stickleback predators prefer to ingest stickleback headfirst suggests an explanation for the anterior position of the spines in stickleback from lakes with predatory fish. A more anterior position of the spines may increase the incidence of escape during prey handling by piscine predators. This hypothesis does not explain, however, why stickleback in relatively low predation risk lakes consistently have more posteriorly positioned spines.

A diversity of vertebrates prey on stickleback (Reimchen, 1994). The behavioral response to threat of predation varies with the type of predator and the context of the interaction (e.g. ontogenetic stage, health, reproductive state, hunger, availability of refuge, presence of other stickleback) (Huntingford, 1976; Kynard, 1978; Milinski, 1985; Fraser & Huntingford, 1986; Foster, 1994; Foster, Garcia & Town, 1988; Foster & Ploch, 1990). In a ten-year study of predation on stickleback within a single lake, Reimchen (1994) observed extensive variation in predation efficiency among piscivorous species. The morphological consequences of these potential sources of variation on anti-predator behaviour have received minimal attention (Reimchen, 1994). Nevertheless, these data and others (Hagen & Gilbertson, 1972; Moodie & Reimchen, 1976; Bell *et al.*, 1993) indicate that the simple presence or absence of NPF is a good predictor of anti-predator morphology. This repeated result is surprising, given that birds are a large source of predation on stickleback (Reimchen, 1980, 1994) and the absence of NPF does not imply the absence of gape-limited predation by birds.

Evolution of foraging design in stickleback

The ecomorphological model predicted truncated, deep body shapes in fish that forage primarily in the littoral zone and elongated, streamlined body shapes in fish

that forage primarily in the limnetic zone. RLA has an effect on foraging design but only in the subset of lakes with NPF. With the exception of two lakes, stickleback from lakes without NPF tend to have intermediate to limnetic foraging designs regardless of RLA. The presence of both RLA and PS effects is consistent with the hypotheses outlined in the introduction that both the (1) relative abundance of limnetic and benthic foraging habitat and (2) predation regime effect foraging habitat use and that variation in these environmental variables among lakes has produced an evolutionary response in foraging morphology. With regard to the effects of predatory fishes on foraging habitat use, these data suggest that there is not a complete shift to littoral foraging when NPF are present. Indeed, stickleback with limnetic body shapes occur in all lakes with low RLA, regardless of the occurrence of NPF.

Hydromechanical models predict that bluff bodies allow greater maneuverability than elongated, streamlined bodies (Alexander, 1967a; Howland, 1974; Webb, 1983; see also Introduction). This greater manoeuvrability, in turn, should facilitate foraging performance in the structurally complex littoral zone. Elongated, streamlined bodies, on the other hand, have lower skin-friction and pressure drag than deep bodies during steady swimming and should, therefore, facilitate open water foraging performance. An association between foraging ecology and body shape consistent with these models is extremely common in fishes (Gregory, 1928; Greenway, 1965; Keast & Webb, 1966; Davis & Birdsong, 1973; Gatz, 1979; Riddell & Leggett, 1981; Webb, 1982b, 1984b; Wikramanayake, 1990; Winemiller, 1991; Robinson *et al.*, 1993; Robinson & Wilson, 1994). A comparison of the distribution of body depth between freshwater and anadromous samples indicates that both truncated, deep profiles and elongated, shallow profiles are derived states: the anadromous form is intermediate to the extreme freshwater forms (Walker, unpublished data). This suggests a history of diverging patterns of selection among freshwater populations. Selection for increased manoeuvrability has resulted in the evolution of truncated, deep bodies in populations colonizing shallow lakes with NPF. The more streamlined body of the stickleback from deep lakes with NPF and in most lakes without NPF compared to those from shallow lakes with NPF is consistent with hydromechanical models but the evolution of *more* streamlined and shallow body profiles compared to the anadromous ancestor is paradoxical. Since the anadromous form makes annual migrations during the breeding season (Wootton, 1976, 1984), all other factors being equal, they should have a more streamlined profile than all freshwater forms.

