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# PHENETIC VARIATION AND HABITAT DIFFERENCES IN *GASTEROSTEUS* POPULATIONS OF THE QUEEN CHARLOTTE ISLANDS

G. E. E. MOODIE AND T. E. REIMCHEN

## Abstract

Moodie, G. E. E., and T. E. Reimchen (Department of Biology, University of Winnipeg, Winnipeg, Manitoba, R3B 2E9, Canada) 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. *Syst. Zool.* 25:49-61.—Lateral plate polymorphism and asymmetry, gill raker number and asymmetry, body size and certain other traits were compared in 25 *Gasterosteus aculeatus* populations. Fluctuating asymmetry and mean number of lateral plates as well as body size and proportions were correlated with the presence of predatory fish. In the absence of other fish species, gill raker number was correlated with lake area. Fluctuating asymmetry of the lateral plates and gill rakers did not appear to decrease with age; in three populations the converse occurred. Directional asymmetry was present in six populations. Fluctuating asymmetry in these populations does not seem to conform well to current concepts concerning developmental stability and asymmetry. [*Gasterosteus*; phenetics; habitat variation; predation; asymmetry.]

Several recent studies have documented the great variability of populations of the threespine stickleback (*Gasterosteus aculeatus* L.) and the adaptive value of certain morphological traits (Semler, 1971; Moodie, 1972a, b; Hagen and Gilbertson, 1972). Much, however, remains to be learned about the adaptive value of such things as lateral plate polymorphism (low, partial or complete), plate numbers and symmetry, body size and proportions. In addition, little is known of how the phenotype is influenced by selective agents other than predation and salinity.

In the Queen Charlotte Islands there are numerous fresh water populations of *G. aculeatus*. Although they are within limited distance of each other, these populations show a range of variation (Fig. 1) practically matching the limits known for this widely distributed species. On these islands, populations may be isolated in small closed lakes or be in large lakes connected to the nearby sea. Some lakes contain only *G. aculeatus*; others contain *G. aculeatus* as well as up to four potential (fish) predators and competitors. The purpose of this study was to determine whether or not phenetic variation was correlated with competition, isolation and habitat or population size as

well as predation. Most of these factors had to be measured indirectly.

Most samples came from Graham Island (53° 49' N, 132° 02' W). Two collections (Awun and Ain Lakes) were obtained in 1929; the others were collected by ourselves between 1966 and 1972. Most of the sites are officially named. To others we applied names which are enclosed in quotation marks when they first appear below. Sticklebacks were usually captured with seines, but a few lakes could be sampled only by using un baited minnow traps. Difficult conditions in Yakoun and Clearwater Lakes forced us to utilize fish succumbing to post-reproductive mortality. (It is possible such samples do not represent the portion of the population one would obtain by seining. However, in Drizzle Lake we compared a sample taken by seining with one composed of victims of post-reproductive mortality. There were no significant differences in the means or variances of the plate and raker counts; sample sizes were 37 and 308.) Gillnets were set wherever possible to help determine the presence or absence of larger species.

Many of the lakes can be visited only by aircraft or on foot through dense vegetation. This created two problems. Firstly, our

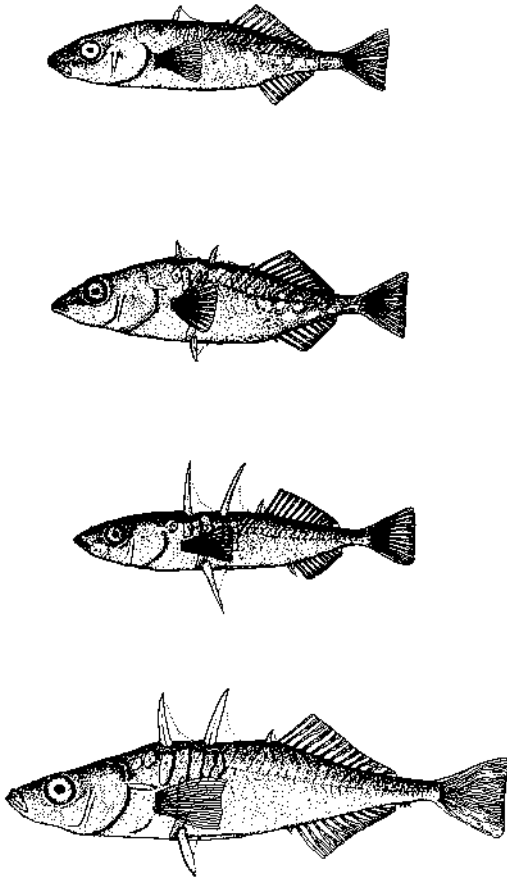


FIG. 1.—Variability among *Gasterosteus aculeatus* populations in the Queen Charlotte Islands. Top to bottom: Boulton Lake, Gold Creek, Yakoun Lake, Mayer Lake. Typical representatives were drawn to the same scale with the aid of a camera lucida, body proportions were measured and transferred to the drawings.

information concerning the status of other fish species may be inaccurate because of the limited time and equipment available at some sites. Secondly, a number of samples are smaller than desirable. Further sampling (being conducted by T.E.R.) thus may alter some of our ecological data and perhaps some of our conclusions.

