PREDATOR-INDUCED CYCLICAL CHANGES IN LATERAL PLATE FREQUENCIES OF GASTEROSTEUS

by

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Summary

This study investigates ecological aspects to intrapopulation variability in the lateral plates of threespine stickleback (*Gasterosteus aculeatus*) at a coastal lake in western Canada. The frequency distribution of the plates, which was slightly skewed to the right and leptokurtic, varied spatially and seasonally. Cyclical frequency changes in plates were most pronounced on sub-adult size classes and these closely tracked (multiple r = 0.77) seasonal differences in the relative proportion of the two major predator groups, trout and diving birds. Trout predation was correlated with an increase in plate number while bird predation was correlated with a reduction in plate number. Such divergent selection pressures, which are probably common in natural populations, would account for the presence of multiple phenotypes and allow for rapid shifts in defensive morphology among different populations where predation regime differs.

Introduction

There has been major empirical and theoretical progress in understanding evolutionary processes in natural populations (reviews in FUTUYMA, 1979; ENDLER, 1986). One of the areas which has received limited attention is evaluating the extent to which intrapopulation variability in continuously distributed traits is functional. Investigations of trophic structures show that variability is advantageous where there is habitat diversity as different phenotypes can exploit slightly different niches (VAN VALEN, 1965; SCHOENER, 1968; POWELL & TAYLOR, 1979; GRANT & PRICE, 1981;

PATTERSON, 1983; HEDRICK, 1985; GRANT & GRANT, 1989; WILSON, 1989; SMITH, 1990). However, direct evidence for such habitat specialization has not been extensively reported in the literature and this has led some workers (*i.e.* FUTUYMA & MORENO, 1988) to suspect that such genotype specialization is probably not important in natural populations.

I have undertaken a study of a meristic trait associated with predator defence to determine, as with previous studies of trophic characters, whether there is a functional context to intrapopulation variability. The bony lateral plates on threespine stickleback (*Gasterosteus aculeatus*), which are associated with predator defense (HAGEN & GILBERTSON, 1972; MOODIE, 1972; MOODIE & REIMCHEN, 1976; GROSS, 1978; REIMCHEN, 1983; BAŃBURA *et al.*, 1989; reviews in WOOTTON, 1984, REIMCHEN, 1994), are highly variable in number and position among individuals and populations. Plate numbers are heritable and controlled at multiple loci (HAGEN & GILBERTSON, 1973a) and they usually exhibit a bell-shaped frequency distribution. Over a four year period I monitored activity of piscivores at a remote lake off the west coast of Canada and intensively tracked both spatial and temporal variability in the lateral plate phenotype frequencies on an endemic population of stickleback. The results provide insight into the functional attributes of lateral plate variability and allow comment on the general importance of microevolutionary processes in population differentiation.

Study area and life history

Drizzle Lake (110 ha) occurs in a low elevation *Sphagnum* bog on the Queen Charlotte Islands off the west coast of Canada. Lake perimeter and bathymetry are simple and there are no physical impediments to fish movement within the lake (Fig. 1). The stickleback are large-bodied forms which are reproductively isolated from small-bodied phenotypes found in adjacent streams (REIMCHEN *et al.*, 1985). Molecular analyses indicate that the population is derived from marine stickleback, probably in post-glacial periods (GACH & REIMCHEN, 1989; O'REILLY *et al.*, 1993). During spring and summer, stickleback occupy diverse habitats in the lake (littoral/limnetic: benthic/pelagic) but during autumn and winter, fish are more abundant offshore than inshore. First reproduction occurs at approximately three years and lifespan can reach at least 8 years in the lake (REIMCHEN, 1992b).

Approximately one-half of the yearly predation on stickleback (N = 562 000) is caused by trout (*Oncorhynchus clarki*) and one-half is caused by avian piscivores, principally loons (*Gavia immer*) and grebes (*Podiceps grisegena*). Trout take primarily small fish (< 50 mm), secondarily sub-adults (50-70 mm) and low numbers of adults (> 70 mm). Birds take primarily sub-adults and adults. Both groups of piscivores are found over much of the lake but trout tend to be more common near the shore and birds are more prevalent in open water (REIMCHEN, 1990, 1994). Proportion of these two predator groups change substantially within and among seasons.
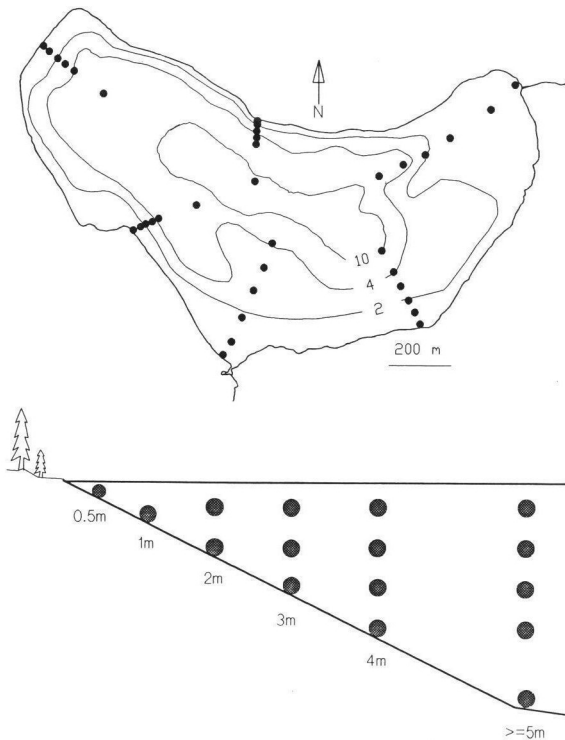
Fig. 1. Outline of Drizzle Lake with and sampling grid. A: bathymetry contours (m) and horizontal sampling sites. B: Trap positions in the water column.

