

**Structural Relationships Between Spines and Lateral Plates in Threespine  
Stickleback (*Gasterosteus aculeatus*)**



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STRUCTURAL RELATIONSHIPS BETWEEN SPINES AND LATERAL  
PLATES IN THREESPINE STICKLEBACK  
(*GASTEROSTEUS ACULEATUS*)

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Of the five genera of stickleback (Gasterosteidae), *Gasterosteus* has the longest dorsal and pelvic spines and the most extensive expression of lateral bony plates (Nelson, 1971). Spines, which can be locked into an erect position (Hoogland, 1951), enlarge the effective body diameter of the stickleback and may pierce the mouthparts of a predator during manipulation, increasing the opportunity for escape (Hoogland et al., 1957). As might be expected, in localities where predatory fish are common, the stickleback spines are relatively longer than in populations where such predators are rare or absent (Hagen and Gilbertson, 1972; Gross, 1978a). Numbers of lateral plates are also geographically variable (for review see Bell, 1976; Wootton, 1976). Most marine populations have a row of 35 lateral plates on each side of the body extending from the head to the caudal peduncle (Fig. 1a). These plates are greatly reduced in number in many freshwater populations in western North America and southwest Europe. While populations are known in which fish lack all lateral plates (Miller and Hubbs, 1969; Moodie and Reimchen, 1973), the majority have from three to eight plates per side in the anterior region of the body (Fig. 1b). Early investigators (Bertin, 1925) considered this variation to be environmentally induced, but subsequent genetic analysis showed that a large component of the variance is heritable (Munzing, 1959; Lindsey, 1962; Hagen, 1973; Hagen and Gilbertson, 1973a; Avise, 1976). However, the adaptive significance

of retaining anterior plates remains obscure.

Predictive associations have been detected between numbers of anterior plates and habitat. For example, in British Columbia, populations exposed to fish predators generally have stickleback with six to eight lateral plates per side (Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976). Differential predation on these phenotypes has been detected in field studies (Moodie, 1972; Hagen and Gilbertson, 1973b) and in experimental chambers (Moodie et al., 1973; Bell and Haglund, 1978). Behavioral traits such as preferences in nesting sites, aggressiveness and responses to predators differ among plate number phenotypes (Moodie, 1972; Moodie et al., 1973; Kynard, 1979; Huntingford, 1981). These associations and the lack of any obvious morphological features which would explain the differential predation have led some investigators (Moodie, 1972; Moodie et al., 1973) to suspect that the numbers of anterior lateral plates might not be directly functional but rather, genetically correlated with advantageous behavioral traits.

During recent investigation into the interactions between avian piscivores and morphology of *G. aculeatus* (Reimchen, 1980; Reimchen and Douglas, 1980), loons (*Gavia*) and grebes (*Podiceps*) were frequently observed feeding on adult three-spine stickleback. Variability in manipulation time by these foragers (2-900 seconds) and occasional escape of the fish (approximately 20%) prompted an examination of the structural characteristics responsible for spine rigidity in the stickleback. This paper examines number and position of lateral plates, structure of spine

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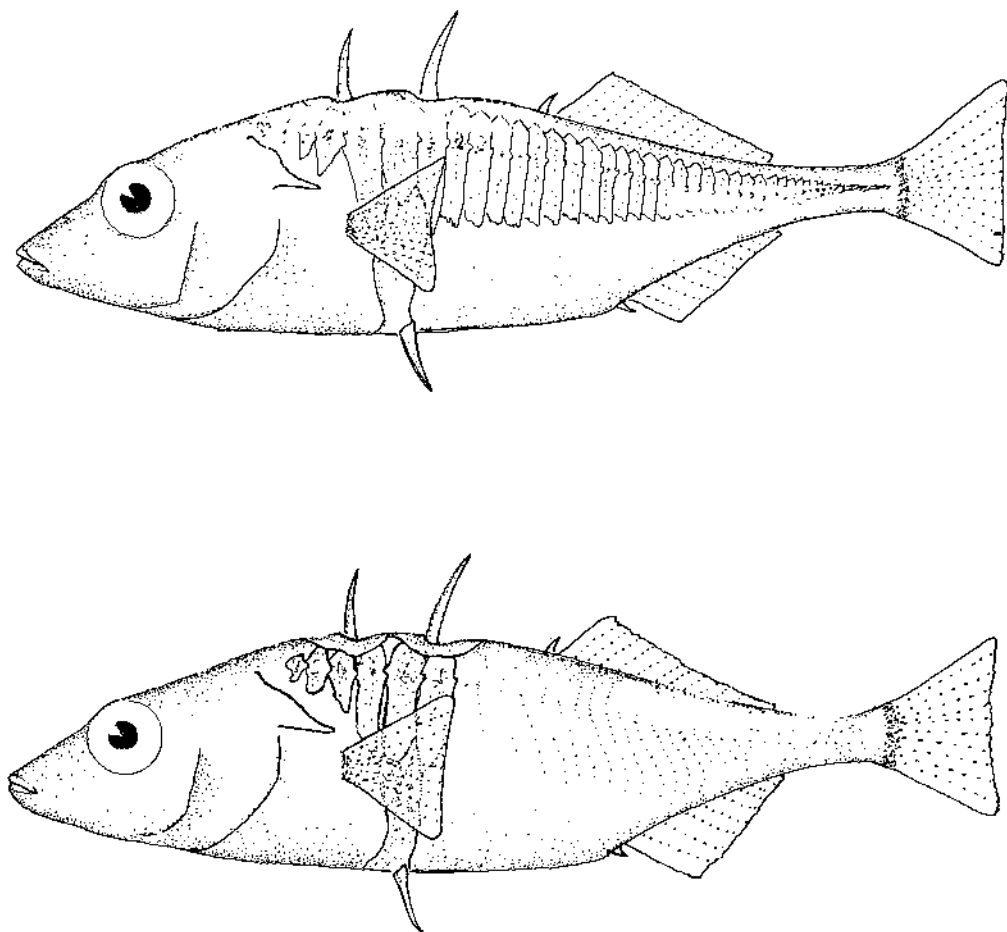


FIG. 1. Examples of completely-plated (upper) and low-plated (lower) morphs. Partially-plated morph (not shown) has keel plates on caudal peduncle in addition to anterior plates.

supports, length of spines and, finally, provides experimental data on spine deflection following removal of lateral plates. A functional interpretation is proposed for the presence of anterior lateral plates in threespine stickleback.

