Inefficient predators and prey injuries in a population of giant stickleback

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I describe predator-induced injuries in a lake population of large-bodied *Gasterosteus aculeatus* from the Queen Charlotte Islands, British Columbia. Injuries, which included structural damage (fractured dorsal and pelvic spines) and skin lacerations (scars, abrasions, and punctures), were observed on 13.4% of the population. Bill imprints ("aviscars") from avian piscivores, including *Podiceps grisegena* and *Gavia immer*, occurred on one-third of the injured fish. Mean aviscar width (4.2 mm) was low in winter and higher in midsummer correlating with seasonal differences in the presence of avian taxa. One-half of the injured fish had fractured spines without any associated skin damage; sources of these injuries could not be verified although they probably resulted from avian piscivores and resident salmonids. Rate of spine regeneration, determined on artifically marked fish, was 1.09 mm over 26 months. Age of injuries, assessed by condition and regrowth of spines, included recent attacks (ca. 1 month or less, 6.3%) and old attacks (1–3 years, 40%). Thirty percent of skin injuries are undetectable after 1 year. Injuries were absent on juvenile fish (<50 mm) but were common on adults, reaching an incidence of 32% on subsamples of the largest fish (>82mm). These data are consistent with theoretical predictions of increased manipulation inefficiencies among gape-limited predators and can account in part for the evolution of large body size in this population. Mark–recapture studies on 12 272 adult stickleback (>70 mm) showed that the probability of incurring a predator injury as an adult fish (0.09/year) is largely a consequence of total length of time in the population; this finding amplifies size-dependent trends in injury frequencies.

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On trouvera ici la description de blessures causées par des prédateurs chez une population de lac de gros *Gasterosteus aculeatus* de l'archipel de la Reine Charlotte en Colombie-Britannique. La présence de blessures profondes (épines dorsales ou pelviennes fracturées) ou superficielles (cicatrices, éraflements, entailles) a été observée chez 13,4% de la population. Des marques de becs infligées par des oiseaux piscivores, notamment *Podiceps grisegena* et *Gavia immer*, ont été retrouvées chez un tiers des poissons blessés. La variation de la largeur moyenne de ces marques (4,2 mm), faible en hiver et plus élevée au milieu de l'été, est associée aux différences saisonnières dans la structure des communautés d'oiseaux. La moitié des poissons blessés avaient des épines cassées, mais pas de blessures superficielles; la cause de ces blessures n'a pu être vérifiée, mais il est probable qu'elles sont dues aux oiseaux piscivores et aux salmonidés résidants. Le taux de regénératon des épines, déterminé sur des poissons marqués artificiellement, a été évalué à 1,1 mm en 26 mois. L'âge des blessures, déterminée par la condition et la regénératon des épines, reflète des attaques récentes (environs 1 mois ou moins, 6,3%) ou des attaques plus anciennes (1–3 ans, 40%). Trente pourcent des blessures superficielles ne sont plus décelables après 1 an. Les blessures étaient absentes chez les jeunes poissons (<50 mm), mais communes chez les adultes, atteignant une fréquence de 32% dans des sous-échantillons des poissons les plus gros (>82 mm). Ces données sont conformes aux prédictions théoriques de l'inefficacité accrue des manipulations chez les poissons à petite bouche et peuvent expliquer en partie l'évolution vers une taille plus grande du corps chez cette population. Les données accumulées par marquage–recapture de 12 272 épinoches adultes (>70 mm) ont démontré que la probabilité pour un poisson adulte (0,09/an) d'être blessé par un prédateur est en grande partie une conséquence de la durée de sa présence dans la population; cela a pour effet d'accentuer la relation qui existe entre la taille et la fréquence des blessures.

[Traduit par la revue]

Introduction

The evolution of defenses in prey populations is dependent on foraging inefficiencies in the predators. Prey may either evade detection, escape during pursuit, or, if captured, escape during manipulation. Such interactions have been examined experimentally and there is a relatively comprehensive literature on theoretical aspects of predator–prey interactions (Curio 1976; Zaret 1980). Yet we do not have a broad framework for assessing how frequently such foraging inefficiencies occur in natural populations. One measure of these inefficiencies is the occurrence of predator-induced injuries such as beak marks in butterfly wings (Carpenter 1942; Robbins 1980), tail loss in lizards (Schoener 1979; Jaksic and Fuentes 1980), shell fractures in molluscs (Vermeij et al. 1981; Reimchen 1982; Vermeij 1982) and brachiopods (Alexander 1981), and spine fractures in cladocerans (Murtaugh 1981). Analyses of these traits for a relatively limited number of taxa have yielded ecological and evolutionary insight into adaptation and there remain major opportunities for exploiting these traits in a broad diversity of taxa (Vermeij 1982).

Extensive investigations of life history and morphological variation in populations of *Gasterosteus aculeatus* (threespine stickleback) indicate that predators are major factors in the evolution of morphological diversity within the species (for review, see Wootton 1984). Large dorsal and pelvic spines offer protection during predator manipulation (Hoogland et al. 1957); individuals surviving attacks should show evidence of injuries. Differences between populations in types or frequencies of injuries would potentially provide information on selective agents and on the intensity of selection. Yet, despite a wide diversity of studies on *Gasterosteus aculeatus*, the characteristics and incidence of predator-induced injuries have not been described for any populations. The data presented here provide an initial effort in this direction.

I examined stickleback from a lake population for which habitat and life history were known and for which a preliminary study had shown predator-induced injuries (Reimchen and

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Douglas 1980, 1984*a*; Reimchen 1983). The sticklebacks in this locality are heavily melanistic and are characterized by exceptionally large body size (70 – 95 mm vs. the more typical 35 – 60 mm). My purposes here are (*i*) to describe the different classes of injuries and identify their sources, (*ii*) examine relationships between frequency of injury and age of fish, and (*iii*) quantify frequencies of predator-induced injuries through time. In a later paper, I will explore evolutionary aspects of unsuccessful predation among different sex, spine, and lateral plate phenotypes.