The populations studied are summarized in Table I. In analyzing the data it was necessary to classify each population as to its exposure to predation. This posed a

problem in the case of two lakes sampled in 1929 and in ones where our sampling was superficial. In a few instances we resorted to an educated guess. In general we assumed if salmon (*Oncorhynchus*) had access to a lake, predatory trout (*Salmo*) and cottids (*Cottus*) would also. Some lakes were exceptional, however. Pure Lake, for example, was sampled twice and yielded only a few salmon and no predators. It is far from the sea and connected by a small, possibly intermittent stream, so we classified this lake as free of predators. Mercer Lake, in contrast, is close to the sea, connected by a larger river and contains many salmon. We therefore assumed trout or cottids or both are present, although none were caught during our brief visit.

Studies in Mayer Lake (Moodie, 1972b) showed that the Cutthroat Trout (*Salmo clarki*) was the major predator of sticklebacks, followed by the Prickly Sculpin (*Cottus asper*) which preys on stickleback eggs and juveniles. Adults of other salmonids enter these lakes only during their reproductive phase at which time they do not feed. Stomachs of juvenile salmon and Dolly Varden (*Salmo malma*) of Mayer Lake were never found to contain fish remains. Greenbank and Nelson (1958) also noted this species does not prey on sticklebacks.

Morphological traits were quantified by methods described previously (Moodie, 1972a) with the exception of lateral plate and gill raker asymmetry which was treated as follows. Fluctuating asymmetry (Van Valen, 1962) was assessed by summing the absolute differences of the count on each side and dividing the sum by the sample size. Others (Thoday, 1958; Soulé, 1967) used the same method. The variance of the absolute asymmetry scores was not independent of the mean. Therefore, prior to regressing asymmetry score on body length we used Taylor's power law (Southwood, 1966) to transform the individual asymmetry scores. In Watt and Skonun Lakes we met a problem not discussed in previous studies of asymmetry. Most fish

TABLE 1. CHARACTERISTICS OF THE HABITATS SAMPLED.<sup>1</sup>

Site	Lake area (hectares)	Drainage	Other species present
Lakes			
Clearwater	60	open <sup>2</sup>	*
Spence	121	open	<i>C. asper</i> , <i>O. kisutch</i> , <i>L. richardsoni</i>
Drizzle	148	open	* <i>S. malma</i> , <i>O. kisutch</i>
Skonun	80	open	*
Pure	41	open (intermittent?)	* <i>O. kisutch</i>
Boulton	10	closed	*
"Kumdis"	33	open	salmonids observed
Watt	5	closed	*
Loon	10	open (intermittent?)	* <i>S. malma</i> , <i>Oncorhynchus</i> sp. (both scarce)
Mayer	627	open	<i>S. clarki</i> , <i>C. asper</i> , <i>S. malma</i> , <i>O. kisutch</i>
Hickey	190	closed?	*
"Woodpile"	5	open	*
Wiggins	33	closed	*
Yakoun	1138	open	salmonids reported
Awun	621	open	salmon and trout reported
Mercer	118	open	<i>O. kisutch</i>
Ain	107	open	salmon and trout reported
"Coates"	124	open	<i>C. asper</i>
Eden	731	open	<i>O. nerka</i>
Marion	192	open	<i>S. clarki</i> , <i>C. asper</i> , <i>O. kisutch</i>
Skidegate	940	open	salmonids reported
Mathers	253	open	<i>C. asper</i> , <i>O. kisutch</i>
Creeks			
"Gold"		open	*
Kumdis (PT)		open	* <i>S. malma</i> , <i>O. kisutch</i>
Kumdis (PM)		open	salmonids observed

<sup>1</sup> Asterisks indicate sites considered to lack predatory fish.

in these lakes completely lack plates. Thus they are "symmetric." The few fish which have plates are quite asymmetric. It seemed most logical to evaluate asymmetry on the basis of individuals which possessed the character in question. Thus we excluded plateless fish from the calculations for these two lakes.

Directional asymmetry (Van Valen, 1962) was determined by a comparison (*t*-test) of the sum of the counts for each side. When the null hypothesis of equal means was rejected at the 0.05 level of significance, we corrected each individual asymmetry score by subtracting the amount of the mean difference (between sides) from the side with the greatest total. Others (*ibid*) have done the same.

We did not test the data for antisymmetry (Van Valen, 1962).

## RESULTS

The morphological traits we considered were: (1) frequency of the three plate morphs described by Hagen and Gilbertson (1972); (2) mean number of plates and plate asymmetry; (3) mean number of gill rakers, raker asymmetry and variance; (4) mean number of vertebrae and variance; (5) maximum body length; (6) number of spines and the ratio of pelvic spine length to standard length; (7) the ratio of body depth to standard length. Each sex was analyzed separately, except in the case of vertebrae, spine number and relative length and plate morph frequencies. The populations are summarized for these traits in Tables 2, 3 and 4.