#### METHODS

Sticklebacks used for description of spines, lateral plates and associated bones were collected from Drizzle Lake, Queen Charlotte Islands, British Columbia. Lake habitat and collecting techniques are reported in Reimchen and Douglas (1980). Other samples of *G. aculeatus* examined were from the Queen Charlotte Islands (62

localities), Vancouver Island (13 localities), Alaska (4 localities), and Japan (5 localities). Adult fish (15–100 per locality) were scored for standard body length, length of first dorsal spine and number and position of lateral plates (LP). Each LP usually overlies a single myomere and accordingly, plate positions are designated P1, P2, P3, etc., beginning with the most anterior. P1–P3 occur above the cleithrum, P4 and P5 beneath the basal plate of the first dorsal spine, P6 above the ascending process and P7 and P8 beneath the second dorsal spine, coincident with the caudal edge of the pectoral fin (see Fig. 6). Since fluctuating asymmetry was com-

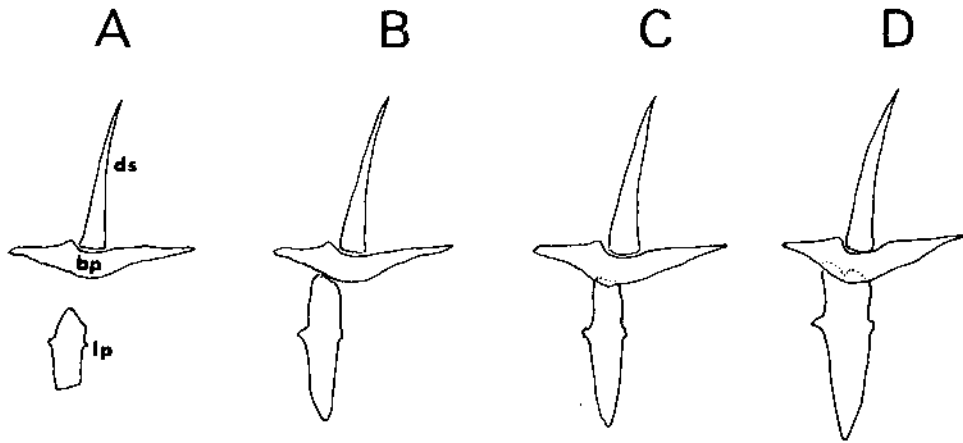


FIG. 2. Categories of overlap between spine supports and lateral plates. Figure shows lateral view of dorsal spine (ds), basal plate (bp) and single lateral plate (lp). A = no overlap (0), B = abutting (1), C = partial overlap (2), D = major overlap (3).

mon, data from both sides of the fish have been included for determining modal positions of LP for the population. Infrequently (<2%), an LP was divided into two narrow segments; these were scored as a single LP.

Some 10–20 fish from each of 27 localities on the Queen Charlotte Islands, including Drizzle Lake, were stained and cleared with the trypsin-alizarin method (Taylor, 1967) and examined for structural associations between vertebrae, pterygiophores, spine supports (basal plates beneath dorsal spine and ascending process of the pelvic girdle) and LP. To evaluate the amount of overlap between spine supports and LP, four categories of association were recognized: no overlap or contact (0), abutting (1), partial overlap (2) and major overlap (3) (Fig. 2). Mean overlap for each LP was calculated for all fish in a sample and a cumulative overlap index derived from the sum of the means.

The structural contribution of LP to spine rigidity was assessed by measuring spine deflection prior to, and following, artificial removal of LP (Fig. 3). Adult stickleback (70–75 mm SL), preserved in 10% formalin for 3 days, were fastened with eight pins to a cork base. These pins

were positioned so as to restrict movement of the trunk when a lateral force was applied to the spine (perpendicular to the longitudinal axis of the body), yet not restrict any relative movement of the spine supports or LP. A narrow aluminum wedge, housed on one arm of a fulcrum balance and counterbalanced with a brass weight, was placed against the erect dorsal spine at a point 5 mm from the base of the spine (see inset, Fig. 3). A weight (30–500 g) was placed on the wedge and horizontal deflection of the spine was measured to the nearest .005 mm with a dial gauge (Baker B02) and converted to degrees. Weights of 200–500 g occasionally resulted in a 30–70 degree spine deflection, permanent displacement from the mid-line or spine breakage. A 50 g weight was chosen as a standard since it generally produced less than 15 degrees deflection, and following removal of the weight, the spine returned to the original position. As well, with a small deflection, the force exerted on the spine remained largely perpendicular to the axis of the spine. Spines in these fish are very stout and did not bend along their length; rather, deflection involved movement of the spine support. Formalin slowly decalcifies bone in pre-

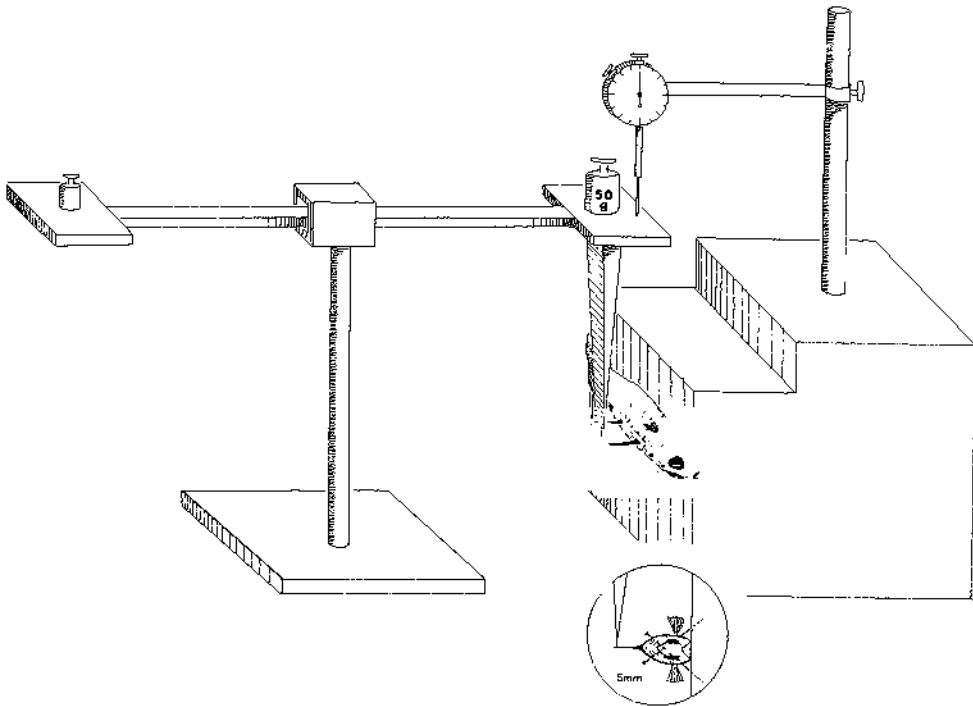


FIG. 3. Apparatus for measuring deflection of spines in relation to the presence or absence of lateral plates. Pelvic spines were folded down in all trials. Position of anterior pins on midline shown as large dots. Inset shows approximate positions of diagonal pins and wedge.

served fish. Fish preserved in buffered formalin for one year showed only partial decalcification, while those preserved for four months had no obvious weakening of the bone (pers. observ.). Therefore, in these experiments, three days of preservation should have no detectable effect.