Predictions are possible on the directionality of spatial and temporal changes in plates. Stickleback with seven or more plates have been previously shown to have advantages against trout predators (HAGEN & GILBERTSON, 1972, 1973b; MOODIE, 1972; MOODIE *et al.*, 1973; MOODIE & REIMCHEN, 1976) while those with fewer plates may have advantages against bird predators (REIMCHEN, 1994). Stickleback in Drizzle Lake typically have from two to eight plates and if the range in plates is an adaptation to trout and bird predators, the frequency distributions should be shifted to higher counts with increased trout predation and to lower counts with increased bird predation. In contrast, uniformity of phenotype frequencies over these spatial and temporal ecological gradients would indicate that the plate variability was not an adaptation to the divergent predation regime.

Methods

Nineteen sampling transects were undertaken from 1980 to 1983 spaced four to ten weeks apart. In each transect, I set 96 wire-mesh funnel traps around the lake to encompass six different geographical sectors, six horizontal sites from shoreline to open water, and one or more sites in the water column (Fig. 1). Horizontal positions corresponded to depth contours of 0.5, 1, 2, 3, 4 and > = 5 m. These were baited (1 cc old cheddar cheese) and left for 48 hours. On retrieval, all adult fish, which comprised about 90% of each sample, were

measured for standard length (SL), first dorsal spine length, position and number of lateral plates (LP) on both sides of the body and occurrence of predator-induced injuries (details in REIMCHEN, 1988). Over the 19 transects, 11146 stickleback were analyzed. Approximately 80% of the fish were released near the site of capture. The remainder, including a random subset of adults, injured fish and all sub-adults were retained for further morphometric analyses in the laboratory. Plates on sub-adults could not be reliably scored in the field and consequently were scored later under a dissecting scope. For this article, I use only plate counts from the left side of the body, which is the convention for studies of *Gasterosteus*. Numbers of fish were low in all traps suspended in the water column. Therefore, grouping of data were necessary for statistical purposes. An upper and lower zone was defined, the former including the surface, 1 and 2 m traps and a lower including all the deeper traps. This grouping essentially corresponds to the photic and aphotic zones.

I estimated total number of stickleback consumed monthly by the major avian and salmonid predators (details in REIMCHEN, 1994). Daily counts of avian piscivores and their foraging activity were recorded throughout much of the study period and during these observations, total daily consumption of stickleback was derived from numbers of stickleback brought to the surface per time block. These values were similar to estimates based on daily caloric requirements (REIMCHEN & DOUGLAS, 1984). Monthly population estimates of trout were determined from mark/release/recapture studies; prey species and prey sizes were determined from trout stomachs collected throughout the year. Trout numbers and diet were then combined to provide total monthly consumption for each size class of stickleback (REIMCHEN, 1990). In the present study, I deal with predation on sub-adult and adult stickleback. Sub-adult ages are 18-32 months while adult ages are 3-8 years (REIMCHEN, 1992b).

For statistical analyses, I used parametric tests (ANOVA, multiple range tests, multiple regression) and non-parametric tests (chi-square, log-likelihood, Fisher Exact, sequential Bonferroni) (SPSS/PC 4.0, STATISTICA^{TM}). For the non-parametric analyses of plate distribution, I grouped the phenotypes into lower-plate group ($< = 4$) and higher-plate group ($> = 5$). This separated the sample into groups of similar size. I also separated the data into two size groups, sub-adults (50-70 mm) and adults (70-95 mm). For estimating directional selection coefficients, I used standard equations from ENDLER (1986).

Results

Overall frequency distribution was unimodal at five plates and was stable over the four years (Fig. 2). The cumulative distribution is slightly skewed to the right (g1 = 0.24, p < 0.001) and moderately leptokurtic (g2 = 2.67, p < 0.001).

Spatial patterns of plates were examined for different depths in the water column (Fig. 3). Among 29 comparisons (19 transects for adults, 10 transects for sub-adults), five (2 adult comparisons, 3 sub-adult comparisons) were statistically significant (p < 0.05). In four of the five tests, lower-plated phenotypes (< = 4LP) were more common than expected in surface traps. However, none of these significance levels reach the table-wide significance level (p = 0.002) for a sequential Bonferroni test.