Taylor & McPhail (1986) observed both significantly larger relative body depth and significantly higher acceleration during a startle response in a sample of stream stickleback compared to a sample of anadromous stickleback. With these observations, it has been argued that the evolution of deep body profiles in stickleback is the consequence of selection for increased burst performance for either evading predators (Taylor & McPhail, 1986) or littoral foraging (Taylor & McPhail, 1986; Baumgartner, Bell & Weinberg, 1988). Both hydromechanical theory and the results of this study do not support the predation hypothesis (see above). While these results do suggest a deep body is an adaptation for littoral foraging, I have argued this reflects selection for increased manoeuvring performance, not (linear) acceleration performance. Compared to streamlined body profiles, bluff body profiles should both increase turning curvature and reduce inertial resistance during slow, precise foraging manoeuvres. On the contrary, a shallow body with posteriorly positioned, large

median fins is the expected body profile for fish specializing on striking prey with large accelerations (see above).

The principal caveat of using the comparative acceleration data (Taylor & McPhail, 1986) to support the burst performance hypothesis of deep body profiles in stickleback is the occurrence of a large suite of morphological and physiological differences between anadromous and stream stickleback with potential influence on acceleration performance. With an effective sample size of two for the comparison, the chance of a spurious association between any two characters is high (Schluter, 1993; Reimchen, 1994; Garland & Adolphe, 1994).

Even if the stream fish have higher accelerations during a C-start as a direct consequence of the deeper bodies, the relevance of this to littoral foraging is unclear. A second kinematic pattern used to accelerate from rest is an S-start, in which the fish bends into an S in the first stage of the fast start. Stickleback (Schluter, 1993; Walker, unpublished data) and other fishes (Hoogland *et al.*, 1957; Janssen, 1978; Rand & Lauder, 1981; Webb & Skadsen, 1981; Vinyard, 1982; Norton, 1991; Harper & Blake, 1991; Beddow, van Leeuwen & Johnston, 1995) employ an S-start to strike prey. In the only study to compare acceleration performance between escape and feeding behaviours, Harper & Blake (1991) found that northern pike accelerate at significantly higher rates during escape responses than feeding strikes. Since we do not know how acceleration in C- and S-starts are related, we should be cautious using C-start data to explain phenotypic variation in foraging behaviour.

More importantly, the available evidence suggests that high accelerations are more characteristic of open water feeding than littoral feeding. The principal prey in the littoral habitat of lakes are chironomid larvae (Rogers, 1968; Manzer, 1976; Lavin & McPhail, 1986; Jakobsen, Johnsen & Larsson, 1988; Schluter, 1993), which are non-evasive and require only a strong suction to capture. In contrast, the principal prey of many limnetic populations are calanoid copepods (Rogers, 1968; Lavin & McPhail, 1986; Schluter, 1993), a highly evasive zooplankton (Drenner, Strickler & O'Brien, 1978). Most fishes feeding on calanoid copepods, including stickleback (Walker, unpublished data), use high accelerations for prey capture (Janssen, 1978; Vinyard, 1980, 1982; Coughlin & Strickler, 1990; Kaiser, Gibson & Hughes, 1992). In summary, the available morphometric, hydromechanical, and behavioral evidence suggests that deep body profiles reflect selection for increased manoeuvrability and not increased burst performance.

The association between relative snout length and PS but not RLA is enigmatic. The mouth and buccal cavity are roughly cone shaped in fishes (Muller & Osse, 1984) and Liem (1993) argues that a long, narrow cone is a better design for planktivorous feeding while a short, broad cone is a better design for benthic feeding. Indeed, feeding trials indicate that limnetic stickleback with long snouts score higher in various zooplanktivorous feeding performance measures than benthic stickleback with short snouts while the reverse relationship holds for feeding on benthic macroinvertebrates (Larson, 1976; Bentzen & McPhail, 1984; Lavin & McPhail, 1986; Ibrahim & Huntingford, 1988a; Schluter, 1993). While the comparative performance measures indicate differences in feeding ability on different diets between stickleback that present different morphologies, they do not allow the determination of the morphological cause of the performance variation.