After measuring the deflection of the first and second dorsal spines, a 3 mm section from the central part of the LP was excised from the most posterior plate on each side of the body (see Fig. 6). Deflection was then remeasured for both dorsal spines. This procedure was repeated for adjacent anterior plates in succession (P10-P1) and spine deflection remeasured after each plate removal. In total, 62 fish were processed. Removal of the LP resulted in minor damage to the sub-cutaneous tissue which could also influence spine deflection. Consequently, further measurements

were obtained from fish in which P7 and P8 were naturally absent and the skin intact.

Magnitudes of forces exerted by predators on stickleback spines were estimated by measuring the forces required to break spines. In Drizzle Lake, 6.6% of the adult stickleback examined ( $N = 3,743$ ) had broken dorsal or pelvic spines, usually associated with body lacerations, teeth marks and bill imprints. Transverse fractures occurred throughout the spine length including the relatively stout base (unpresented data). These injuries are assumed to have resulted from attacks by resident avian and salmonid piscivores. Approximately 15% of the adult stickleback found in trout (*Salmo clarki*) stomachs had broken spines. As an average estimate, I determined fracture force at the mid-point of the spine. Spines were removed from freshly pre-

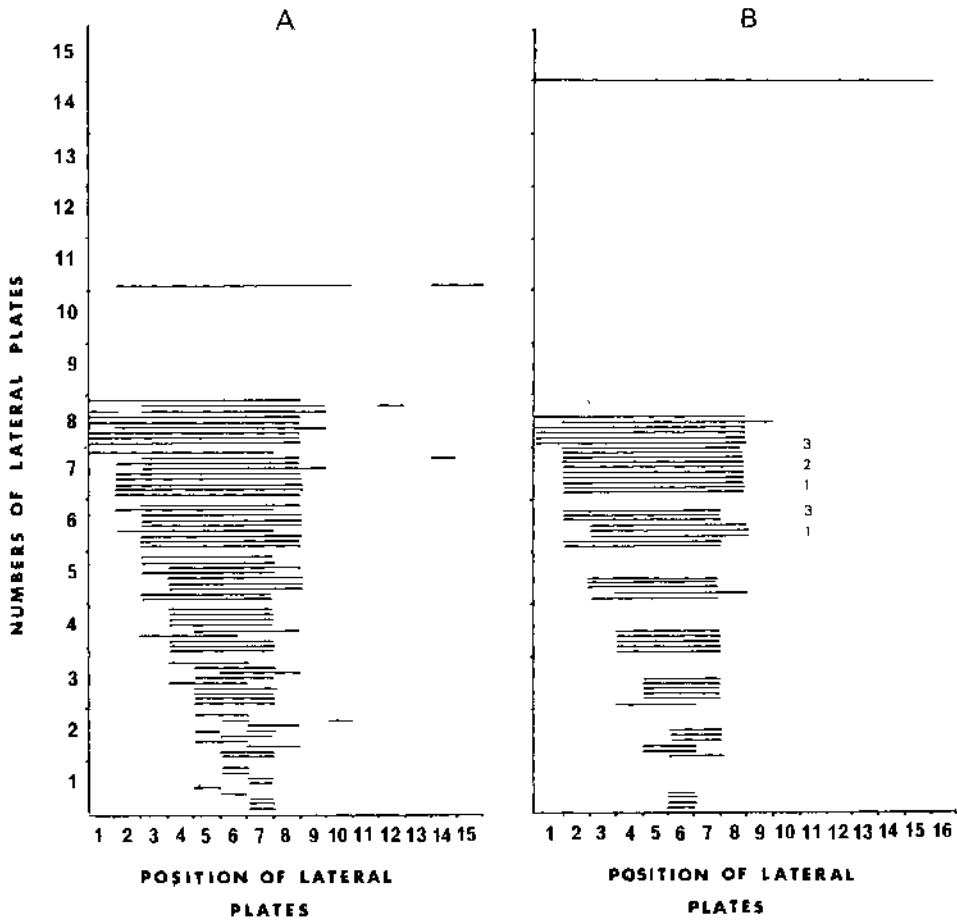


FIG. 4. Relationship between number and position of lateral plates (see Fig. 1 or Fig. 6). Left graph (A) shows positions of lateral plates in adult stickleback from Drizzle Lake. Each horizontal line represents the positions of lateral plates on a single fish. Vertical axis shows total number of lateral plates (0-15) per fish. Attempts were made to include about 10 fish in each plate number category as well as unusual fish with discontinuous series. Fish with four lateral plates were most frequent in the population. Right graph (B) shows modal position of lateral plates in other freshwater populations on the Queen Charlotte Islands, Vancouver Island, Alaska and Japan. Each line represents the most frequent position of lateral plates for the population. This was determined by calculating mean numbers of lateral plates in the sample and then choosing the most common positions for that particular plate number phenotype. Numbers at right refer to localities from Vancouver Island (1), Alaska (2) and Japan (3). Nine additional populations, all with seven lateral plates at P2-P8, are not shown. Keel plates (P26-P35), which occurred in one partially-plated ( $\bar{x}$  = 14 LP) population from the Queen Charlotte Islands, are not shown.

served adult fish, measured for total length and then clamped at the mid-point so that the distal end extended above the clamp. A loop, connected by thin wire to a spring balance (0-1,000 g) was attached 2 mm from the tip of the spine. The tension on

the spine was slowly increased (30 g/second) until the spine failed (at the mid-point), at which point the g-force was recorded. All spines were attached such that the pressure was exerted on the lateral edges of the spine (see Fig. 3) rather than