Study area and methods

The investigation was carried out at Drizzle Lake, a small bog lake (112 ha) on the Queen Charlotte Islands, British Columbia. The lake has a diversity of avian and salmonid predators on the stickleback, including loons (*Gavia immer* and *Gavia stellata*), grebes (*Podiceps grisegena*, *Podiceps auritus*), Belted Kingfisher (*Ceryle alcyon*), and cutthroat trout (*Salmo clarki*) (Reimchen and Douglas 1980, 1984*a*). General morphology of these stickleback and those from surrounding populations are described in Moodie and Reimchen (1976) and Reimchen et al. (1985).

Standard mesh minnow traps were set every 4 – 8 weeks over a 3-year period (15 times) in a three-dimensional grid of the lake (100 sites). In each of the 15 surveys, traps were collected after 48 h and the fish were scored for standard body length (SL), length of first dorsal spine, and positions of lateral plates. Each fish was visually inspected for damage to the first and second dorsal spines, to the left and right pelvic spines (fracture, bend, fork), and to the integument (puncture, abrasion, scar); those with injuries were preserved for later analyses. For convenience, I will refer to the former group as structural injuries and to the latter as skin injuries. Most uninjured fish were released at the site of capture; a random subset from each trap was retained for morphological comparison with injured fish. Over the 15 surveys, 8718 stickleback were examined.

Preserved fish were measured for 18 morphological and meristic traits. In this paper I deal principally with body length. Terminology for lateral plates and pelvic girdle follows Reimchen (1983). Distance of the spine fracture from the base was measured along the length of the spine. These data were partitioned into three groups depending on the relative position of the spine fracture (base, middle, tip), with base fractures ocurring within the proximal 30% of the spine and tip fractures occurring on the distal 30%. Spine regeneration was often present at the position of the fracture (Fig. 1B). I measured the length of spine regrowth (± 0.1 mm) to obtain a general index of how recently the spine fracture occurred. In fish with bent spines, the angle of spine deflection from the normal axis was measured to the nearest 10°. For analyses, I recognized three groups: major bend (>45°), minor bend (20 – 45°), and forked spines. I excluded fish with bends less than 20°. While these may also have been injuries, they were indistinguishable from natural growth variation. For example, fish with unusually long dorsal or pelvic spines occasionally have a 10 – 20° left or right lateral deflection of the distal 1 – 2 mm of the spine. This deflection reduces overlap of the spine tip with the more posterior spine or fin.

General characteristics of integumentary damage on each fish were recorded, including trunk position and type of injuries (punctures, bill scars and bilateral compression of the trunk, irregular scratches, skin removal, and diffuse areas of depigmentation). For most analyses, fish were subjectively assigned to one of four categories dependent on the characteristics and extent of damage: (*i*) no damage, (*ii*) minor injury including diffuse areas of depigmentation and scratches on less than 25% of the body surface, (*iii*) major injury including punctures, multiple curvilinear stratches, skin removal, and major diffuse depigmentation (>25% surface area), and (*iv*) bill imprints or "aviscars." These categories were not discrete but formed a continuum. On a subsample of fish with minor injuries ($N = 376$), I further partitioned the data into abrasions, vertical scratches, horizontal scratches (<45°), and crescent scars. Fish occasionally exhibit scratches over a small region near the insertion of either the dorsal or the anal fin. These are the consequences of recurring abrasion from the tips of the depressed dorsal or pelvic spines and such fish were categorized as nondamaged.

Maximum widths of aviscars (distance between parallel scars at midpoint of the scar) were recorded to distinguish avian piscivores with different bill sizes. Video recordings were made (Sony Portable VTR with 1000-mm lens) of the foraging and prey manipulation behaviour of Red-necked Grebe and Common Loon, the two dominant avian piscivores on the lake (Reimchen and Douglas 1984*a*). On 43 sequences in which the bill was held perpendicular to the axis of the television lens, I recorded the position of the fish (usually held crosswise in the bill) along the length of the bill. Mean relative distance from the bill tip was calculated. Bill diameters along the bill were measured on skeletal material (*P. grisegena*, five specimens, *G. immer*, three specimens, University of Alberta Museum of Zoology) to provide a general comparison with aviscars. Data on predation efficiency and manipulation technique are not analyzed here and will be treated in a separate paper (T. E. Reimchen, unpublished data).

I carried out a mark – release experiment of 12 272 adult fish to estimate the rate at which new injuries appeared in the population. Traps were set throughout the lake in March, April, and May, 1985, and all uninjured adult fish were marked (transverse clip at the midpoint of the second dorsal spine) and released at the site of capture. SL was recorded on a random subset of this sample. From 1985 to 1987, I resampled the population on 10 occasions and recorded the presence or absence of predator-induced injuries on all recaptured fish. Amount of spine regrowth at the apex of the clipped spine was measured (with ocular micrometer) on 39 fish recaptured in July 1987 to estimate the rate of spine regeneration. Artificial injuries (transverse spine clips) were easily distinguishable from predator-induced injuries by the smooth and perpendicular surface of the fracture in contrast to the angular and rough profile of natural fractures.