The functional and ecological significance of variation in snout length is poorly understood. Pietsch (1978) argued the extremely long snout in *Stylephorus chordatus* produces large suction forces during zooplanktivorous feeding. On the contrary,

Liem (1993) argued that a deep buccal cavity in combination with short snouts produces large suction forces and is expected of benthivorous feeders. Finally, Hobson & Chess (1978) argued that long snouts preclude binocular vision and, therefore, zooplanktivorous fishes are expected to have short snouts.

Comparative morphology fails to enlighten our inference on the functional consequences of variation in snout length. In the sympatric populations of stickleback from British Columbia, the limnetic form has a longer snout than the benthic form (Baumgartner *et al.*, 1988). On the other hand, anadromous stickleback, which spend large portions of the year in the open ocean feeding on pelagic zooplankton (Wootton, 1976; Williams & Delbeek, 1989; Quinn & Light 1989; Cowen *et al.*, 1991) have extremely short snouts compared to most lacustrine forms (Walker, unpublished data). In some trophically polymorphic fish, long snouts are associated with zooplanktivory (Meyer, 1990a,b; Malmquist, 1992; Liem, 1993; Skúlason & Smith, 1995). In a large study on stream fishes, Winemiller (1991) found an association between long snouts and a limnetic body shape. Nevertheless, there are numerous exceptions to this trend, especially in coral reef fishes (Davis & Birdsong, 1973; Hobson, 1974; Hobson & Chess, 1978).

Baumgartner *et al.* (1988), following Pietsch (1978), argued that the long snout in the limnetic species of the sympatric stickleback from British Columbia evolved to increase suction performance during zooplanktivorous feeding. In general, however, large suction forces are more characteristic of benthic feeders than limnetic feeders. In the open water, fish capture evasive prey with high body acceleration (ram strikes or jaw protrusion (ram-jaw) strikes either in place of or in addition to suction (Lauder & Liem, 1981; Vinyard, 1982; Coughlin & Strickler, 1990; Harper & Blake, 1991; Norton, 1991; Norton & Brainerd, 1993). Because rapid body acceleration strikes are not typically used when feeding on the bottom, suction is probably more important for littoral feeders. Indeed, within centrarchids, suction and strike velocities are inversely related (Lauder, 1983). In addition, Norton & Brainerd (1993) created the ram-suction suction index and found that phylogenetically distant littoral feeders were closer to the suction extreme while phylogenetically distant water column feeders were closer to the ram extreme.

Stickleback feeding on the evasive calanoid copepod, *Epischuria*, a common open water prey, use much greater accelerations during the strike than when feeding on *Tubifex*, a benthic prey item (Walker, unpublished data). In contrast, suction is clearly important for stickleback feeding on prey that are partially or completely buried in the substrate (Alexander, 1967b; Walker, unpublished data). These preliminary data suggest that stickleback conform to the general pattern described by Liem (1993) and indicate that increased suction performance is probably not the explanation for elongated snouts in the limnetic form of the species pairs. It is possible that snout length is related to the geometry of the head. The pressure generated during suction is proportional to the volume of the buccal cavity. Fish with deep heads and short snouts probably have similar buccal volumes to fish with shallow heads and long snouts. Since head depth effects locomotor performance, locomotor behaviour may be an important determinant of snout length in addition to feeding behaviour.

Adaptive phenotypic plasticity vs. adaptive genetic differentiation

The range of phenotypes produced by a genotype under natural environmental variation is the norm of reaction (Schmalhausen, 1949; Lewontin, 1974). Theoretical

models suggest the norm of reaction can evolve in an adaptive direction as a consequence of selection for different phenotypes between habitats, a process that leads to adaptive phenotypic plasticity (Via & Lande, 1985; Via, 1993; Gomulkiewicz & Kirkpatrick, 1992). Do the ecomorphological correlations observed in these data reflect adaptive phenotypic plasticity or genetic divergence?