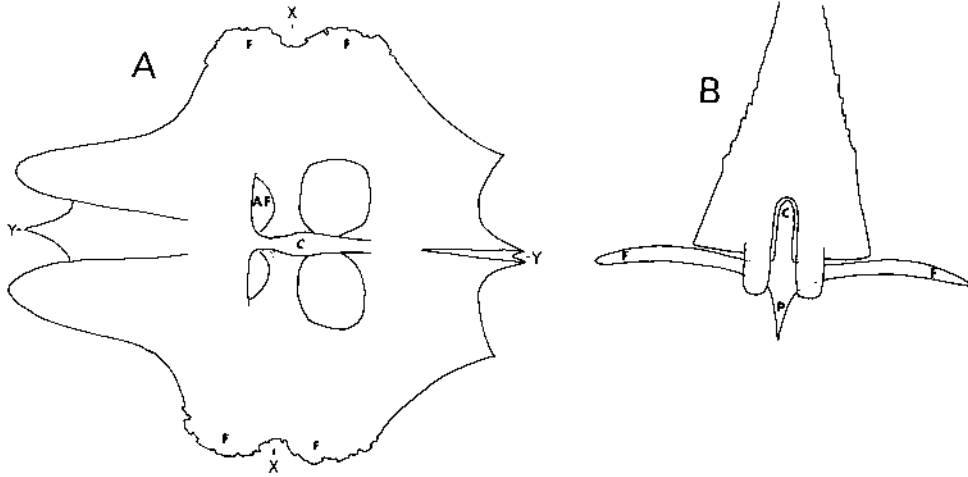


FIG. 5. Structure of second basal. A. Dorsal view of basal. B. Cross section (X—X) through second basal at position of condyle with dorsal spine drawn to scale. AF—anterior fossae, C—condyle, F—flange, P—pterygiophore.

the leading or trailing edges. The fracture force was determined for 70 moist spines ranging from 8–15 mm.

## RESULTS

### *Position and Number of Lateral Plates*

There was a consistent relationship between the number of LP and the positions which they occupy. In the Drizzle Lake population (Fig. 4A), individuals with 9 LP generally had P1–P9 or less frequently, P2–P10. With reduction in numbers, there was a sequential loss of P9, P1 and P2, followed by P3 or P8. Most fish with four lateral plates, which is the mode for the population, had P4–P7 or infrequently, P3–P6 or P5–P8. With further reduction, there was a loss of P4 and P5; among fish with only 1 LP, P6, or occasionally P5, predominated. About 10% of the fish had missing LP within the usually continuous series or an additional LP at P12 or P13.

Modal LP positions in freshwater localities from the Queen Charlotte Islands, Vancouver Island, Alaska and Japan are shown in Figure 4B. While mean number of LP was highly variable among these populations (range 1–26), there was a very

similar relationship to LP positions observed in the Drizzle Lake fish. When populations are ranked in order of decreasing number of LP, it is apparent that there was generally a sequential loss of P9, P1, P2, P3, P8, P4, P5 and P7. Plate 6 was the least variable of all the LP.

### *Morphology of Spine Supports and Lateral Plates*

Each of the two large dorsal spines articulates on a condyle extending vertically from the basal plate (Fig. 5A). Small processes, which form the socket of the spine, project into the anterior fossae of the basal, while the base of the spine, when erect, abuts against a flattened area of the basal (Fig. 5B). The characteristics of this articulation limit any lateral movement of the spine on the basal yet allow erection of spines along the mid-line. Flanges on the lateral edge of the basal (Fig. 5A, B) extend over the dorsal trunk musculature and overlie one or more LP. Usually the first basal overlies P5, while the second basal overlies P7 (Fig. 6). A broadly expanded pterygiophore, continuous with the mid-ventral line of the basal, extends antero-ventrally towards the vertebral column.