Horizontal distributions of the plate phenotypes were also examined. In all seven of the nineteen transects where there were significant differ-
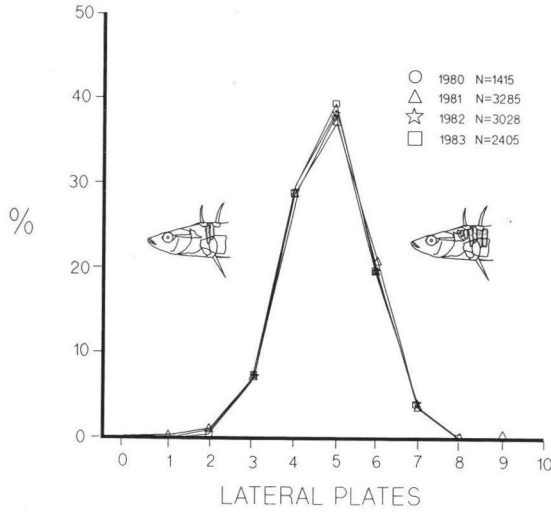
Fig. 2. Frequency distribution of number of lateral plates on stickleback from Drizzle Lake (1980-1984). Insets shows schematic phenotypes with two and seven lateral plates.
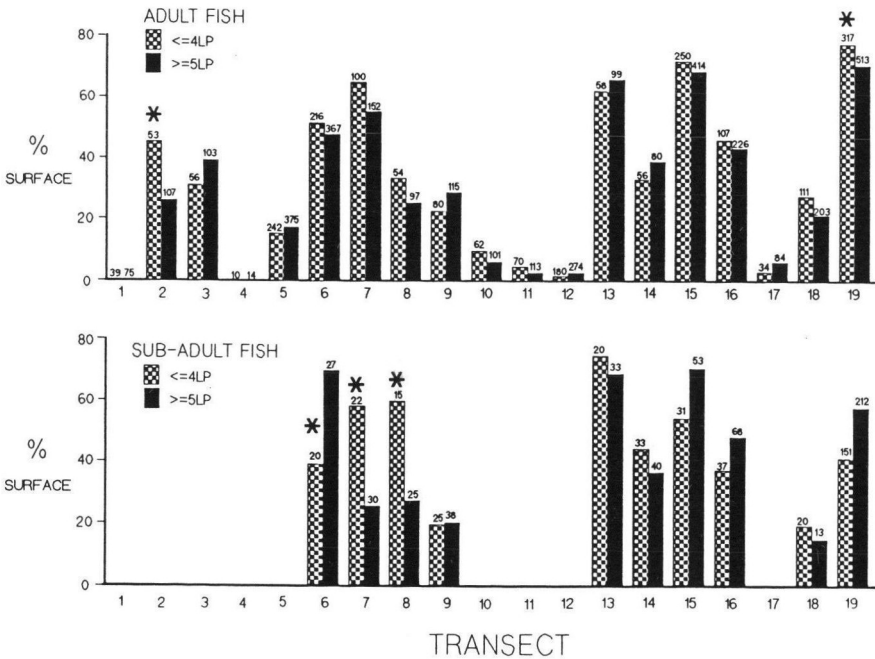

Fig. 3. Distribution of lateral plate phenotypes in relation to depth in the water column. Vertical axis shows frequency of low and high plated phenotype in surface traps. *: p < 0.05.

ences among horizontal zones (pairwise means tests, p < 0.05), the littoral sample closest to the shore had significantly higher plate counts than the adjacent sample (Fig. 4). Similar comparisons for sub-adults are not possible as these size classes are primarily in open water habitats.

Lateral plate variability among lake sectors was examined. Among 30 comparisons (19 transects for adults, 11 transects for sub-adults), chi-square analyses for plate group (< = 4, > = 5) and sector (NW *vs* SE) demonstrate that two of 30 comparisons were significant. This proportion could be expected by chance alone. As well, there were no trends among samples as 14 comparisons had an excess and 16 had a deficiency of higher plate counts in the south-east sectors.
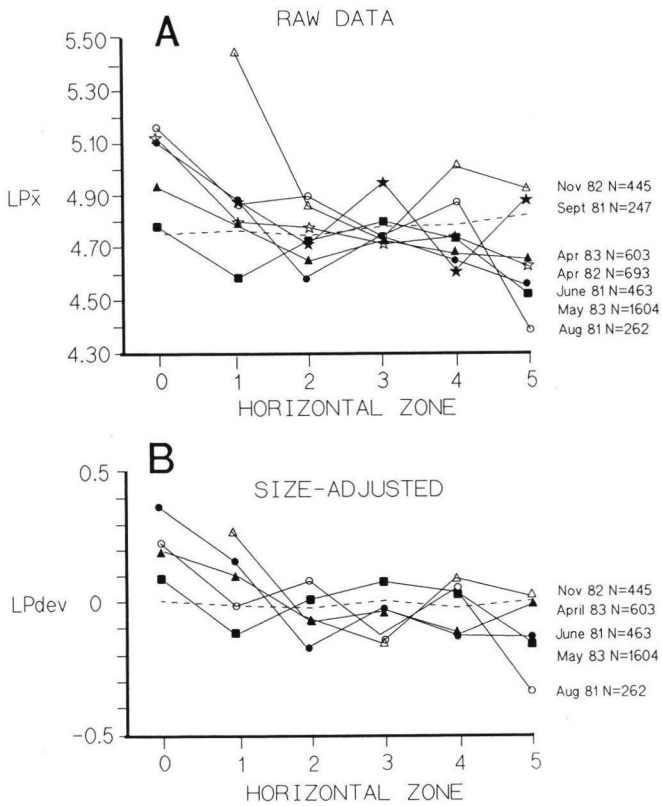

Fig. 4. Relationship between lateral plates and horizontal zone in lake. Continuous lines represent each transect with significant pairwise comparisons among means. Dashed line is the cumulative means for all remaining transects. A: Mean number of lateral plates. B: Lateral plate residuals (influence of body size removed).