The relative effects of phenotypic plasticity and genetic differentiation on Cook Inlet populations have not been investigated but evidence from other stickleback suggests that phenotypic differences among lakes are largely due to genetic differentiation. In a sample of stream threespine stickleback from California, the average magnitude of the degree of genetic determination on a suite of body shape traits was relatively high (0.57), indicating a large genetic component to morphological differentiation (Baumgartner, 1995). Among the British Columbia populations, common garden experiments provide evidence for a strong genetic effect on major phenotypic traits (McPhail, 1984, 1992, 1994; Lavin & McPhail, 1993). Finally, Day, Pritchard & Schluter (1994) designed a breeding experiment directly investigating the effects of phenotypic plasticity and genetic differentiation on trophic traits between one of the pairs of sympatric species from British Columbia. They found no plasticity in gill raker number and moderate plasticity in snout length and head depth. Importantly, the observed plasticity was in the expected direction for increased feeding performance. Nevertheless, the magnitude of the plasticity was not enough to account for observed variation among the sympatric populations.

Interaction effects on body shape

In lakes with NPF, stickleback from shallow lakes have the expected benthic foraging design and stickleback from deep lakes have the expected limnetic foraging design. In lakes without NPF, only two of the shallow lakes have stickleback with a benthic body shape; in general, stickleback from lakes without NPF have intermediate or limnetic body shapes, regardless of RLA. The two exceptions are from lakes that are extremely shallow and support dense aquatic vegetation across most of the lake area. A similar interaction, between presence or absence of predatory fish, lake area and trophic morphology, was observed among samples of stickleback from British Columbia, but no explanation for this interaction was offered (Moodie & Reimchen, 1976).

The energetic contents of benthic and limnetic prey are similar (Wootton, 1994). Nevertheless, relative profitability between benthic and limnetic foraging habitats may differ if the density of prey (in units of energy) differs between habitats, if prey are simply easier to locate in one habitat, or if the energetic cost of the predation cycle differs between habitats (Werner *et al.*, 1983b; Kaiser *et al.*, 1992).

The benefit of foraging in the most profitable habitat must be weighed against the relative safety from predation in the habitat. Stickleback encounter vertebrate piscivores in both the littoral and limnetic habitats (Reimchen, 1980, 1994) but the relative risk of predation between these habitats has not been measured. Predation experiments indicate that littoral vegetation provides a partial refuge from predation for many organisms (Savino & Stein, 1982, 1989a,b; Werner *et al.*, 1983a,b; Gilinsky, 1984; Diehl, 1988; Gotceitas & Colgan, 1989; Dionne & Folt, 1991; Brabrand & Faafeng, 1993) although this has not been investigated in stickleback. Stickleback are famously bold for their body size and threat of predation may have little

consequence on the long term feeding behaviour in some populations. Early natural historians were amused while observing stickleback harass larger predatory fish (Houghton, 1981). More rigorous, contemporary laboratory and field studies indicate that stickleback rarely flee into cover unless the predator attempts a strike (Hoogland *et al.*, 1957; McLean & Godin, 1989; Foster & Ploch, 1990; Bishop & Brown, 1992). Experimental studies do indicate that stickleback modify foraging behaviour as a response to direct threat of predation (Milinski & Heller, 1978; Fraser & Huntingford, 1986; Foster *et al.*, 1988; Ibrahim & Huntingford, 1988b; Huntingford & Wright, 1989, 1992; Jakobsen *et al.*, 1988). Stickleback reduce both the amount of time foraging (Fraser & Huntingford, 1986) and time spent in the water column (Ibrahim & Huntingford, 1988b) in the presence of predators and they learn to avoid food patches with higher threat of predation (Huntingford & Wright, 1989, 1992). Nevertheless, limnetic stickleback are frequently observed foraging high in the water column despite abundant piscine predators (Foster *et al.*, 1992; Walker, pers. observ.).