Results

Representative structural injuries are shown in Fig. 1. Broken spines, usually with transverse but occasionally with oblique fractures, were the most frequently observed injury, occurring in 9.9% of the fish. Although spines become progressively narrow and weak distally, the number of fractures was greatest in the middle region of the spine rather than at the end. Injuries could be roughly aged (recent vs. old) based on the amount of repair and regrowth. Among the 759 fish with fractured spines, 48 (6.3%) were judged to have been injured recently because the distal spine fragments were still attached to the basal portion of the spines with damaged membranes. A total of 381 (50.2%) fish had slightly older injuries, as assessed by melanistic tissue overgrowing the distal edge of the fracture. Regrowth of the spines, indicating substantially older injuries, was observed on the remaining fish: 224 had up to 1 mm regrowth, 79 had 1 – 2 mm regrowth while 27 had 2 – 4 mm of regrowth. Mean spine regrowth after 26 months on adult fish with artificially clipped spines was 1.09 mm (range 0.10 – 2.47 mm).

Bent spines, which occurred on 2.6% of the fish, included major bends (0.65%), minor bends (1.40%), and forks (0.55%) (Figs. 1E – 1G). Spines on adult stickleback are rigid and cannot be bent with pressure (Reimchen 1983); therefore, bends result either from growth anomalies or from lateral forces applied to the less rigid spines of juvenile fish. Forks result from disruption to the normal growth of the spine during ontogeny. In some instances, the disruption is a fracture; two diagonal apices of regrowth on artificially clipped spines were

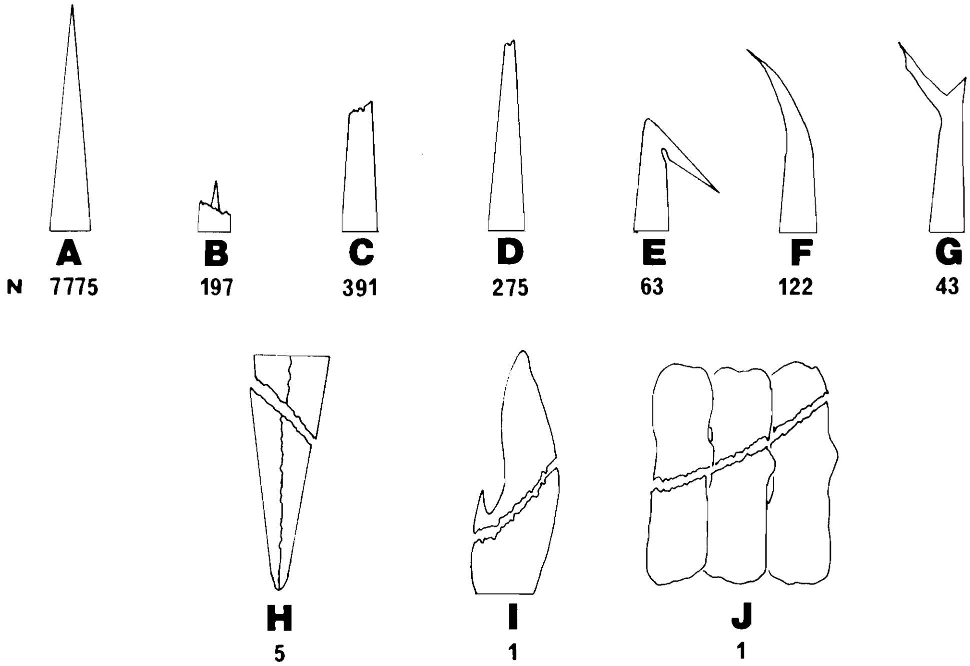

FIG. 1. Classes of structural injuries on stickleback. (A) Uninjured spine. (B) Base fracture with representative spine regeneration on fracture surface. (C) Intermediate fracture. (D) Tip fracture. (E) Major bend. (F) Minor bend. (G) Fork. (H) Ventral plate fracture of the pelvic girdle. (I) Ascending process fracture of the pelvic girdle. (J) Lateral plate fracture. Sample size (N) shows total number of fish with each injury. A single fish (category J) with two broken plates is not shown.

observed on some of the recaptured fish. Forks also may be developmental in origin; several fish had symmetrical forks on each spine with the same point of bifurcation, suggesting a growth anomaly rather than an injury.

There were several additional structural injuries observed on the fish (Figs. 1H–1J). The ventral plate of the pelvic girdle was transversely fractured in five fish (0.06%) and the ascending process was fractured in one fish (0.01%). In two individuals, some or all of the major lateral plates (positions 5, 6, 7) were horizontally fractured near their midpoint.

Skin injuries occurred on 11.3% of the fish (Table 1). The most frequent (4.5%) and distinctive of these injuries were aviscars, which are generally vertical in orientation (Fig. 2A) and symmetrical on both sides of the body. They varied in number from single to multiple overlapping sets per individual (Fig. 2B), differed in size (Fig. 2C), and regularly occurred amid other diffuse abrasions or scratches on the trunk. These scars were the consequences of attacks from avian piscivores (Fig. 2D). Contact between the bill and the trunk results in two widely spaced linear scars. Examination of museum specimens (*Podiceps*, *Gavia*, and *Ceryle*) showed that the edge of the bill that is the principal contact zone with the fish is ridged. Aviscars occurred over most of the body but they were more difficult to detect in the anterior region since this area is encased in body armour. Erect dorsal and pelvic spines restrict symmetrical contact of the bill with the body, producing atypical scratches and diffuse abrasions. Among the 391 fish with aviscars, 78 (19.9%) also exhibited bilateral compression of the trunk musculature directly beneath the scars. Extent of this compression was highly variable, from slight depressions of the body surface to major compression in which the body diameter was reduced by approximately half its original width.