Temporal changes in mean plate number occurred over the study period. Among adults, mean plates varied by 4%, lowest values ($\bar{x} = 4.73$) occurring during winter/spring of 1981 and spring of 1983 and highest values ($\bar{x} = 4.93$) occurring in winter 1982/1983 (Fig. 5a). Single factor ANOVA on plates for all transects was not significant ($F = 1.40$, $p = 0.12$) although LSD and Duncan's multiple range test show differences ($p < 0.05$) between means in February and April, 1983. However, among sub-adult stickleback (Fig. 5b), mean plate number was much more variable than that of adults (Variance ratio-test, $F = 19.5_{15,18}$, $p < 0.001$) with
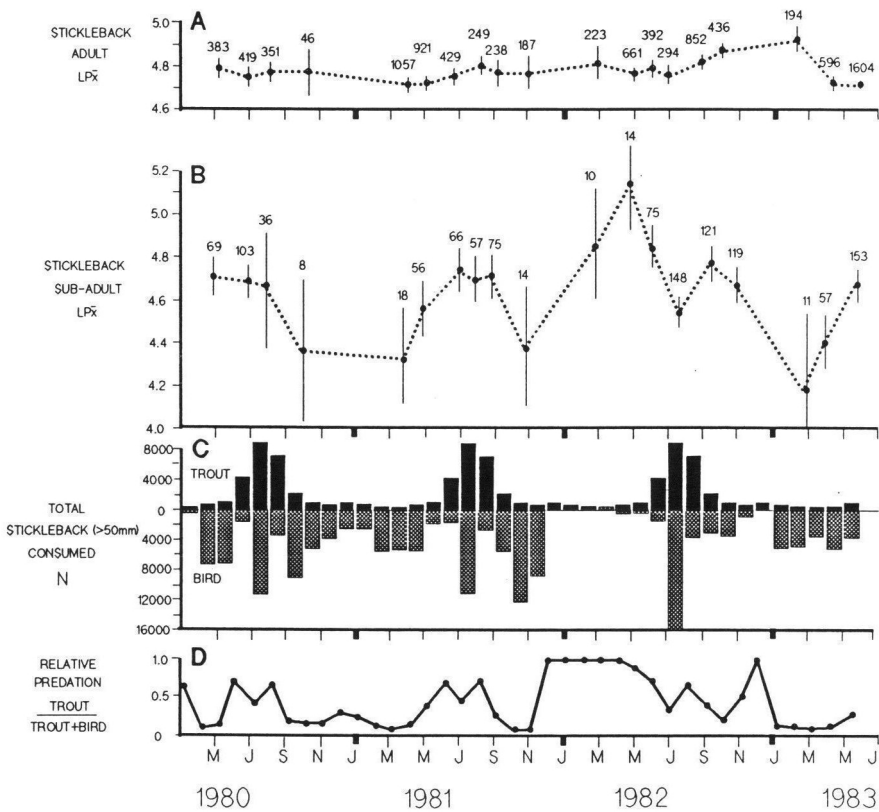
Fig. 5. Temporal variability in lateral plates and predation regime at Drizzle Lake. A: Mean number of lateral plate (± 1 SE) for adult stickleback. Sample sizes shown for each transect. B: Mean number of lateral plate (± 1 SE) for sub-adult stickleback. Sample sizes shown for each transect. C: Total stickleback consumed monthly by trout (black histogram) and diving birds (hatched histogram) over duration of study period. D: Ratio of trout to bird predation over duration of study period.

means varying by 21% among transects (4.18 to 5.18). ANOVA of plates among transects is significant ($F = 1.74$, $p = 0.039$). In each year, elevated plate means tended to occur during spring and summer while lowest means occurred during winter. These results, while statistically informative, must be interpreted cautiously given some of the small sample sizes.

Estimates of total monthly predation levels on stickleback ranged from 440 to 25,000 (Figure 5c). Consumption by trout was highest in summer (9000 stickleback per month) and lowest in winter (440 per month), largely as a consequence of temperature-related differences in metabolic rate (REIMCHEN, 1990). Avian piscivores varied in abundance among seasons and years (REIMCHEN & DOUGLAS, 1984). Average monthly consumption of stickleback by birds was about 4000 during spring, autumn and winter and up to 16,000 during summer. The major exception to these seasonal trends occurred from December 1981 to May 1982 when birds were absent due to prolonged winter ice cover and cool spring temperatures.

Proportional consumption of stickleback by the two major predator groups (Fig. 5d) shows bird predominance (low ratios) during spring and autumn, roughly equal consumption by the two groups during summer and an extended period of trout predominance (high ratios) during the first half of 1982.