The pattern of the interaction in this study is consistent with recent optimal foraging theory that models diet or foraging habitat preference as a balance between profitability and risk of predation (Werner *et al.*, 1983a,b; Milinski, 1986; Gilliam, 1990; Godin, 1990; Hart & Gill, 1994). Neither PS nor RLA can explain patterns of foraging morphology alone. Instead, the comparative morphometric data suggest that the transition from more limnetic feeding to more littoral feeding occurs in shallower lakes when NPF are present. Stickleback do feed in the littoral zone when NPF are absent, but these data suggest this occurs only in lakes with abundant aquatic vegetation across the entire lake area.

Alternatively, the interaction may reflect the effects of competition for resources when NPF are present. In the littoral zone of Great Central Lake, Vancouver Island, stickleback and juvenile sockeye salmon (*Oncorhynchus nerka*) have similar diets but the density of salmon is low relative to the limnetic zone. In contrast, in the Wood River lakes of Alaska, sockeye salmon fry have very similar diets to limnetic threespine stickleback and interspecific competition in the limnetic zone has been suggested (Rogers, 1968). In deep lakes, there may be a large enough zooplankton biomass to support both zooplanktivorous stickleback and salmonids. In shallower lakes, however, interspecific competition may be intense enough to cause a foraging habitat transition in stickleback, from the limnetic to littoral zones.

The presence of an interaction between PS and RLA on foraging morphology is typical of the relationship between many morphological and environmental variables. Interactions confound estimates of ecomorphological associations unless techniques that specifically model interactions are employed. This suggests that results from comparisons of large sets of morphological and environmental variables using simple bivariate correlations, multiple regression without interaction effects, or canonical correspondence analysis, should be interpreted cautiously.

Comparisons with sympatric populations from British Columbia

Six lakes in southwestern British Columbia each support species pairs—two populations of stickleback with extreme trophic and locomotor morphologies associated with benthic and limnetic foraging behaviour (Larson, 1976; McPhail, 1984, 1992, 1993, 1994; Bentzen & McPhail, 1984; Baumgartner *et al.*, 1988; Schluter & McPhail, 1992, 1993). Body shape variation among solitary Cook Inlet

populations is nearly, if not equally, as large as the variation present among the sympatric species. Unfortunately, the body shape variables in this study cannot be quantitatively compared with the published shape variables of the sympatric samples because of slight differences in both the variables measured and the method of size adjustment. Nevertheless, the mean number of gill rakers for each sample can be directly compared. Gill rakers are believed to facilitate feeding by sieving small prey from the flow out of the buccopharyngeal cavity (Wright, O'Brien & Luecke, 1983) or blocking flow altogether (Sanderson, Cech & Patterson, 1991). Among fishes in general, zooplanktivore specialists have longer and more numerous gill rakers than closely related non-planktivores (Schluter & McPhail, 1993). Gill raker number differs between limnetic and benthic populations from British Columbia (Schluter & McPhail, 1992; McPhail, 1993) and among marine, lake, and pond populations from Europe (Gross & Anderson, 1984). Nevertheless, gill raker number is not always a reliable indicator of foraging habitat preference among lake populations of stickleback (Foster *et al.*, 1992). This lack of association may result if fewer, wider gill rakers have the same functional effect as more, narrower gill rakers (Robinson *et al.*, 1993). The significant positive association between mean gill raker count and RLA within the subset of lakes without NPF is consistent with the ecomorphological hypothesis that stickleback from deep lakes should present a better functional design for feeding on zooplankton than do those from shallow lakes.

Schluter & McPhail (1992) give the mean gill raker counts for samples of both males and females of all benthic, all limnetic and 10 solitary populations but all comparisons with the Cook Inlet samples will refer to the male subsamples only. The lower end of the range of mean gill raker counts from Cook Inlet samples overlaps that of the British Columbian benthic samples, which, perhaps surprisingly, have very similar counts to the British Columbian solitary samples. Mean gill raker count from one Cook Inlet lake (Visnaw Lake, $Y = 23.2$) lies within the range of the British Columbian limnetics ($Y = 23.03-25.00$), while two more (Zero Lake, $Y = 22.6$, Lorraine Lake $Y = 22.35$) fall only slightly below this range. A large proportion (37.5%) of the Cook Inlet samples have higher counts than all British Columbian solitary samples. It is noteworthy that these high gill raker counts are observed in lakes that fall within the range of lake size from Schluter and McPhail's study (species-pair lakes, 5–44 ha; Visnaw Lake, 14.4 ha; Lorraine Lake, 13.1 ha; Zero Lake, 25.7 ha).