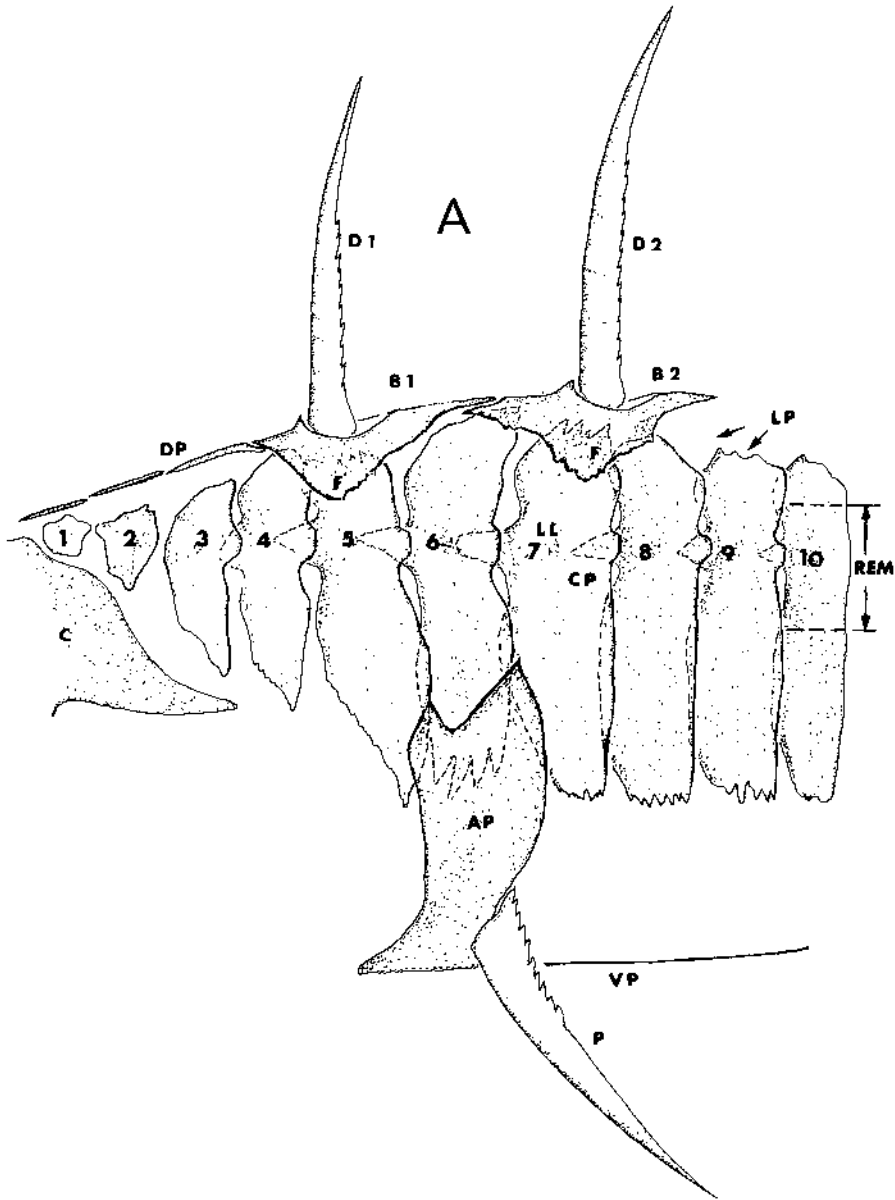
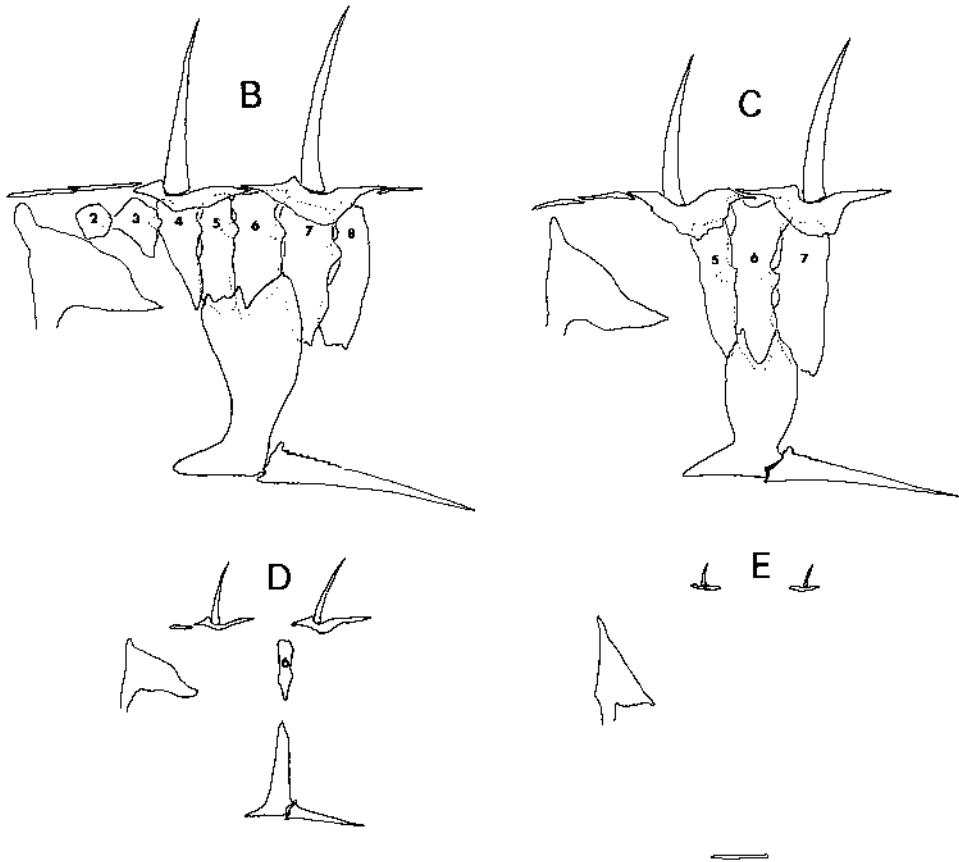


FIG. 6. A: Structural associations between spines and lateral plates on adult stickleback from Drizzle Lake. B-E: General structure of spines, basals, ascending process and lateral plates from four localities on the Queen Charlotte Islands. B—Eden Lake, C—Hickey Lake, D—Solstice Lake, E—Serendipity Lake. All specimens are representative adults (body length 60–75 mm) from each population, although structures

Pelvic spines are attached to the girdle with a peg and socket articulation, similar to that of the dorsal spines. No internal bones, equivalent to the pterygiophores,

are present. Rather, an ascending process of the pelvis extends vertically (Fig. 6) approximately 40% of the body depth on each side of the body and overlies the LP (prin-





are quite variable. AP—ascending process of the pelvis, B1—first basal, B2—second basal, C—cleithrum, CP—central process of the lateral plates, D1—first dorsal spine, D2—second dorsal spine, DP—dorsal plates, F—basal flanges, LL—lateral line pores, LP—lateral plates numbered from 1-10, P—pelvic spine, REM—section of lateral plates removed for deflection measurements, VP—ventral plates.

cipally P6). A ventral plate, fused at the mid-line to its complement, forms the base of the ascending process.

Lateral plates are oval to rectangular in shape and overlap each other along their posterior edges (Fig. 6). Bony processes at the level of the lateral line pores extend anteriorly beneath the adjacent LP. On P5-P7, these processes are relatively large, reaching the mid-line of the adjacent plate, while on P2 and P3, they are small or often absent. Dorsal sections of the LP frequently have variation in edge contours which are directed either anterior or posterior to the dorso-ventral axis of the LP. For example, P6 normally has a small pos-

terior process which underlies the anterior section of the second basal, but in some individuals, an additional anterior process abuts against the first basal. In exceptional cases, in which fish lack P1-P5, this process on P6 is often greatly enlarged and extends under the flange of the first basal.

Relationships between spine supports and LP were examined from 26 additional localities on the Queen Charlotte Islands (Table 1). In 17 of these (#1-17), which had population means of greater than 4 LP, the structural associations were similar to those described for the Drizzle Lake fish (#13). That is, the first basal overlapped P4 and P5, the second basal P6-



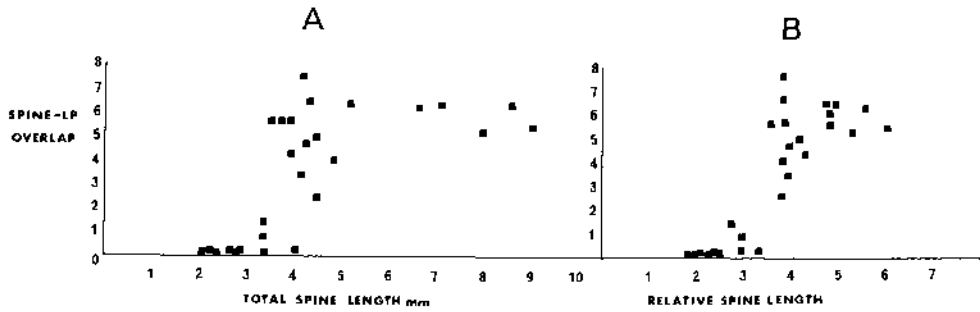


FIG. 7. Relationship between dorsal spine length and the amount of basal overlap with lateral plates from 27 populations on the Queen Charlotte Islands (see Table 1). Left graph (A) shows total basal overlap against mean length of first dorsal spine on adult fish from each locality. (Range of body lengths 40–80 mm). Right graph (B) shows basal overlap against relative dorsal spine length adjusted for a body length of 50 mm.