### Lateral Plates

Three plate morphs have been described for freshwater populations of *G. aculeatus*.

TABLE 2(a). PHENETIC CHARACTERISTICS OF EACH POPULATION.<sup>1</sup>

Site	Sex	Mode	Plates			Rakers		Maximum body length	$\bar{x}$ Body length/body depth	N
			$\bar{x}$	Variance	Asymmetry	$\bar{x}$	Variance			
Clearwater	♀	3	2.9	1.718	.714	18.7	1.506	65.6		28
	♂	3	2.8	1.321	.643	19.1	1.266	63.7		14
Spence	♀	7	6.7	.386	.583	21.3	1.617	81.3	4.37	12
	♂	7	7.5	.439	.389	20.3	2.425	75.3		18
Drizzle	♀	4	4.5	1.187	.658	20.7	1.547	85.2	5.34	164
	♂	5	4.6	1.17	.715	21.3	1.487	78.6	5.26	144
Skonun	♀	0	1	1.611	.575	18.8	1.395	55		39
	♂	0	1.5	2.112	.333	18.9	.648	52		22
Pure	♀	5	5	.387	.426	19.2	.98	63.6	4.94	47
	♂	5	6.6	.699	.544	19.2	.918	77.1	4.85	57
Boulton	♀	3	3.2	.515	.85	18.8	1.023	55.5	5.61	20
	♂	3	3.2	.656	.68	19.1	1.327	54.5		25
Kumdis	♀	6	5.6	.319	.333	20.1	1.111	53		9
	♂	6	6.4	.447	.267	20.1	2.067	55		15
Watt	♀	0	.4	.236	.222	17.9	1.111	48		9
	♂	0	.5	.476	.4	18.7	2.067	66		15
Loon	♀	2	2.6	.498	.5	17.7	1.869	65.9		18
	♂	3	2.9	.919	.594	17.7	1.374	60		101
Mayer	♀	7	6.6	.289	.367	21.1	2.33	99.7		67
	♂	7	6.6	.315	.255	21.2	2.061	91		186
Hickey	♀	4	4.2	.993	.63	20.8	1.767	60	5.22	22
	♂	4	4.8	1.146	.732	20.6	1.077	79.7	4.99	44
Woodpile	♀	5	5.	.734	.609	18	1.31	68.1	4.48	69
	♂	5	5.3	.727	.466	17.9	1.541	59.5	4.46	58
Wiggins	♀	2	1.2	.967	.55	19.9	1.748	63.4		20
	♂	2	1.7	1.082	.94	19.7	1.36	63.3	5.12	80
Yakoun	♀	6	5.8	.967	.667	19.5	2.667	52.3		6
	♂	7	6.5	.291	.25	20	.7	48	5.29	4
Awun	♀	7	6.6	.286	.66	20.3	1.571	66.6		7
	♂	7	6.6	.866	.66	20.6	2.712	75		27
Mercer	♀	7	6.8	.743	.4	18.9	.717	55	3.99	15
	♂	7	6.6	.9	.4	19	1.1	51.3		5
Ain	♀	5	6	.781	.364	19.3	1.301	79.7	3.96	22
	♂	6	6	.637	.385	19.3	1.409	60.4	4.02	26
Coates	♂	7	7.9	2.491	.727	20.4	1.082	71	4.8	11
Eden	♀	7	6.8	.38	.298	19.3	1.589	87.2	4.43	124
	♂	7	7	.339	.318	19.8	1.853	72.8	4.51	168
Marion	♀	7	6.4	.426	.473	21.4	1.453	76.5	4.7	88
	♂	7	6.8	.578	.437	21.3	1.462	71.9	4.75	107
Skidegate	♀	7	6.3	.44	.423		2.84	77.2	4.92	26
	♂	7	6.7	.291	.636		1.6	69.3	4.63	11
Mathers	♀	8	8.3	2.58	.741	22	1.355		4.64	27
	♂	7	8.4	19.65	.683	21.7	2.006	62	4.69	41
Gold	♀	5	4.7			17.3	2.4	69		
	♂	5	4.7			17.3	2.4	69		
Kumdis PM	♀	4	3.7	.82	.625	17.3	1.342	54.8	4.7	52
	♂	4	3.9	.621	.4	17.1	1.66	55.8	4.47	32
Kumdis PT	♀	5	4.8	.814	.615	15.8	1.758	62.6	4.28	32
	♂	6	5.3	.84	.594	16.2	1.9	53.2	4.36	20

<sup>1</sup> Sexes were not differentiated in assessing raker asymmetry, vertebral means, and the ratios of body length: spine length.