I predicted that trout predation should result in higher plate means while bird predation should lead to lower plate means. Multiple regression was carried out on data from adult and sub-adult stickleback using the following variables: TOTAL (total stickleback consumption by trout and birds), RATIO (proportion trout/trout+bird) and SL (standard length of stickleback). Among adult stickleback, the regression was not significant (multiple $R^2 = 0.15$, $F_{3,15} = 0.92$, $p = 0.46$, adjusted $R^2 = 0.00$) and none of the variables were significantly correlated with LP (partial correlation TOTAL $= 0.20$, $p = 0.44$; RATIO $= 0.01$, $p = 0.96$; SLADULT $= 0.27$, $p = 0.3$). Comparable analyses on sub-adults yielded a highly significant association (multiple $R^2 = 0.77$, $F_{3,15} = 7.1$, $p < 0.004$, adjusted $R^2 = 0.50$) of which RATIO was the only variable that contributed a significant effect (standardized regression coefficient $= 0.72$, $p < 0.002$). Partial correlations were -0.09, 0.69 and -0.04 for TOTAL, RATIO and SLSBADULT respectively. This association is not a consequence of several outliers contributing disproportional statistical effects.
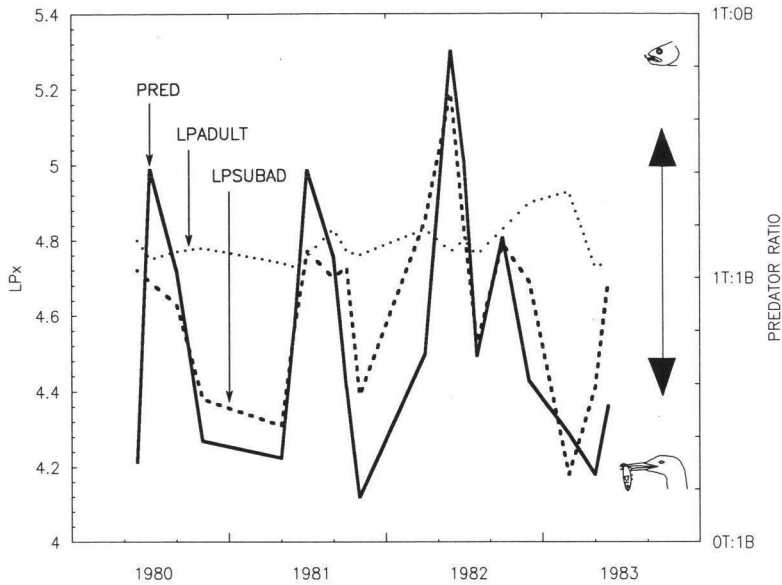
Fig. 6. Summary plot of mean number of lateral plates for adult (LPADULT) and sub-adult (LPSUBAD) stickleback against predation regime (PRED) over the study period. Right axis shows relative predation by the major groups (trout - T and diving birds - B).

Rather, it is due to the cyclical tracking between RATIO and LP (Fig. 6). The three major periods with increased bird predation over the 4 years were in each case followed by a sharp reduction in LPx.

Directional selection differentials were calculated for mean LP between sequential samples among the 19 transects (Table 1). For adults, absolute values for directional selection (i, sign ignored) ranged from 0.01 to 0.25 ($\bar{x}$ = 0.05) of which a single comparison (Trans #18) reached statistical significance (p < 0.02). For sub-adults, i (sign ignored) ranged from 0.02 to 0.69 ($\bar{x}$ = 0.25), three of which (Trans #14, #15, #19) were statistically significant (p < 0.05). Direction of change (+/-) was largely symmetrical for both adults and sub-adults. Two of the significant values were negative and two were positive.

Discussion

These data suggest that predator-mediated cyclical selection is occurring on the lateral plates in sub-adult stickleback, with trout predation tending to produce an increase in plate means and bird predation tending to

TABLE 1. Directional selection differentials (i) on lateral plates for adult and sub-adult stickleback at Drizzle Lake

Transect	Adult			Sub-adult		
	i	t	df	i	t	df
2	0.05	0.72	802	-0.04	0.23	172
3	0.02	0.28	770	0.32	1.65	139
4	0.01	0.07	397	-0.69	1.72	44
5	-0.05	0.27*	1113	-0.05	0.15	101
6	-0.01	0.23	1978	0.26	0.95	74
7	0.03	0.56	1350	0.22	1.29	122
8	0.08	0.96	678	-0.08	0.45	123
9	-0.06	0.68	587	0.02	0.13	130
10	-0.01	0.11	425	-0.39	1.28	87
11	0.08	0.71*	424	0.43	1.13	24
12	-0.06	0.80*	884	0.27	0.69	24
13	0.03	0.51	1053	-0.32	0.97	88
14	-0.04	0.57	678	-0.33	2.43	217
15	0.08	1.08	1142	0.31	2.30*	264
16	0.07	1.24	1294	0.10	0.77	239
17	0.03	0.39	630	-0.51	1.59	129
18	-0.25	2.73*	790	0.20	0.73	86
19	0.01	0.22	1934	0.30	2.03	210

T-values show statistical significance of i. *: $p < 0.05$.

reduce plate means. Although there were slight spatial associations in the lake between plate frequencies and predator group, it was primarily temporal variability in the relative proportion of each predator group that produced the recurrent changes within and between seasons. Such a bi-directional selective regime will contribute to the maintenance of lateral plate variability within the population as there are multiple optima. These data are consistent with hypotheses of adaptive variation for continuously distributed traits (VAN VALEN, 1965; GRANT & PRICE, 1981; WILSON, 1989) and extend the conclusions from previous studies of gasterosteids that have demonstrated close associations between morphology and predation among different geographical localities (e.g. HAGEN & GILBERTSON, 1972; MOODIE, 1972; MOODIE & REIMCHEN, 1976; GROSS, 1978; REIMCHEN, 1980; review in REIMCHEN, 1994). If the changes observed are in fact the result of differential predation, then the data also suggest that population differentiation could occur very quickly when predation regimes change.