P8 and the ascending process P5–P8. Differences were evident in the amount of overlap for some LP. Stickleback from Dead Toad (#1) (which were fully-plated) showed only negligible association between P6 and the second basal. In Eden (#5), P4 was often elongated and obliquely positioned such that the ventral aspect abutted against the ascending process (Fig. 6B). In Sundew (#11) and in several individuals from Hickey (#14), the anterior dorsal process of P6 was well-developed and consistently underlay the first basal, producing a broad overlap zone (see Fig. 6C).

Comparisons were made of the cumulative overlap for each spine support among the 17 localities. The ascending process had greater overlap with the LP ( $\bar{x} = 7.0$ ) than did the first basal ( $\bar{x} = 5.4$ ,  $t = 4.85$ ,  $d.f. = 16$ ,  $P < .001$ , paired  $t$ -test) or the second basal ( $\bar{x} = 5.6$ ,  $t = 5.28$ ,  $d.f. = 16$ ,  $P < .001$ ).

In populations from the remaining localities, all with mean counts of fewer than 4 LP, LP were either absent (#25, #27) or greatly reduced in size such that no overlap occurred with the basal or ascending process (Fig. 6D, E).

There was a general relationship between mean dorsal spine length and cumulative LP overlap of the first basal (Fig. 7A). All of the populations in which individuals had dorsal spines less than 3.5

mm in length had no significant overlap of the LP, while those with spine lengths greater than 4 mm showed extensive overlap. Since body length differs in these populations (39–75 mm), spine length was adjusted to a standard body length of 50 mm; the resulting relationship (Fig. 7B) is similar to that for total spine length. A related variable to this correlation is the shape and size of the ascending process of the pelvis. This process was absent in two populations (#18, #26) where pelvic spines were also lacking. It consisted of a single narrow fork in eight populations where individuals had less than 4 LP. Finally, it was wider, with two, three or occasionally four forks which overlapped up to 5 LP in the remaining populations. There is a significant correlation ( $r = .45$ ,  $d.f. = 26$ ,  $P < .02$ ) between the mean number of forks and the length of dorsal spines.

#### *Spine Deflection*

A lateral force exerted on the dorsal spine produced a rotational movement of the basal, rather than movement of the spine on the central condyle. Since the basal flanges overlies the LP, rotation of the basal was restricted. On sticklebacks with a full series of anterior LP (P1–P10), dorsal spines deflected approximately 4°–6° from the mid-line when subjected to a 50 g force. Sequential removal of small segments of P10 through P1 produced an

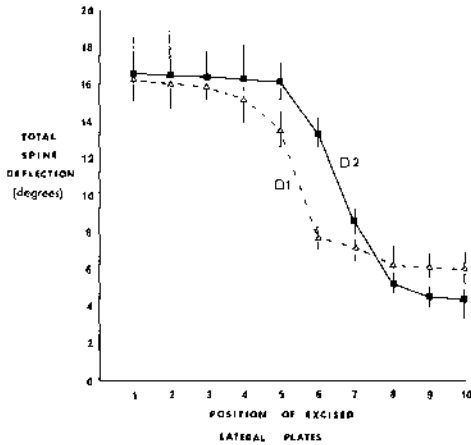


FIG. 8. Angular deflection of dorsal spines following sequential removal of lateral plates from P10–P1. Each point shows the mean spine deflection ( $\pm 1$  SE) for the first dorsal (D1) and second (D2) spine after the lateral plate from that position was removed.

increase of at least 267% in the deflection to approximately  $16^\circ$ . It is evident (Fig. 8) that removal of P7 and P6 produced the major deflection in the second dorsal, and removal of P5 and P4, the major effect on the first dorsal. P1–P3 and P9–P10 did not provide any substantial contribution to spine stability.

Tissue damage resulting from removal of LP influenced the stability of spines. Deflection measurements were obtained in two groups of stickleback, the first ( $N = 13$ ) having P2–P8 and the second ( $N = 8$ ), with P2–P6, lacking the 2 LP (P7, P8) which underlie the second basal. Mean deflection in the second dorsal spine was 4.4 degrees and 7.0 degrees for the two groups respectively ( $t = 4.06$ ,  $P < .001$ , unpaired  $t$ -test). The raw data from LP removal experiments show that surgical removal of P7 and P8 increased deflection from 4.7 degrees to 8.7 degrees; the difference between the two data sets indicates that 35% of the deflection shown in Figure 8 was due to tissue damage.

No realistic force vectors can be deduced from the data, but it is possible to roughly distinguish direction and distribution of forces (Fig. 9). A force exerted

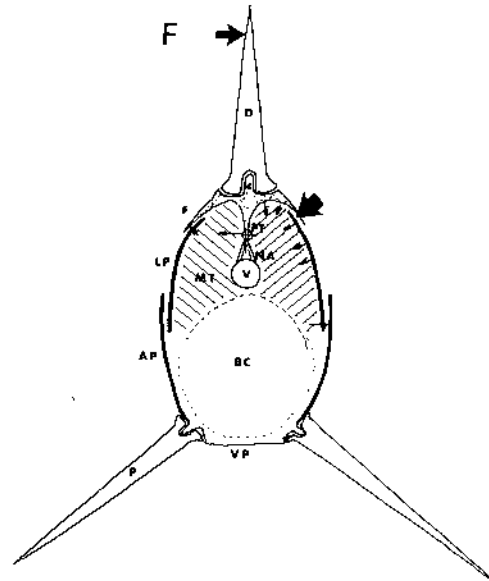


FIG. 9. Oblique cross-section of adult stickleback showing relationship among different structures and estimates on the distribution of lateral force (F) exerted by a predator. Lines of force shown do not represent vector quantities. Distance between overlapping elements is accentuated in diagram. AP—ascending process, BC—body cavity, BF—basal flange, C—condyle, D—dorsal spine, LP—lateral plate, MT—muscle tissue, NA—neural arch, P—pelvic spine, PT—pterygiophore, V—vertebra.

on the spine produces a moment about the basal proportional to the distance through which the force is applied. In the absence of LP, the force is distributed from the basal flanges directly to the dorso-lateral muscles and from the central pterygiophore to the two bilateral muscle blocks. When LP are present, the force on the basal flange is distributed to the dorsal region of the LP and in turn to the dorso-lateral muscle. Since the LP extend ventrally some 70% of the body depth, the force exerted at a single point of basal overlap is distributed over a wider area. Each LP overlaps the long central process and the anterior edges of the adjacent LP (Fig. 6) and therefore, force on any single LP will be, in part, distributed to other LP. For example, on a fish 75 mm in length, the basal (on one side of the midline) and pterygiophore have a combined

surface area of 14 mm<sup>2</sup> on which the forces exerted on the spine are distributed. The presence of P6, P7 and P8 increases the surface area to 68 mm<sup>2</sup>.