TABLE 2(b). PHENETIC CHARACTERISTICS OF EACH POPULATION.<sup>1</sup>

Site	Rakers	Vertebrae		$\bar{x}$ Body length/ spine length	N
	Asymmetry	$\bar{x}$	Variance		
Clearwater	.865	31.83	.295		44
Spence	1.226	32.55	.256	6.4	30
Drizzle	1.054	33	.34	5.9	308
Skonun		32.85	.344		121
Pure	.836	32.54	.319	5.58	110
Boulton		32.81	.25	12.55	45
Kumdis		31.58	.265		44
Watt		32.27	.618	8.17	49
Loon	.943	32.27	.368		120
Mayer		34.01	.263	5.3	254
Hickey	.987	32.94	.74	5.97	76
Woodpile		32.78	.318	5.87	129
Wiggins	1	32.34	.411	8.23	100
Yakoun		32.5	.323	5.04	43
Awun		32.48	.259		34
Mercer	.667			6.23	22
Ain	.783	32.07	.158	5.17	50
Coates	.909	32.37	.245	6.06	130
Eden	.964	32.42	.353	5.06	422
Marion	.869	32.97	.251	5.18	195
Skidegate				5.75	37
Mathers	1.352			5.95	68
Gold		32.48	.367	6.4	146
Kumdis PM	1.038	31.91	.21	8.28	86
Kumdis PT	1.127	31.69	.402	9.11	52

<sup>1</sup> Sexes were not differentiated in assessing raker asymmetry, vertebral means, and the ratios of body length: spine length.

"Lows" have plates only on the anterior portion of the body. "Completes" have a continuous series of plates from the pectoral region to the caudal peduncle. "Partials" have a gap so that there are anterior plates followed by a naked zone and then plates again on the caudal peduncle.

In the Queen Charlotte Islands most populations are monomorphically low. One, in Mathers Lake is virtually monomorphic for partials. Populations in Eden and Coates Lakes are mainly low but a few partials and completes are present (Table 3).

Within the low and partial morphs there is sexual dimorphism in the number of plates. Males had more plates than females in 20 of 22 populations (in 9 of the 20  $p < 0.05$ ,  $t$ -test). Variance of plate number was also more often greater ( $\chi^2_{(1)} = 3.52$ ,  $p = 0.062$ ) in males than females.

Some of the variance in plate number seems related to the presence of predators. Ten lakes have modes at seven plates. Six

of these lakes contain either *S. clarki*, *C. asper* or both. We suspect (because of other species present, location, drainage, or anglers' reports) that these two predators are also in the other four lakes. *Salmo clarki* and *C. asper* are apparently absent from the other 14 lakes and streams which generally have modal plate counts of less than seven.

We studied fluctuating asymmetry of lateral plate number because it has been considered (Mather, 1953) an indicator of development homeostasis and Soulé (1967) has suggested that the level of asymmetry may be related to rate of immigration and ratio of directional to stabilizing selection.

Plate asymmetry was not influenced by the scaling effect encountered by others (Van Valen, 1962; Soulé, 1967). However, there was an "inverse scaling" effect; populations with a higher mean plate count were more symmetric than those with low means. For males the significance level of the correlation coefficient for mean population

TABLE 3. FREQUENCIES OF PLATE MORPHS IN LAKES WHERE MORPHS OTHER THAN LOWS OCCUR.

Site	Low	Partial	Complete
Marion	148	2	
Eden	295		1
Coates	100	18	
Mathers		67	1

plate count and mean asymmetry score was  $<0.05$ , for females  $<0.10$ . Two populations containing the partial morph do not conform to the pattern. If they (Mathers and Coates Lakes) are excluded, the significance level rises to  $p < 0.01$  for females. Both plate asymmetry and number are correlated with the presence of predators and predation respectively. We found mean asymmetry was lowest in the presence of predators ( $p < 0.01$  for males,  $p < 0.05$  for females; Mann-Whitney  $U$  test). Plate count has been correlated with predation in two field studies based on gut analyses of predators (Moodie, 1972b; Hagen and Gilbertson, 1973) and in a laboratory study in which symmetric fish of various plate counts were offered to predators (Moodie, McPhail and Hagen, 1973).

Differences in fluctuating asymmetry were not correlated with lake size or drainage type.

If developmental instability interferes with the expression of an optimum phenotype, it should be selected against. We therefore tried to determine whether fluctuating asymmetry, an indicator of developmental instability, decreased during the life of a cohort. We were especially interested in seeing whether asymmetric fish were eliminated in populations subject to predation. In practice we had to use fish from different year classes. Our estimate of age was based on length, which others (Greenbank and Nelson, 1958; Hagen and Gilbertson, 1972; Hay, 1974) have found correlates well with other methods of ageing in this species.

Analysis consisted of regressing transformed, absolute asymmetry (corrected for directional asymmetry if present) against

TABLE 4. FREQUENCIES OF FISH WITH MISSING SPINES.