Lake populations from the northern hemisphere exhibit regular seasonal differences in a diversity of biophysical parameters each of which

might influence strength and direction of selection. Predatory fish forage throughout the year but their consumption rate drops during winter while avian piscivores will forage throughout the year unless excluded by winter ice cover. In coastal British Columbia, large flocks of non-breeding common loons move from marine waters onto some freshwater lakes only during July and forage extensively on stickleback during a three week period (REIMCHEN & DOUGLAS, 1980). Red-necked grebe occur on coastal lakes in autumn, winter and early spring but are absent during summer. Doubled-crested cormorant (*Phalacrocorax auritus*) occur on lakes during January and February but not during the rest of the year. Common merganser (*Mergus merganser*) occur in large numbers during early spring and late autumn and occasionally forage extensively on threespine stickleback at the lake surface during twilight (REIMCHEN & DOUGLAS, 1984). In some streams of northern Europe, mergansers forage extensively on *Gasterosteus* only in spring (RAD, 1980). Anadromous cutthroat trout enter rivers during high runoff in October and November and migrate into lakes where they overwinter (REIMCHEN, 1990). When these seasonal differences are combined with yearly fluctuations in the proportion of each species, there is ample opportunity for temporal variability in selective regime and therefore, it seems reasonable that short term temporal variation in selection would be common in these populations. Such cyclical selection has been observed in other taxa (*e.g.* SHEPPARD, 1951; FORD, 1964; SAMOLLOW, 1980; review in ENDLER, 1986).

Gene flow between populations can also be expected to contribute to the persistence of variability in a strongly selected population (FALCONER, 1967). Investigations of the large-bodied stickleback from Mayer Lake show evidence for hybridization near the stream mouths between the lake and stream form (MOODIE, 1970). The large-bodied stickleback in Drizzle Lake spatially overlap with a small- bodied stickleback which breeds in streams that flow into and out of the lake. These forms differ in multiple morphological traits and there is no evidence for hybridization (REIMCHEN *et al.*, 1985). Recent mitochondrial DNA analyses of numerous freshwater and marine stickleback from the Queen Charlotte Islands demonstrate that most populations have multiple haplotypes while Drizzle Lake stickleback have only a single haplotype (O'REILLY *et al.*, 1993) which further suggests that gene flow is not a substantive cause for plate variability in this population.

Some of the phenotypic variability within populations may be associated with habitat differences among the sexes (SELANDER, 1966; SLATKIN, 1984; BOROWSKY, 1990). In stickleback populations on the Queen Charlotte Islands, males have slightly higher plate counts than females (MOODIE, 1972; MOODIE & REIMCHEN, 1976; REIMCHEN et al., 1985) and therefore, sex ratio differences within the lake could shift plate distribution. I compared plate distribution of 812 males and 1289 females from Drizzle Lake; mean plate counts differed by 1.9% (male = 4.78, female = 4.69). If all of the adults near the shore were males, this would account for less than one-quarter of the 10% change in plate frequencies in the littoral habitat. In actuality, there was only a marginal excess of males near the shore (57%, N = 310) which shows that habitat differences between the sexes only contribute a small proportion to the spatial differences in plate frequencies.

It was primarily variation in sub-adults rather than adults that tracked the divergent predation regime. Presumably, this is because sub-adults are a more defined age cohort than those of the adults and are subject to much higher levels of predation. Such a trend has also been observed in studies on polymorphic traits in several diverse taxa (i.e. GIESEL, 1970; REIMCHEN, 1979, 1980; SAMALLOW, 1980). Seasonal movement of adults over multiple seasons would obscure site-specific or time-specific differentiation that could have developed during earlier periods in the life history.

ENDLER (1986) summarized published data on selection differentials in natural populations and calculated an average value of 0.59 among 36 species (maximum 2.0). In the current study, average values tend to be low (sub-adults = 0.27, adults = 0.05) and in most cases statistically non-significant. Because there was such close temporal tracking of the plates to predation regime, these non-significant differentials would appear to be biologically relevant. Small differentials such as these are probably the norm and distinguishing these from random sampling effects requires either exceptionally large samples or alternatively, sequential sampling over temporally varying selective pressures.

I have currently assumed that the changes in plate frequencies are the immediate result of differential predation but there are several issues which suggest that additional factors must be operating. To establish whether the observed predation rate will produce the observed changes in plate frequencies, I modelled the tracking between predation regime and

lateral plates for period between June 1982 and July 1982 when plate means dropped about 6%, from 4.83 to 4.53. Total population size estimates for adult stickleback (which comprise at least five separate year classes, REIMCHEN, 1992b) ranged from 30,000 to 120,000 (REIMCHEN, 1990); for sub-adults (which comprise a single year class), I estimate a population of 80,000. Birds consumed approximately 8000 more stickleback than trout during this period, most of which were sub-adults. Initial lateral plate frequencies were 0.41, 0.35 and 0.24 for LP4, LP5 and LP6 respectively for an average of 4.83 (see Fig. 1). Let us initially assume that plate phenotypes have a capture probability by birds of 1, 1.1 and 1.2 for LP4, LP5 and LP6 respectively. After one month, mean plates for the population would decline from 4.830 to 4.824, which is about 2% of the observed decline. If we assume that LP6 had twice the capture rate of LP4 (LP4 = 1, LP5 = 1.5, LP6 = 2), mean plate number would decline from 4.830 to 4.806, only 8% of the observed decline. To produce the observed change would require either a substantially lower population estimate or a greater differential among the phenotypes.