Width of aviscars varied from 2 to 8 mm ($\bar{x} = 4.2$, $N = 339$) with a positively skewed distribution (Fig. 3). Examination of video tapes of foraging Red-necked Grebe indicated that the relative positions of stickleback in their bills ranged from 9 to 50% ($\bar{x} = 21.2\%$, $N = 48$) along the length of the bill measured from the tip. Bill diameters over these positions increased from 1.5 to 7.0 mm, respectively, with a mean width of 3.4 mm at the average fish position along the bill. Similar data could not be obtained for the Common Loon since the bill was generally held partially submerged during manipulation, obscuring the view of the exact fish position. I reexamined video tapes taken during a previous study on foraging in Red-throated Loon (Reimchen and Douglas 1984*b*) and determined the position of fish (*Ammodytes* and *Clupea*) along the length of the bill. This position ranged from 9 to 45% ($\bar{x} = 26.3\%$, $N = 18$) indicating similar handling techniques to those observed in the grebe. Bill widths over these distances in Common Loon, assuming comparable prey handling to Red-throated Loon, ranges from 2 to 12 mm ($\bar{x} = 5.8$ mm). These values, therefore, are congruent with the mean and range of aviscar widths observed on the fish.

Seasonal effects in mean aviscar width were present, with fish collected during winter months having narrower scars than those taken in midsummer (Fig. 4). Although width is highly variable within each season, mean differences appear to be real ($F = 3.1$, $P < 0.03$, ANOVA).

Major damage to the skin occurred on 219 fish (2.5%). Within this group, small punctures in the integument, each generally less than 1 mm^2, occurred on five fish and appeared to be the result of tooth penetration by cutthroat trout, the major tooth-bearing predator in the lake. Ripped skin (Fig. 5A), which may be an extension of multiple punctures or intense abrasion from bill contact, occurred on eight fish. The remaining fish had diffuse trunk abrasions (Fig. 5B), which probably result from frictional damage during bill manipulation by birds because comparable abrasions were also observed on fish with aviscars.

Among fish with minor skin damage (4.3%), weak vertical

TABLE 1. Raw data matrix of interactions between structural injuries and integumentary abrasions (values in parentheses are row percentages to the right and column percentages below)

	Spine condition			
	No damage	Bend	Break	Total
Integument				
No abrasions	7243 (93.7) (93.2)	111 (1.4) (60.3)	377 (4.9) (49.7)	7731 (88.7)
Minor	172 (46.1) (2.2)	31 (8.3) (16.8)	170 (45.6) (22.4)	373 (4.3)
Major	107 (48.0) (1.4)	13 (5.8) (7.1)	103 (46.2) (13.6)	223 (2.6)
Aviscar	253 (64.7) (3.3)	29 (7.4) (15.8)	109 (27.9) (14.4)	391 (4.5)
Total	7775 (89.2)	184 (2.1)	759 (8.7)	8718

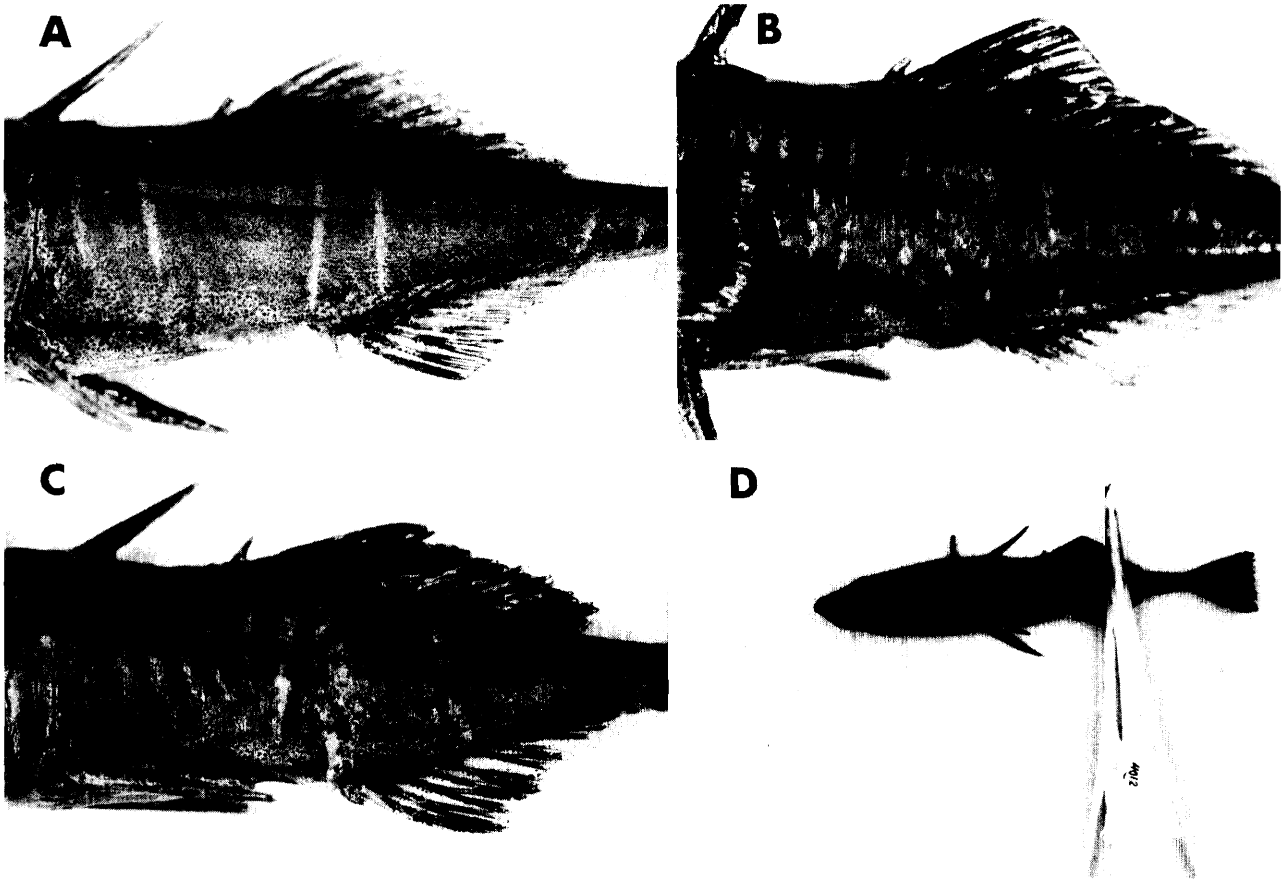

FIG. 2. Representative aviscars (A–C) from *Gasterosteus* at Drizzle Lake. Figure 2B shows multiple overlapping sets of scars on a single fish and Fig. 2C illustrates different sizes of scars on one fish. (D) Modal position of fish in bill of *Podiceps grisegena*.