Lake	Missing spines			Total sample size
	Pelvics	One dorsal	Two dorsals	
Loon		14	1	102
Boulton	111	96	5	221
Imber		1		3
"Rouge"		5		9

body length. In most populations we found no significant change in the amount of asymmetry from young to old fish. Only in the Spence Lake population was there a significant ( $p < 0.025$ ) negative slope and that only among females. In contrast both sexes in Skonun Lake showed a significant ( $p < 0.005$  for females;  $p < 0.01$  for males) increase in asymmetry with age. Females in Mercer and males in Marion Lakes also underwent a relative increase with age ( $p < 0.05$  and  $p < 0.005$  respectively). Details for all populations are provided in Table 5.

Directional asymmetry was present ( $p < 0.05$ ) in males of populations in Wiggins and Hickey Lakes and in females of the Marion, Spence, Mayer and Boulton Lake populations.

#### Gill Rakers

We compared gill raker means and variances to discover whether differences could be related to habitat differences or potential interspecific competition for food. We found only an indirect relationship. In lakes where no other species were present regression analysis revealed raker number was positively related to lake size ( $p < 0.01$ ). In lakes containing other species, no such correlation existed, although there tended to be more rakers. Because lakes with other species were also larger we can not say whether the raker difference is due to the presence of other species, greater lake size, both, or some other concomitant variable.

We also found mean gill raker number is positively related to maximum body length

TABLE 5. DATA FOR THE REGRESSIONS OF FLUCTUATING ASYMMETRY OF THE LATERAL PLATES AGAINST STANDARD LENGTH.<sup>1</sup>

Site	Sex	b	Standard error of b	r <sup>2</sup>	F	d.f.
Clearwater	♀	-.005	.026	.002	.043	1;26
	♂	.014	.024	.028	.350	1;12
Spence	♀	-.009	.003	.443	7.954**	1;10
	♂	.006	.032	.002	.036	1;16
Drizzle	♀	.016	.008	.024	3.867	1;159
	♂	-.002	.003	.003	.487	1;142
Skonun	♀	.040	.010	.292	15.64****	1;38
	♂	.057	.018	.343	9.937****	1;19
Pure	♀	-.023	.014	.055	2.636	1;45
	♂	-.003	.007	.003	.157	1;55
Boulton	♀	-.017	.017	.054	1.037	1;18
	♂	.012	.048	.003	.061	1;23
Kumdis	♀	.018	.024	.071	.533	1;7
	♂	-.010	.015	.034	.458	1;13
Watt	♀	-.034	.039	.100	.777	1;7
	♂	.014	.017	.048	.654	1;13
Loon	♀	.010	.012	.041	.877	1;16
	♂	.002	.007	.001	.058	1;99
Mayer	♀	-.002	.008	.002	.086	1;48
	♂	.011	.009	.008	1.264	1;147
Hickey	♀	-.020	.012	.102	2.828	1;25
	♂	.034	.035	.021	.941	1;43
Woodpile	♀	.009	.009	.016	1.098	1;87
	♂	.022	.012	.056	3.353	1;56
Wiggins	♀	.006	.025	.004	.065	1;18
	♂	.024	.090	.0009	.074	1;78
Yakoun	♀	-.096	.114	.150	.707	1;4
Mercer	♀	.040	.018	.285	5.185*	1;13
	♂	-.068	.077	.206	.778	1;3
Ain	♀	-.015	.010	.099	2.196	1;20
	♂	-.009	.020	.008	.199	1;24
Coates	♂	.004	.027	.002	.023	1;9
Eden	♀	-0.0003	.003	.0001	.010	1;122
	♂	.005	.004	.010	1.672	1;168
Marion	♀	.001	.004	.001	.080	1;54
	♂	.012	.005	.122	11.821****	1;85
Skidegate	♀	-.008	.012	.021	.515	1;24
	♂	-.02	.01	.127	1.312	1;9
Mathers	♀	-.003	.072	.00005	.001	1;25
	♂	.022	.014	.055	2.28	1;39
Kumdis PM	♀	-.001	.012	.0001	.003	1;30
	♂	.015	.012	.085	1.664	1;18
Kumdis PT	♀	-.015	.012	.020	1.48	1;47
	♂	.028	.028	.039	1.044	1;26

<sup>1</sup> Slope of the regression (b), coefficient of determination (r<sup>2</sup>), significance of the regression (F), degrees of freedom (d.f.), p < 0.05 (\*), p < 0.025 (\*\*), p < 0.01 (\*\*\*), p < 0.001 (\*\*\*\*).

( $p < 0.05$  for females,  $p < 0.01$  for males). This is apparently not caused by an increase in the number of rakers as an individual grows: there were no significant correla-

tions between raker number and body length within populations.

The variance of raker number of males was less in lakes with no other species



present than in those with either or both competitors and predators ( $p < 0.05$ , Mann-Whitney  $U$  test).

Gill raker asymmetry was not correlated with any of the physical or biotic variables we considered. As in the case of plates, raker asymmetry seldom changed with age. A significant regression was obtained only in Pure Lake where asymmetry decreased with age amongst females. For the number of tests (30) one significant case could be expected on the basis of chance alone.

Directional raker asymmetry was present ( $p < 0.05$ ) only among males of Woodpile and Boulton Lakes.