Experimental data yielded an estimate of forces which would be required to break spines. Regressing breakage force ( $y$ ) against spine length ( $x$ ) approximated the power curve  $y = 7.52x^{1.55}$  ( $r = .60$ ,  $P < .001$ ,  $d.f. = 68$ ). Assuming minimum values required for breakage, that is if the force was exerted at the tip of the spine rather than at the mid-point, a 9 mm spine and a 14 mm spine would fracture at 228 g and 452 g, respectively. The presence of broken spines in the Drizzle Lake population (see Methods) indicates that one or more of the predators (*Salmo clarki*, *Gavia immer*, *Podiceps grisegena*) is capable of exerting forces of this magnitude. During preliminary deflection measurements, a 200 g force applied to the second dorsal spine produced a 14 degree displacement in fish with P2–P8 but a 50 degree deflection in fish with P2–P6. In the latter case, basal flanges penetrated the tissues, and during maximum deflection, the spine disarticulated from the basal. Therefore, if the spines and basals are not buttressed by lateral plates, the rigidity, and presumably, effectiveness of the spine will be greatly reduced and the dorso-lateral trunk musculature vulnerable to damage during deflection of the spines.

#### DISCUSSION

Three lateral plate morphs are recognized in the threespine stickleback (Hagen and Gilbertson, 1972): *complete*, with a continuous row of plates from the head to the caudal peduncle, *partial*, with anterior plates and keel plates (on the caudal peduncle), and *low*, with only anterior plates (see Fig. 1). Despite extensive investigations of geographical variation in this trait (Heuts, 1947; Munzing, 1963; Miller and Hubbs, 1969; Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Bell and Haglund, 1978; Gross, 1978a; Bell, 1981, 1982; Bell and Richkind, 1981; Hagen and Moodie, 1982), functional aspects of plates remain unknown. Evidence presented here

suggests that the anterior plates, which occur on each of the morphs, provide the major structural support for dorsal and pelvic spines. Different lines of evidence are consistent with this interpretation: the geographical trends in positions of LP (Fig. 4), the development of bony processes on the LP which are positioned so as to increase the articulation with the basals of the dorsal spines and the ascending processes of the pelvis (Fig. 6, Table 1), the positive correlation between length of spine and amount of overlap with the LP (Fig. 7) and the increased deflection of dorsal spines and compression of tissues when lateral plates are absent (Fig. 8).

This structural model appears to account for some of the broad geographical patterns in number and position of anterior plates. Modes of 5 LP predominate in California (Bell and Haglund, 1978), as well as in central and southern Europe (data extracted from Gross, 1977). In populations from the Queen Charlotte Islands, Vancouver Island, Alaska and Japan, examined in the present study, this mode occurs at P3–P7 or P4–P8, the major positions for spine stability. Ranking these populations in order of reduced numbers of plates, the reduction proceeded from caudal positions anteriorly to P8, and thereafter to P1, P2 and P3, again indicating loss of LP not directly associated with the spines. Plate 6 was the least variable of all LP and contributed to the stability of the pelvic, second dorsal, and occasionally, the first dorsal spine. The importance of P6 and adjacent plates is also implicit in the ontogenetic sequence, as these LP are the first to form and ossify even in the completely plated morph (Igarashi, 1970; Bell, 1981).

Observations on behavior of salmonid and avian predators (Hoogland et al., 1957; Moodie, 1972; Moodie et al., 1973; Reimchen, 1980; Reimchen and Douglas, 1980, unpubl. data) show that erect spines are broken or forced down by compression, torsion and bending before the stickleback is swallowed. The force on the spine supports will be directly proportional to the distance vector through which the

forces act. Consequently, one would predict that if long spines are to remain rigid, or in other words, if the force per unit area exerted on the muscle tissue is to remain similar to that for shorter spines, there should be a positive correlation between length of spines and overlap of the LP. The data presented on cumulative overlap (Fig. 7) are in agreement with this prediction. This relationship was also applicable to differences in spine length within individuals. Pelvic spines are about 35% longer than the first dorsal spine (Potapova, 1972); the ascending process, which supports the pelvic spine, had significantly greater overlap with the LP than did the first and second basals. This increased overlap of the ascending process with LP may also be related to the type of tissue underlying the ascending process. Unlike the basals and a large segment of the LP, both of which overlie the major trunk musculature, much of the ascending process overlies the body cavity (see Fig. 9) which will not provide any substantial resistance to compression.

In populations with exceptionally long spines, such as Drizzle and Eden Lake, up to three adjacent lateral plates were occasionally fused into a single broad plate, which, in contact with the pelvis and the basals, produced a rigid bony exoskeleton around the trunk. Such circular fusion of bones (and occasionally stout spines) was prevalent in early vertebrates, such as the ostracoderms and placoderms, and in extant groups such as Ostraciidae (trunkfish), Callichthyidae and Loricariidae (armoured catfish). While this would result in a maximum dispersion of forces on underlying tissues, it would occur at the expense of swimming speed and maneuverability (Aleyev, 1977). Overlapping bony plates, as in *Gasterosteus*, retain some of the mechanical strength of fused plates yet allow body flexibility during swimming.