scars occurred on 2.02%, horizontal scars on 1.08%, abrasions on 0.86%, and crescent-shaped scars on 0.09%. Some of these scars (Fig. 5C) probably resulted from superficial raking by trout teeth, while abrasions may have been caused by manipulation by birds. Not all of the injuries were predator induced. Crescent-shaped scars (Fig. 5D) in six fish closely resembled the gape of an adult stickleback; these injuries were presumably incurred during courtship and territorial biting. Other reproductive activities such as nest construction (glueing) and nest entry, which involve contact with abrasive substrata, could contribute to the minor injuries in this group. The trapping and collecting process are also a possible source of injuries. For example, during occasional storms, midwater traps suspended with surface floats oscillated vertically with the passage of wave crests and fish in the traps were killed (N = 272) from recurrent abrasion against the traps. However, frequencies of spine fractures and skin injuries of these fish were not significantly different from those in stationary traps (χ^2 = 1.2, 1 df, ns). A regression of the incidence of storm-killed fish against frequency of fish with skin injuries (excluding avi-

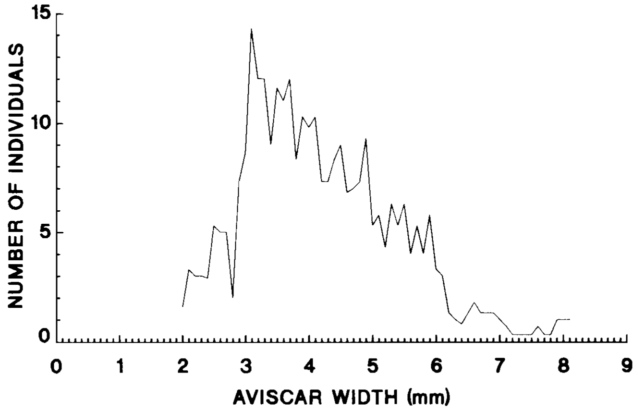

FIG. 3. Width of aviscars found on *Gasterosteus*. Raw data measured to ± 0.1 mm. Graph shows three-point moving average.

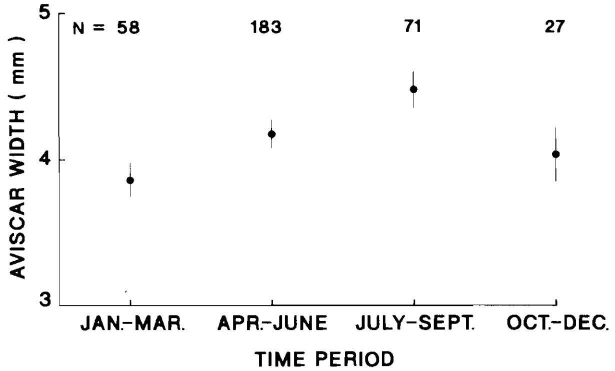

FIG. 4. Seasonal effects on mean aviscar width (± 1 SE). Multiple means comparisons (Student – Newman – Keuls test) show significance ($P<0.05$) only for differences between January – March and July – September.

scars) among the 15 surveys was not significant (*F*-ratio = 1.6, $P = 0.24$, ANOVA).

Nonrandom associations occur between structural injuries and skin injuries ($\chi^2 = 1558.3$, $P<0.001$), which provide information on the injury-producing process (Table 1). Among the 1475 injured fish, 31% had both structural and skin injuries, 34% had only structural injuries while 36% had only skin injuries. An additional category of attacked fish, lacking both structural and skin injuries, is probable, although its proportions cannot be reliably predicted with the current data. Fish with bent spines, which are equivocal in origin, had intermediate frequencies of skin injuries when compared with fish that had no spine damage and those with broken spines. This result suggests that the injuries result from developmental anomalies in some cases and from predator activity in others. Minor skin injuries, also equivocal in origin, occurred on 2.2% of all fish without structural injuries, yet occurred on 22% of fish with fractured spines, indicating that the majority of minor skin abrasions were the consequence of predator manipulation. If such abrasions were primarily from agonistic encounters with conspecifics, nest construction, and abrasion with the substrate, frequencies of minor skin injuries should be independent of structural injuries.

Some injuries will not be visible if there are effective repair processes that mask the injury over time. For structural injuries, such processes seems unlikely because spines that have fused and regrown are visually distinct from undamaged spines. However, skin injuries might be less evident after repair. To test this possibility, I compared the extent of skin damage on fish attacked recently with that of fish with progressively older attacks (judged by amount of spine regrowth). I assumed that spine and skin injury were incurred during the same attack. The data (Fig. 6) indicate that many skin injuries are as persistent as spine injuries over time. However, there is an approximately 30% loss of major injuries (including aviscars) for each 1 mm spine regrowth (possibly 1 year) and a corresponding increase in the percentage of fish without detectable skin injuries. This loss of major skin injuries could also reflect increased mortality from trauma as I observed that several of these fish had extensive edema in the region of the injury.

Total incidence of injuries was 16.9% in the population. As a conservative classification, I include spine fractures, aviscars, and major skin damage as predator induced, excluding forked spines, bent spines, and minor skin injuries. This definition reduces the incidence to 13.4% for predator-induced injuries. The proportion of attacked fish will be underestimated by this value since it does not include fish that escaped without injuries or fish with fully repaired (not detectable) injuries.