### *Body Length*

In the Queen Charlotte Islands populations vary greatly in maximum body length (Table 2). In some populations lengths are comparable to those on the mainland but others, as in Mayer and Spence Lakes, have large mean and maximum lengths.

In lakes where the predators *S. clarki* and *C. asper* occur, maximum length of both sexes was greater than that in lakes where neither species was present ( $p < 0.01$  for females,  $p < 0.05$  for males; Mann-Whitney  $U$  test).

Maximum length was also positively correlated with mean vertebral number ( $p < 0.001$ ). The relationship between maximum body length and gill raker number has been noted.

There was no correlation ( $p > 0.1$ ) between length and lake area. However, populations with a short maximum length seem most common in small lakes and larger fish tend to be in larger lakes (Tables 1 and 2).

### *Ratio of Body Depth to Standard Length*

We found the most streamlined fish were in lakes where there were no predators. Lake populations exposed to *S. clarki* and *C. asper* had relatively deeper bodies ( $p < 0.02$  for each sex, Mann-Whitney  $U$  test). Body depth was not correlated with raker number, length or lake area.

### *Spines*

In several of the lakes many fish lack dorsal or pelvic spines. The frequencies of missing spines in the four populations concerned are shown in Table 4. Dorsal spines I, II and III may be missing as well as the pelvics. Loon and Boulton Lakes were extensively sampled and we are confident there were no predatory fish in them. We suspect predatory fish were also absent from Imber and "Rouge" Lakes, which together with "Naked" Lake (below) are not otherwise discussed because their sample sizes were inadequate for most purposes.

We found, as have other studies, (Moodie, 1972b; Hagen and Gilbertson, 1972) that relative length of the pelvic spines was greater in populations subject to predation. However, the differences were not significant.

### DISCUSSION

#### *Lateral Plates*

In a survey of mainland populations 2 of 15 lakes contained populations monomorphic for the low plate morph (Hagen and Gilbertson, 1972). In the present study, 18 of 22 lakes contained monomorphic low populations. Hagen and Gilbertson were uncertain of the causes of differences in the relative frequencies of the three morphs. The reason for the general differences between the mainland and the island is also unclear. The island lakes differ from many of those surveyed on the mainland in containing fewer species and being much less disturbed environments. The island lakes (Coates, Mathers) which contain the highest frequencies of the partial and complete morphs are physically somewhat different from the others. Coates Lake consists of crystal clear water running off adjacent mountains. Mathers Lake also contained fairly transparent water and is situated among low mountains. Most of the other lakes (including Clearwater and Pure) are in the lowlands and are filled by darkly stained seepage water. The lakes occupied by monomorphic low populations have a

slightly smaller mean area ( $p < 0.1$ ) than the four lakes where the other two morphs occur.

The extreme reduction in the number of plates in the populations of Watt, Wiggins, Skonun and Naked (18 of 21 fish in this lake had no plates) Lakes has few parallels elsewhere. The only comparable cases we know of are populations on Texada Island, Canada, in Southern California, U.S.A. and in Algeria. The reduction in the Queen Charlotte Islands seems related to the absence of predators. When the number of plates is reduced to about one to three, they usually link the pelvic girdle to the supporting bones of the first and second dorsal spines (Hay, 1974 and personal observations). Presumably by completing a bony ring around the body these plates stabilize the bones with which the major dorsal and pelvic spines articulate. In the absence of predation the supportive function of these plates may be unnecessary. The above four lakes are smaller than most ( $p < 0.05$ , Mann-Whitney  $U$  test) and at least three appear to be closed drainages. Although Skonun Lake has an outlet it is uncertain to what extent this permits gene exchange with other populations.

The impact of open and closed drainage on the genetics of these populations is difficult to assess. With the possible exceptions of spine loss and extreme plate reduction, we failed to correlate drainage type with morphological variation and asymmetry. Fresh water sticklebacks are known to be quite sedentary (Hagen, 1967; McLean, 1974). Populations in lakes with open drainage may be almost or as isolated as those in a closed drainage. Some connecting streams seem to offer unfavorable habitats which must augment the effects of sedentary behavior on migration.

Skonun and Drizzle Lakes empty into the same river: Woodpile Lake drains into Mayer Lake yet the populations in each pair are quite different. Selection could maintain these differences in the face of gene flow but it may be that there is in

addition little movement between populations.

The prevalence of modes at seven plates where predators occur is also characteristic of mainland populations (Hagen and Gilbertson, 1972) and the selective advantage of various plate counts has been discussed elsewhere (Moodie, 1972b; Moodie, McPhail and Hagen, 1973).

Differential predation during the reproductive cycle was suggested by Moodie (1972b) as an explanation for sexual dimorphism in plate number. However, additional factors may be involved because the dimorphism is present in both populations exposed and unexposed to predation. At present we can not account for its presence in unexposed populations.