Temporal changes in phenotype frequencies might also result from behavioural differences among the phenotypes. For example, if phenotypes with increased plates became less attractive during periods of increased bird predation, they would be underrepresented in the trapping grid. There is precedence for this suggestion. At Mayer Lake, stickleback with seven plates differ in their nesting habitat and responses to disturbance compared with non-sevens (MOODIE, 1970). Stickleback with seven plates from other populations in coastal British Columbia are less likely to approach a predatory fish than non-sevens (MOODIE et al., 1973). In a stickleback population from western Europe, those with four or five plates are more aggressive than those with ten or twelve plates (HUNTINGFORD, 1981). Spatial variability in plate morph frequencies in a large quarry has also been detected with respect to depths in the water column and horizontal positions along the shore (MACLEAN, 1980). Stream channels have sharp clines in plate expression (HEUTS, 1947; BELL & RICHKIND, 1981; BAUMGARTNER, 1992). Dorsal and pelvic spine expression in stickleback from Boulton Lake, Queen Charlotte Islands, differed between littoral and limnetic habitats (REIMCHEN, 1980). Apart from the defensive complex of stickleback, other characters also exhibit within-locality variability including trophic structures (SCHLUTER & MCPHAIL, 1993) and

vertebral phenotypes (REIMCHEN & NELSON, 1987). If some phenotypes have higher fitness in one habitat than another, then a behaviour that produces a preference for the appropriate habitat will be strongly favoured (POWELL & TAYLOR, 1979, GARCIA-DORADO, 1986).

Morphological and behavioral differences within threespine stickleback populations have been described at different geographical and temporal scales. Currently, the differences at each scale broadly appear to be functionally associated with ecological differences (HAGEN & GILBERTSON, 1972; MOODIE & REIMCHEN, 1976; GROSS, 1978; BELL & RICHKIND, 1981; SCHLUTER & MCPHAIL, 1993; BELL, 1994; this study) indicating that microevolutionary forces are important in shaping population differentiation. Such a conclusion reinforces the traditional paradigm of adaptive radiation of form (MAYR, 1966; CAIN, 1971) and does not support developing views (*i.e.* GOULD, 1984) that much of the geographical variation within species is a non-adaptive product of history.

References

BAŃBURA, J., PRZYBYLSKI, M. & FRANIEWICZ, P. (1989). Selective predation of the pike *Esox lucius*: comparison of lateral plates and some metric features of the three-spined stickleback *Gasterosteus aculeatus*. — Zool. Scripta 18, p. 303-309.

BAUMGARTNER, J.V. (1992). Spatial variation of morphology in a freshwater population of the threespine stickleback, *Gasterosteus aculeatus*. — Can. J. Zool. 70, p. 1140-1148.

BELL, M.A. (1994). Paleobiology and evolution of threespine stickleback. — In: The evolutionary biology of the threespine stickleback (M.A. BELL & S.A. FOSTER, eds). Oxford University Press, Oxford, p. 438-471.

—— & RICHKIND, K. A. (1981). Clinal variation of lateral plates in threespine stickleback fish. — Am. Nat. 117, p. 113-132.

BOROWSKY, R. (1990). Habitat choice by allelic variants in *Xiphophorus variatus* (Pisces: Poeciliidae) and implications for maintenance of genetic polymorphism. — Evolution 44, p.1338-1345.

CAIN, A.J. (1971). Animal species and their evolution. — Hutchinson University Library, London, 192 pp.

ENDLER, J.A. (1977). Geographic variation, speciation and clines. — Princeton University Press, Princeton, New Jersey, 246 pp.

—— (1986). Natural selection in the wild. — Princeton University Press, Princeton, New Jersey, 337 pp.

FALCONER, D.S. (1967). Introduction to quantitative genetics. — The Ronald Press Company, New York, 365 pp.

FORD, E.B. (1964). Ecological genetics. — Methuen, London.

FUTUYMA, D.J. (1979). Evolutionary biology. — Sinauer Associates, Sunderland, Mass.

—— & MORENO, G. (1988). The evolution of ecological specialization. — Ann. Rev. Ecol. Syst. 19, p. 207-233.

GACH, M.H. & REIMCHEN, T.E. (1989). Mitochondrial DNA patterns among endemic stickleback from the Queen Charlotte Islands: a preliminary survey. — Can. J. Zool. 67, p. 1324-1328.

GARCIA-DORADO, A. (1986). The effect of niche preferences on polymorphism protection in a heterogeneous environment. — Evolution 40, p. 936-945.

GIESEL, J. T. (1970). On the maintenance of shell pattern and behaviour polymorphism in *Acmaea digitalis*, a limpet. — Evolution 24, p. 98-119.

GOULD, S.J. (1984). Covariance sets and ordered geographic variation in Cerion from Aruba, Bonaire and Curacao: a way of studying nonadaptation. — Syst. Zool. 33, p. 217-237.

GRANT, B.R. & GRANT, P.R. (1989). Evolutionary dynamics of a natural population: The large cactus finch of the Galapagos. — University of Chicago Press, Chicago.

GRANT, P.R. & PRICE, T.D. (1981). Population variation in continuously varying traits as an ecological genetics problem. — Am. Zool. 21, p. 795-811.

GROSS, H.P. (1978). Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L. — Can. J. Zool. 56, p. 398-413.

HAGEN, D.W. & GILBERTSON, L.G. (1972). Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific northwest, America. — Evolution 26, p. 32-51.

—— & —— (1973a). The genetics of plate morphs in freshwater threespine sticklebacks. — Heredity 31, p. 75-84.

—— & —— (1973b). Selective predation and the intensity of selection acting upon the lateral plates of threespine sticklebacks. — Heredity 30, p. 273-287.

HEDRICK, P.W. (1986). Genetic polymorphism in heterogeneous environments: a decade later. — Ann. Rev. Ecol. Syst. 17, p. 535-566.

HEUTS, M.J. (1947). Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. — Evolution 1, p. 89-102.