Body size and frequency of injury are strongly correlated. Injuries were absent among juvenile fish (<50 mm), rare among subadult fish (50 – 70 mm), and common among adults, with frequencies increasing among progressively larger adult fish. In the largest length group (84 – 95 mm), an average of 16% (range 6 – 32%) of the fish were injured. Partitioning the data between years indicated a similar pattern in 1981, 1982, and 1983 (Fig. 7).

Average injury frequencies fluctuated from a low of 6% to a high of 18% over the study period (Fig. 8). Minimum values, which occurred in early summer, were followed by a doubling of the frequencies during late summer and early fall. These values remained elevated until late spring. Differences in mean body size among the 15 surveys accounted for some of the temporal fluctuations; for example, reduced injury frequencies coincided with smaller standard length in 1982 (Fig. 8). To estimate temporal patterns of injuries, independent of body size, I regressed injury frequency against body length for each of the 15 surveys and calculated the incidence for the average adult body size ($\bar{x} = 80$ mm). However, seasonal trends in adjusted frequencies were similar to the unadjusted data.

Stickleback marked and released as adults incurred predator injuries during their subsequent 2 or 3 years of life. Linear regression of injury frequency of recaptured fish against time shows that the probability of incurring a predator-induced injury as an adult was 0.09/year (Fig. 9). Rates were not constant, since in both 1986 and 1987 there was an approximate doubling of the incidence of injuries during the month of July. This increase coincided with the major seasonal incursion of foraging Common Loon onto the lake (Reimchen and Douglas 1980).

Discussion

A general conclusion emerging from evolutionary studies of *Gasterosteus aculeatus* is that predation exerts a major effect on morphological differentiation among populations (Hagen and Gilbertson 1972; Moodie 1972; Moodie and Reimchen 1976; Reimchen 1983; Bell 1984*a*; Wootton 1984). Results of the present study provide some of the first empirical evidence that substantial numbers of stickleback escape during predator

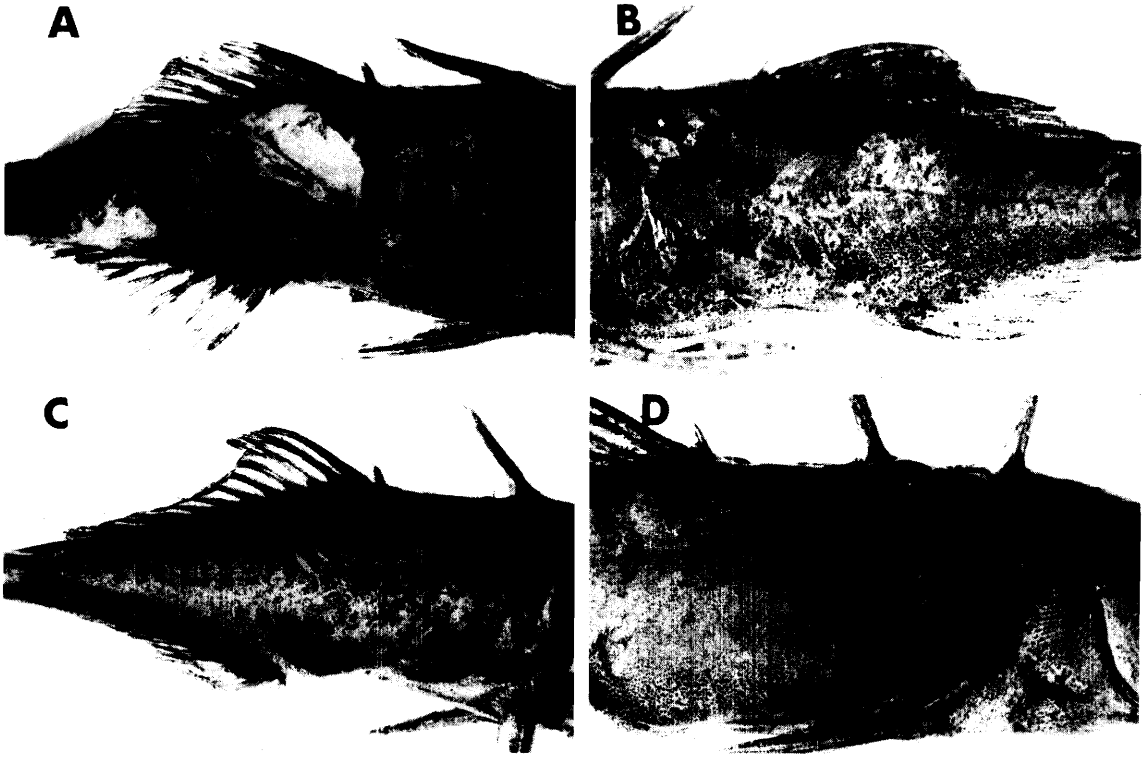

FIG. 5. Representative skin injuries on Drizzle Lake *Gasterosteus*. (A) Ripped skin. (B) General abrasion. (C) Curvilinear scratches. (D) Crescent scars.

manipulation, recover from injuries, and retain a record of the attack.

External spines provide diverse advantages to prey. They increase effective body size, which is known to prolong manipulation time for gape-limited predators (Werner 1974; Zaret 1980; Hoyle and Keast 1987); they pierce the mouthparts of the predator causing temporary release of the prey (Hoogland et al. 1957). The prevalence of spine fractures among survivors of predator attacks attests to the effectiveness of spines in these stickleback as a defense against predator manipulation. That many of the fish with fractures had no skin injuries suggests that another function of spines is to minimize injurious contact between the mouthparts of the predator and the body of the prey. This factor would be particularly important against a tooth-bearing predator from which skin punctures, with resultant infection or osmotic shock, could potentially reduce survivorship.