#### *Asymmetry*

The lateral plates seem to offer an ideal opportunity to study asymmetry. With this trait particular numbers of plates are known to be of adaptive importance. It is thus reasonable to assume symmetry of this trait will also be important (Thoday, 1958). We thought there might be stronger selection for developmental stability where predation existed because of the relationship between predation and lateral plate number (this is not to imply predation is the only selective agent acting on plate number; merely that we hoped the others would be acting equally in populations exposed or not exposed to predators). We also initially felt there would be less immigration and therefore more genetic stability in isolated small lakes than in larger ones containing numerous sub-populations and open to the sea or to other lakes or streams. Because the islands were glaciated about 10,000 years ago (Sutherland Brown and Nasmith, 1962) and the environment has been relatively undisturbed by man, the ratio of directional to stabilizing selection may be about the same in each population. Previous studies of asymmetry in nature (Soulé, 1967; Jackson, 1973) have dealt with such things as scale counts, where although the mean is doubtless subject to selection it is unlikely

or at least undemonstrated that small differences about the mean or between the total on each side of an animal greatly affect its fitness. In spite of the seeming suitability of the plates, our efforts to relate their level of fluctuating asymmetry to environmental characteristics were only partly successful. One of the problems in assessing asymmetry was discussed by Van Valen (1962), who pointed out that individual microchaetae on each side of *Drosophila melanogaster* may be individually homologous. Mere counting may give only a "course" estimate of their asymmetry if in fact genetically different chaetae are present on each side. This difficulty may be relevant to *G. aculeatus* because Hay (1974) believes each anterior plate represents a discrete unit of a polymorphism. The sides could be numerically equal but genetically unequal if different units of the polymorphism are represented. Future study will have to determine the comparability of asymmetry evaluated by our simple numerical method and that of Hay's (*ibid*).

The inverse relationship between mean plate number and plate asymmetry can be related to potential predation. High plate counts of seven are associated with the presence of predators; counts of less than seven with their absence. Similarly, excesses of fish with counts other than seven were found in the guts of predators by Hagen and Gilbertson (1973). Mean plate asymmetry, conversely, was reduced in the presence of predators in our study. There remains, however, considerable variation in asymmetry among populations not exposed to predation and it would be simplistic to think variation among exposed populations was only a reflection of differences in intensity of predation. In a recent study of lizard populations, Jackson (1973) found that levels of asymmetry were generally similar. He attributed this to environmental uniformity from site to site. Many of our lowlands sites were similar (at least superficially) yet in this instance there are great differences in asymmetry.

We expected smaller lakes might contain

smaller populations with more genetic coadaptation than the larger and often open lakes. This may have been an erroneous viewpoint because all lakes probably contain many populations due to the sedentary behaviour of the species. The effective population sizes may be similar regardless of lake size.

Asymmetry in at least one population of *G. aculeatus* is a heritable trait (Hagen, 1973) and Beardmore (in Thoday, 1958) showed that asymmetry decreased in adapting laboratory populations of *D. melanogaster*. We expected to detect changes in asymmetry from young to adult fish. The failure to detect significant change in asymmetry with age could be because either no such selection takes place in nature (Fox, 1975) or that our methods were inadequate. Plates can not be reliably counted until a fish is about 30 mm long (Hagen and McPhail, 1970; Hagen and Gilbertson, 1972) thus we could not measure selection during the early part of the life span. We were also dealing with different year classes and in a few cases with small sample sizes.

Nevertheless, the data analyses may be reliable and there is accumulating evidence that asymmetry can be selected for. Where we did find a significant change in asymmetry with age it was usually an increase. J. D. McPhail (*pers. com.*) has also observed such an increase. Furthermore, Hagen and Gilbertson (1973), who studied a true cohort of large size, found the optimum plate phenotype in Lake Wapato was an asymmetric one.

Gill raker asymmetry varied considerably from one population to another but we could not relate the variation to the environmental parameters studied. As with plates, selection seemed to favor asymmetric fish in one population. Rakers may be a character like reptile scales in which slight differences in asymmetry may not be very important to their function.

Soulé (1967) found some populations tended to have similar asymmetry levels for a number of characters. This concordance of asymmetries he termed the Popu-

lation Asymmetry Parameter (PAP). Jackson (1973) failed to find a PAP in a study of six characters in twenty populations. In our survey, the use of only two traits hardly offers an opportunity for a rigorous search for a PAP in these populations. However, we did check plate and raker asymmetries for concordance and found none. In three cases (of 15) we found a correlation between the asymmetry of the two traits within individuals (females of Mercer and Ain Lakes and males of Wiggins Lake,  $p < 0.05$ ). This is a greater number of significant results than could be expected due to chance in a total of 15 tests. A study of the same characters in another stickleback, *Culaea inconstans*, also showed such a correlation within individuals in 12 of 45 populations (unpublished, G.E.E.M.). These cases contrast with the findings of Van Valen (1962) and Soulé (1967) who found no concordance of asymmetry within individuals.

#### Gill Raker Variation

The number of rakers indicates the space between each which may in turn be correlated with the size of food items taken (Hildebrand, in Brooks and Dodson, 1965).