HUNTINGFORD, F.A. (1981). Further evidence for an association between lateral scute number and aggressiveness in the threespine stickleback, *Gasterosteus aculeatus*. — Copeia 1981, p. 717-719.

MACLEAN J. (1980). Ecological genetics of threespine sticklebacks in Heisholt Lake. — Can. J. Zool. 58, p. 2026-2039.

MAYR, E. (1966). Animal species and evolution. — The Belknap Press of Harvard University Press, Cambridge, Massachusetts, 797 pp.

MOODIE, G.E.E. (1970). Predation as a mechanism in the evolution of an unusual population of stickleback in the Queen Charlotte Islands, Canada (Pisces: Gasterosteidae). — PhD thesis, Univ. Alberta, Edmonton, Alberta, Canada.

—— (1972). Predation, natural selection and adaptation in an unusual stickleback. — Heredity 28, p. 155-167.

—— & REIMCHEN, T.E. (1976). Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. — Syst. Zool. 25, p. 49-61.

——, McPHAIL, J.D. & HAGEN, D.W. (1973). Experimental demonstration of selective predation on *Gasterosteus aculeatus*. — Behaviour 47, p. 95-105.

O'REILLY, P., REIMCHEN, T.E., BEECH, R. & STROBECK, C. (1993). Mitochondrial DNA in *Gasterosteus* and Pleistocene glacial refugium on the Queen Charlotte Islands, British Columbia. — Evolution 47, p. 678-684.

PATTERSON, B.D. (1983). Grasshopper mandibles and the niche variation hypothesis. — Evolution 37, p. 375-388.

POWELL, J.R. & TAYLOR, C.E. (1979). Genetic variation in ecologically diverse environments. — Am. Sci. 67, p. 590-596.

RAD, O. (1980). Breeding distribution and habitat selection of Red-breasted Mergansers *Mergus serrator* in fresh water in western Norway. — Wildfowl 31, p. 53-56.

REIMCHEN, T.E. (1979). Substrate heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina mariae*). — Can. J. Zool. 57, p. 1070-1085.

—— (1980). Spine-deficiency and polymorphism in a population of *Gasterosteus aculeatus*,: an adaptation to predators? — Can. J. Zool. 58, p. 1232-1244.

—— (1983). Structural relationships between spines and lateral plates in threespine stickleback (*Gasterosteus aculeatus*). — Evolution 37, p. 931-946.

—— (1988). Inefficient predators and prey injuries in a population of giant stickleback. — Can. J. Zool. 66, p. 2036-2044.

—— (1990). Size-structured mortality in a threespine stickleback (*Gasterosteus aculeatus*) — cutthroat trout (*Oncorhynchus clarki*) community. — Can. J. Fish. Aquat. Sci. 47, p. 1194-1205.

—— (1991). Trout foraging failures and the evolution of body size in stickleback. — Copeia 1991, p. 1098-1104.

—— (1992a). Injuries on stickleback from attacks by a toothed predator (*Oncorhynchus*) and some implications for the evolution of lateral plates. — Evolution 46, p. 1224-1230.

—— (1992b). Extended longevity in a large-bodied *Gasterosteus* population. — Can. Field-Naturalist 106, p. 122-125.

—— (1994). Predators and evolution in threespine stickleback. — In: The evolutionary biology of the threespine stickleback (M.A. BELL & S.A. FOSTER, eds). Oxford University Press, Oxford, p. 240-276.

—— & DOUGLAS, S.D. (1980). Observations of loons (*Gavia immer* and *G. stellata*) at a bog lake on the Queen Charlotte Islands. — Can. Field-Naturalist 94, p. 398-404.

—— & —— (1984). Seasonal and diurnal activity of aquatic birds on a coastal lake in British Columbia. — Can. Field-Naturalist 98, p. 22-28.

—— & NELSON, J.S. (1987). Habitat and morphological correlates to vertebral number as shown in a teleost, *Gasterosteus aculeatus*. — Copeia 1987, p. 868-874.

——, STINSON, E. & NELSON, J.S. (1985). Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. — Can. J. Zool. 63, p. 2944-2951.

SAMOLLOW, P.B. (1980). Selective mortality and reproduction in a natural population of *Bufo boreas*. — Evolution 34, p. 18-39.

SCHOENER, T.W. (1968). The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. — Ecology 49, p. 704-726.

SCHLUTER, D. & McPHAIL, J.D. (1993). Character displacement and replicate adaptive radiation. — Trends Ecol. Evol. 8, p. 197-200.

SELANDER, R.K. (1966). Sexual dimorphism and differential niche utilization in birds. — Condor 68, p. 113-151.

SHEPPARD, P.M. (1951). Fluctuations in the selective values of certain phenotypes in the polymorphic land snail *Cepaea nemoralis*. — Heredity 5, p. 125-134.

SLATKIN, M. (1984). Ecological causes of sexual dimorphism. — Evolution 38, p. 622-630.

SMITH, T.B. (1990). Natural selection on bill characters in the two bill morphs of the African finch *Pyrenestes ostrinus*. — Evolution 44, p. 832-842.

VAN VALEN, L. (1965). Morphological variation and width of ecological niche. — Am. Nat. 99, p. 377-389.

WILSON, D.S. (1989). The diversification of single gene-pools by density- and frequency-dependent selection. — In: Speciation and its consequences (D. OTTE & J.A. ENDLER, eds). p. 366-385.

WOOTTON, R.J. (1984). A functional biology of sticklebacks. — University of California Press, Berkeley and Los Angeles, 265 p.