Force exerted on *Gasterosteus* spines by a predator is transferred initially to the central condyles of the basal plates, from central regions of the plates to the lateral flanges, and from the flanges to the lateral plates (Reimchen 1983). Each of the components is theoretically capable of mechanical failure. However, the vast majority of failures occurred on the spine rather than on the condyle, flange, and lateral plates; this pattern emphasizes the efficiency of these support structures in the redistribution of forces applied to the spines.

Recognizing the source of injuries remains problematic in most studies, since the manipulation event is rarely observed. At least one-third of the injuries in the present study were the result of attacks by avian piscivores as evidenced by aviscars. These highly characteristic scars are regularly observed in other populations of *Gasterosteus* (T. E. Reimchen, personal observation) and in other taxa including *Pimephales* (Smith and Lemley 1986) and *Oncorhynchus* (R. Le Brasseur, personal communication). Since manipulation failures of avian piscivores are generally greater than 25% (for review, see Vermeij 1982), populations subjected to these predators could be expected to exhibit aviscars. Prefledged Red-throated Loons have a 20% failure rate in manipulating relatively small prey and a 100% failure rate in manipulating large-bodied prey (Reimchen and Douglas 1984*b*). Approximately 20% of the stickleback escape from adult Red-necked Grebes (Reimchen 1983), while subadult and inexperienced grebes have about 80% manipulation failure (T. E. Reimchen, personal observation). Width of the aviscar provides clues to species, although extensive variability in position of the fish in the bill constrains any simple association between aviscar width, bill width, and species. In the present study, Red-necked Grebes and Common Loons were the dominant avian species that foraged regularly on the lake, the former from September to May and the latter in mid-July (Reimchen and Douglas 1980, 1984*a*), a distribution which is consistent with the seasonal changes in mean aviscar width.

An unresolved issue in this study is identification of the sources of those injuries not associated with aviscars (skin lacerations, spine fractures). Some of these injuries were likely from avian subjugation in which bill contact was asymmetrial and irregular, or in which there was only contact with the spines. Among all fish with aviscars, 72.1% lacked fractured spines, indicating that fractures are not the usual consequence of an unsuccessful attack by avian piscivores. Therefore, some other predator is implicated. Piscivorous fish are major causes of mortality of stickleback (for review, see Wootton 1984) and large-bodied predatory fish (*Esox*, *Perca*, *Salmo*) have diffi-

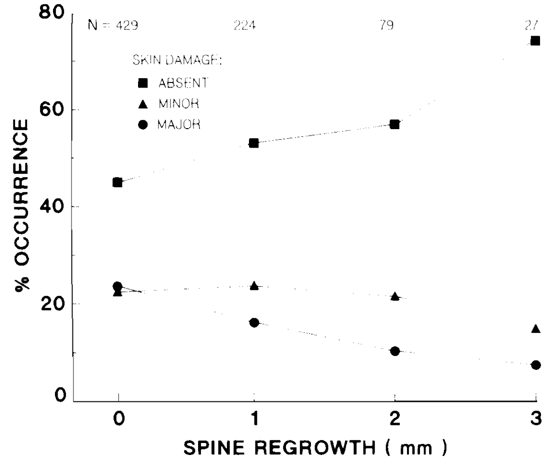

FIG. 6. Relationship between skin injuries and age of fracture as assessed by spine regrowth.

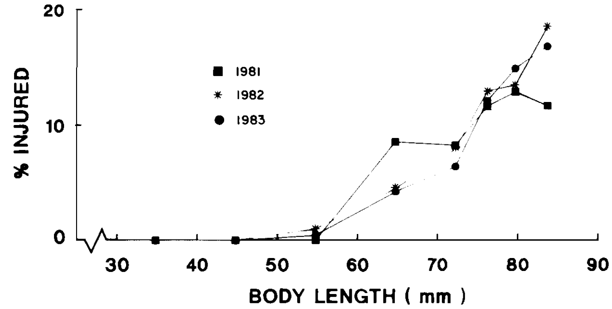

FIG. 7. Incidence of predator-induced injuries at different body lengths (SL) of fish.

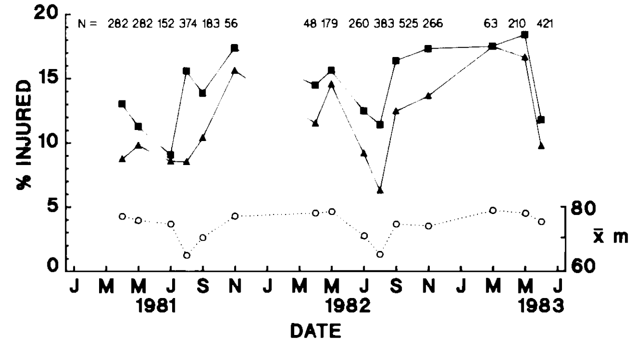

FIG. 8. Incidence of predator-induced injuries over time. Square, frequencies adjusted to standard length of 80 mm; triangle, unadjusted frequencies; dotted line shows mean body length (SL) for each survey.