Using an elegant series of comparative morphometric, feeding performance, and experimentally induced competition studies, Schluter (1993, 1994; Schluter & McPhail, 1992) has argued the extreme divergence in the sympatric populations from British Columbia is the consequence of character displacement (Brown & Wilson, 1956). The broad range of trophic and locomotor morphologies among solitary populations from Cook Inlet suggests that extreme levels of behavioral and morphological divergence can occur among closely related populations in the absence of interspecific competition. The lakes in this study were not randomly sampled but were chosen to maximize differences among lakes for two environmental variables that were believed *a priori* to have potential effects on the evolution of foraging and evasive morphology. The observed associations between foraging and evasive morphology, RLA, and PS suggests that extreme ecotypes can evolve when stickleback colonize lakes with extreme environments but lacking interspecific competition.

Effects of history

The global distribution of phenotypic traits in stickleback suggests that derived phenotypes have independently evolved numerous times (Bell & Foster, 1994b). At what geographic scale, however, does a shared derived trait reflect common ancestry or geneflow and not independent evolution? Parapatric stream populations or from lakes and their inlet or outlet streams, adjacent lakes, or even sympatric populations within single lakes frequently present divergent derived phenotypes (Bell, 1982; Reimchen, Stinson & Nelson, 1985; Lavin & McPhail, 1985, 1993; Baumgartner, 1992; Bell & Ortí, 1994; McPhail, 1994), suggesting that many characters can evolve independently at an extreme microgeographic scale.

In order to minimize the influence of common ancestry or geneflow on the association between morphology and environment, stickleback from lakes with similar environments were sampled from distinct drainages. Nevertheless, it is doubtful the 40 populations sampled for this study were each independently derived from a common anadromous ancestor and have been genetically isolated since colonizing the lake. I used the Smouse-Long-Sokal test to remove residual effects of ancestry and geneflow on the ecomorphological correlations (for related methods, see Felsenstein, 1985; Cheverud, Dow & Leutenegger, 1985; Grafen, 1989; Lynch, 1991; Harvey & Pagel, 1991). The extremely low correlations between the morphometric and geographic distance matrices and the high partial correlations between morphometric and environmental matrices holding geography constant are consistent with the hypothesis that the effects of RLA and PS on body shape reflect the independent, parallel evolution of derived traits following colonization of lacustrine environments.

CONCLUSION

The presence of multiple stickleback populations with the same suite of derived traits suggests a history of extensive parallel evolution. Associations between morphological and environmental variation supports this hypothesis. The efficacy of the mechanical models to predict the pattern of environmental effects on body shape provides further support for the hypothesis. The absence of a geographic effect on the distribution of phenotypes is evidence that the ecomorphological associations are not an artifact of spatial autocorrelation. Given these results, the repeated occurrence of derived trophic, armor, and locomotor traits within the Cook Inlet system is consistent with the hypothesis that phenotypic evolution in this radiation has proceeded by extensive parallel selection.

In this study, I have attempted to identify both the environmental sources and the morphological targets of selection. My inference is based on the comparison of observed and expected effects of specific environmental variables on the morphometric variables. This method has the disadvantage of not controlling for correlated effects of unmeasured environmental or morphological variables. Measuring multiple environmental variables and controlling for correlated effects by using path, partial correlation, or canonical correlation analysis is an alternative comparative method to infer causation. A problem with these multivariate approaches is that results can be extremely misleading if there are large interaction effects between environmental

variables. Experimental designs that manipulate morphological or environmental variation also control for correlated effects. Although many relevant manipulations, especially on morphological variation, are impractical, an experimental approach addressing the hypotheses outlined in this study is clearly the next step in the investigation of body shape evolution in threespine stickleback.

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