While 5 LP appear to be the mode in many freshwater populations, an unusual finding in recent surveys in western North America is that modes of 7 LP occur where predatory fish are present (Hagen and Gilbertson, 1972; Moodie and Reimchen,

1976). This relationship appears to be causal, as there is evidence, from examination of trout stomach contents, that stickleback with 7 LP are consumed less frequently than fish with greater or fewer number of plates (Hagen and Gilbertson, 1973b). The increase in number of LP involves the addition of the most anterior plates (P1, P2 and P3) rather than those posterior to P8. It appears unlikely that this higher mode can be interpreted from the structural model. Occasionally P3 abutted against the first basal and in such cases, may provide an additional support to the spine, but in most fish, these anterior LP did not articulate with the spine supports. One possibility is that these plates act as protective armour. On the anterior half of the stickleback, a large segment of the body is heavily ossified, including the cranium, cleithrum, dorsal plates, lateral plates and ventral plates (see Fig. 6A). In the absence of P1-P3, there is a relatively large area of exposed tissue between the cranium and first dorsal spine (see Fig. 6C). Since trout use teeth during prey capture, penetration of tissue unprotected by bone seems probable. Plates in this region may be particularly important for the protection of lateral line nerves and other branches of the vagus nerve which lie close to the surface beneath P2 and P3 (Reimchen and Nelson, unpubl. data). If the lateral line nerve was severed near the origin, sensory input would be eliminated from the entire trunk.

Two experimental studies have examined the influence of predation on numbers of LP in *G. aculeatus* (Moodie et al., 1973; Bell and Haglund, 1978). Although some of the results are consistent with the above proposals, the design of the experiments limits their usefulness in assessing structural aspects of LP. The importance of P4-P8 for spine stability or P1-P3 for tissue protection, would only be expressed following initial capture by the predator. Thus, a test of the proposal would require a comparison of "escaped" fish to those which had been eaten. In both laboratory studies, investigators noted that sticklebacks rarely escaped following capture,

which was probably a reflection of the confined chambers and therefore, lack of a normal escape opportunity. As a result of this, survivors represented fish which had avoided capture, rather than fish which had escaped after capture. Consequently, behavioral differences associated with LP phenotypes have been advocated as a cause for geographical and temporal variation in the frequency of LP phenotypes (Hagen and Gilbertson, 1972; Moodie, 1972; Moodie et al., 1973; Kynard, 1979).

Some exceptions are evident in the structural associations between spine supports and LP. All of the populations with small dorsal spines (<3 mm) had reduced numbers of LP (<4) and no significant overlap of the spine supports. Structurally, this represents both a reduction in the width of the basals and ascending process of the pelvis and a reduction in the size of the LP. Similar relationships between small spines and reduced numbers of LP in *Gasterosteus* have been reported by Hagen and Gilbertson (1972), Moodie and Reimchen (1976), Gross (1977), Campbell (1979) and Bell (pers. comm.). Such parallel reduction of spines and plates has been interpreted as an evolutionary regression of defensive structures since these populations generally occur in small lakes, ponds and streams that lack predatory fish (Bell, 1976; Moodie and Reimchen, 1976). This interpretation can be criticized for several reasons. Firstly, the localities, at least on the Queen Charlotte Islands, which lack predatory fish have one or more avian piscivores including *Gavia*, *Podiceps*, *Lophodytes* and *Megaceryle* (Reimchen, 1980; Reimchen and Douglas, 1980, unpubl. data) and therefore, the spines and LP should be subject to selection. Secondly, in other members of the Gasterosteidae, including *Apeltes* (four-spine stickleback), *Culaea* (fivespine), *Pungitius* (ninespine) and *Spinachia* (fifteen-spine), lateral plates are absent or poorly developed (Nelson, 1971). Each of these species has small dorsal spines, generally from 1–4 mm in length, yet many populations are subject to vertebrate pre-

dation (Nelson, 1969; Wootton, 1976; Gross, 1978b, 1979; Reist, 1980a; Blouw and Hagen, 1981). Therefore, the broad correlation between small spines and LP reduction cannot be ascribed to a lack of predation.

It is not clear what evolutionary constraints are operating to limit length of spines in these taxa, although Nelson (1969) suggests that reduced weight and stream-lining could be advantageous during predator avoidance in *Culaea inconstans*. Even small spines are capable of piercing the mouthparts of predators, providing some advantage over fish without spines (Hoogland et al., 1957). Extrapolation of the power curve for spine length and fracture force predicts that a 6 mm spine will fail at mid-point with a 121 g force applied near the point of fracture, while a 4 mm spine will fail at 65 g. Since magnitude of forces exerted by predators is inferred to equal 100 g and may exceed 500 g, small spines would easily break during manipulation. Under these conditions, there may be a disadvantage to having LP underlying the spine supports, since this would increase the rigidity of the spines. Rather, small spines may be most effective if they are capable of piercing the mouthparts during compressional forces yet deflecting during lateral forces.

The data presented in this paper demonstrate that the position and development of some anterior lateral plates are functionally correlated with the length of dorsal and pelvic spines. Clearly, much additional work is required on defining the significance of LP at P1–P3 and P9–P35 as well as distinguishing magnitude and direction of forces exerted on the spines and LP. Predators differ in their foraging and manipulative techniques (Hoogland et al., 1957; Moodie et al., 1973; Bell and Haglund, 1978; Reimchen, 1980; Reist, 1980b) which, in combination with physical differences in habitats (for example, Hagen and Moodie, 1982), could produce different optimal behavioral and morphological defenses in the prey species. There is a lack of pertinent data on sources of mortality among different age-cohorts and

among different populations. When such information is obtained, it may be possible to evaluate the significance of intra-population variability and broad geographical patterns in defensive structures of the stickleback without recourse to postulates such as introgression, linkage effects or other default explanations.

#### SUMMARY

Numerous freshwater populations of threespine stickleback (*Gasterosteus aculeatus*) have a series of three to eight bony lateral plates restricted to the anterior region of the body. There was a close relationship between total number of plates on individual fish and the positions which the plates occupied. Those positioned between the dorsal and pelvic spines are the least variable in occurrence of all lateral plates. Basal plates and ascending processes which support the dorsal and pelvic spines, respectively, overlap the central lateral plates and the amount of overlap is greatest in populations with long spines (>5 mm). A lateral force (50 g) exerted on the spine produced a significant increase in the angular spine deflection when lateral plates were artificially removed; a 200 g force resulted in penetration of the basal plate into the muscle tissue. Forces exerted by avian and salmonid predators, as deduced from the incidence of broken spines in one population and the force required to experimentally break the spines, range from 100 to 500 g. Lateral plates provide a structural base for the spine supports and a greater surface area over which the forces on the spines are distributed; it is proposed that the principal function of these plates is for stability of long erect spines during manipulation by predators. A rigorous analysis of strength of spines, force vectors on the body, and methods of manipulation for different species of predators should provide further information on functional aspects of these characters.

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