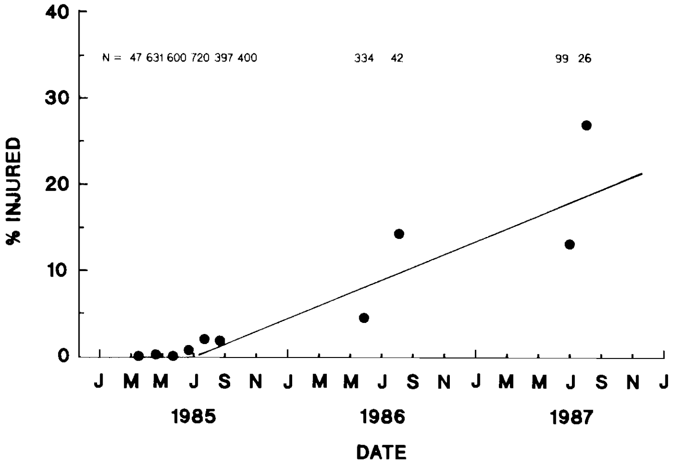

FIG. 9. Rate of injury formation among recaptured adult stickleback. Data points represent frequencies of predator-induced injuries among stickleback recaptured at increasing time intervals from release date (March–May 1985). The number of uninjured fish marked was 12 272. The regression line was calculated for data points extending from date of first recapture (April 1985).

culty in subjugating relatively large-bodied stickleback (Hoogland et al. 1957; Moodie et al. 1973). In the present study, *Salmo clarki* could be the principal source of spine injuries; it is a major predator in this population and is capable of producing the forces required for spine fracture (Reimchen 1983). If it is also assumed that the minor and major curvilinear scratches are the consequence of raking of vomerine teeth (e.g., Reist et al. 1987), this predator could account for up to 50% of total injuries. However, its actual contribution cannot be resolved without further information on manipulation techniques and efficiencies.

Frequencies of predator-induced injuries represent a complex of interacting factors including predation rate, predator inefficiency, age structure of the prey population, and survivorship of injured individuals (Edmunds 1974; Schoener 1979; Schoener and Schoener 1980). Consequently, differences in injury frequency between seasons, populations, or species may result from fundamentally different causes. The reduction and subsequent increase in injuries during summer months observed in the present study is multifactorial. Although adjusting mean frequencies to a standard body length did not substantially reduce these seasonal shifts relative to unadjusted values, I suspect that there is an age effect that is not reflected in these length measurements. During late spring there was a major increase in the numbers of prereproductive adults entering the traps (T. E. Reimchen, unpublished data). These individuals, which would not breed until the following year, could be distinguished from older adults of the same size in part by their retention of pigmentation patterns (countershading) characteristically found on subadult and juvenile fish. Since younger fish had very low incidences of injuries, this could produce the observed seasonal reduction in injury frequencies. The trend could also be accentuated since old fish (which have the highest injury frequencies) tended to be found close to shore (Reimchen and Nelson 1987) and as such were not equally represented in the full-lake collections. As well, old fish die after their final spring spawning season (Wootton 1976), which would be expected to further reduce the proportion of injured fish during late spring. In contrast, the rapid increase in injury rate following this initial reduction was probably largely due to increased predation rate resulting from the major incursion of foraging Common Loon onto the lake in July (Reimchen and Douglas 1980).

One of the clear patterns to emerge in the present study was the absence of injuries among juvenile fish (<50 mm). This observation is puzzling because these size classes are subject to predation by small-bodied avian piscivores (*Podiceps auritus*) (Reimchen and Douglas 1984*a*) and by a broad size range of *Salmo clarki* (16–42 cm) (T. E. Reimchen, unpublished data). Repair processes are probably rapid and efficient during early ontogeny and, consequently, if injuries were incurred, they may not have been detectable, a characteristic recently described in coral reef fish (Foster 1985). Bent and forked spines on adult fish possibly represent these juvenile injuries. Alternatively, if the absence of injuries among juveniles is real, there is a threshold near 50 mm under which manipulation efficiencies are very high in the complex of predators at this locality.

Among subadult and adult sticklebacks, injury frequency was strongly correlated with body size. Increased size is known to provide a refuge against predation since most predators are limited by gape (Werner 1974; Zaret 1980). Thus, manipulation efficiency is high when prey are well within the gape capabilities but declines rapidly as maximum gape is approached (Hoyle and Keast 1987). Observations on foraging behaviour of Red-necked Grebe (see methods) show that adult stickleback from this locality clearly approach the gape limitations of the bird since fish are regularly rejected after prolonged bouts of manipulation. While experimental observations have not been carried out, it is highly plausible that the rise in injury rate on fish between 70 and 90 mm is a direct result of increasing manipulation inefficiency of predators.

Yet injury frequencies among adults will show a similar increase, independent of body size, if the likelihood of predator escape is constant over time (for example, Schoener and Schoener 1980). Recapture data, which are consistent with this process, showed that adult sticklebacks (>70 mm) had a 9% chance/year of incurring an injury. Since sticklebacks in this population reach maturity at ca. 24 months of age and can survive for at least 2–3 years as adults, one would expect at least 18% injury frequencies among the largest adults; this is close to the observed value (see Fig. 7). Therefore, the relationship between body size and injury frequency may be fundamentally a consequence of increased manipulation inefficiencies accentuated by the longevity of individuals in the population.

Large body size (>80 mm) in *Gasterosteus* is exceptionally uncommon, being recorded only from six localities on the Queen Charlotte Islands (Moodie and Reimchen 1976; T. E. Reimchen, unpublished data) and at least one locality in Alaska (Bell 1984*b*). In the detailed study of one of these populations (Mayer Lake, Queen Charlotte Islands), Moodie (1972) concluded that large body size was an adaptation to extensive vertebrate predation although the actual mechanism could not be identified. Numerous factors could be involved in selection for large body size including longevity, gravidity, and swimming speed. The present study shows that manipulation inefficiencies would contribute an additional and perhaps major component to the evolution of gigantism.

In conclusion, the current data on classes of injuries and their size-dependent frequencies establish a framework for examining these traits in other populations. The prevalence of manipulation failures provides unique opportunities for analysing components of fitness among diverse phenotypes. Since different predators are suspected of producing opposing selective pressures on the morphology of *Gasterosteus* (Reimchen 1980, 1983), characterizing injuries produced by each predator is critical to further investigation of these phenomena.

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