Preliminary examination of a few lakes led us to think other species were influencing gill raker number, either as competitors with sticklebacks or possibly as predators forcing the sticklebacks into a different microhabitat. Some salmonids have raker numbers comparable to sticklebacks and the latter have been accused of competing with the juveniles of certain salmonids (Krogus and Krokhin, 1948; Rodgers, 1968). Analysis of the complete data, however, failed to reveal significant raker differences correlated with the presence of other species. Populations sympatric with other species did have mean raker counts higher than populations where no other species were found. However, an interaction with lake area in the former populations but absent in the latter made a statistical test of the difference in raker counts impossible. Not only was there no

evidence of character divergence in the mean number of gill rakers, the increase in variance where other species are present suggests there is no contraction of the feeding niche induced by competition.

The direct correlation between raker number and lake area in lakes with no predators may be a reflection of the relatively greater littoral zone in the smaller lakes. Fish feeding in the littoral zone often take larger items than species utilizing food of the limnetic zone.

The correlation between raker number and maximum body length may represent a need for different swimming speeds when feeding on different classes of prey: fish taking larger items may follow a halting "search and grab" pattern, whereas those utilizing smaller, aggregated planktonic organisms may move more smoothly and quickly.

Stream dwelling populations on the mainland had lower mean raker counts than lake populations (Hagen and Gilbertson, 1972). The three stream populations in our study also had mean raker counts lower than those of the 21 lake populations. Hagen and Gilbertson concluded there were probably differences in the types of food available in the two habitats.

#### Body Size and Proportions

One of the most remarkable features of the different *Gasterosteus* populations in the Queen Charlotte Islands is the great differences in body size that occur. Often lakes containing very large fish are within three kilometers of others containing small fish, for example Mayer and Boulton, Mayer and Watt or Drizzle and Skonun Lakes. In such cases the physical environment (watershed, climate) must be similar and one thus suspects biotic factors to be causative. Evidently the presence of *S. clarki* and *C. asper* affects body size. This is further supported by analysis of gut samples from Mayer Lake which showed large sticklebacks were swallowed mainly by the larger and scarcer trout (Moodie, 1972a). Experimental work by Hay (1974) revealed *S.*

*clarki* selectively captured smaller sticklebacks so that large size is favored. Larger fish may also have a better chance of reaching shelter when pursued by trout and may be more able to drive nest robbing sculpins from the territory. Additionally, body size may be influenced by the type of food available, as noted above (Gill Rakers).

To summarize, predation remains the selective agent most readily correlated with phenetic variation of the type quantified to date. However, differences in lake area are related to variation in a trophic adaptation, namely gill raker number. Potential competition did not affect the mean number of gill rakers but variance increases among males in lakes where other fish species occur. Several phenetic traits are correlated with each other in these populations. This study, as well as data of others, suggest fluctuating asymmetry in this species may be selected for. If this is indeed the case, it appears to us that the concept of fluctuating asymmetry as simply an inverse measure of buffering against developmental "accidents" will have to be reassessed and modified.

Although our data on fluctuating asymmetry are not as exhaustive as we would prefer, we feel they together with Jackson's (1973) contribution suggest that our understanding of asymmetry may not yet be at the point where we can make valid generalizations about its relevance to developmental biology and adaptation.

The biological significance of directional asymmetry also concerns us. In past studies (Soulé, 1967; Jackson, 1973) directional asymmetry has been minimal and thus perhaps justifiably ignored or attributed to sampling error. Fox (1975), however, found considerable directional asymmetry in a population of lizards. In the present study directional plate or raker asymmetry appeared in one sex or the other of six populations. Of greater interest is the directional asymmetry in pelvic spine loss in Boulton Lake. Here there is a polymorphism, either transient or balanced, such that fish may have both the left and right spines, neither

spine or only one. In the latter case the missing spine is consistently the right (Reimchen, unpublished). McPhail (pers. com.) reports a similar phenomenon in a distant population on Texada Island. Clearly the cause is genetic or developmental; we wonder if the less obvious but more numerous cases involving meristic traits may also have biological bases rather than be sampling artifacts.

#### RÉSUMÉ

Vingt-cinq bancs de *Gasterosteus aculeatus* ont été étudiés pour comparer les variations morphologiques et asymétriques des scutelles latérales, le nombre et l'asymétrie des opercules, la taille du corps et autres traits. Les fluctuations dans l'asymétrie et le nombre moyen des scutelles latérales ainsi que les dimensions et les proportions du corps sont corrélatif à la présence d'un poisson (prédateur) rapace. En l'absence de d'autre espèce de poissons, le nombre d'opercules est corrélatif à la superficie du lac. Les fluctuations dans l'asymétrie des scutelles latérales et des opercules ne semblent pas diminuer avec l'âge; dans trois des bancs, l'inverse s'est produit. Six des bancs présentaient une direction dans l'asymétrie. Les fluctuations d'asymétries dans ces bancs ne semblent pas se conformer aux concepts actuels de stabilité de développement et d'asymétrie.

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