TWELVE YEARS OF CONTEMPORARY ARMOR EVOLUTION IN A THREESPINE STICKLEBACK POPULATION

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Abstract.—Loberg Lake, Alaska was colonized by sea-run *Gasterosteus aculeatus* between 1983 and 1988, after the original stickleback population was exterminated. Annual samples from 1990 to 2001 reveal substantial evolution of lateral plate (armor) phenotypes. The 1990 sample was nearly monomorphic for the complete plate morph, which is monomorphic in local sea-run populations; the low plate morph, which is usually monomorphic in local freshwater populations, was absent. By 2001, the frequency of completes had declined to 11%, and lows had increased to 75%. The partial plate morph and two unusual intermediate plate phenotypes were generally rare, but occurrence of the intermediates was unexpected. These intermediate phenotypes rarely occur in other, presumably older, polymorphic populations. When low morphs first appeared, they averaged 6.8 plates per side, indicating that the ancestral plate number of low morphs is high, and their mean has subsequently declined. Contemporary evolution in this population indicates that threespine stickleback adapt to freshwater habitats within decades after invasion from the ocean, and thus phenotypes in most populations are adapted to current conditions.

Key words.—Adaptive radiation, allopatric divergence, contemporary evolution, *Gasterosteus aculeatus*, invasion, lateral plates, postglacial evolution.

Postglacial adaptive radiation of the threespine stickleback, *Gasterosteus aculeatus*, provides one of our most enlightening cases of evolutionary diversification (reviewed by Bell and Foster 1994a, Schluter 2000; McKinnon and Rundle 2002). It has been studied most intensively in northwestern North America, which was heavily glaciated until about 20,000 years ago. During deglaciation, sea-run (anadromous) and marine-resident threespine stickleback (collectively oceanic) invaded lakes and streams to found resident populations that diverged innumerable times from their oceanic ancestors.

Lateral plate (LP) phenotypes vary conspicuously among freshwater *G. aculeatus* populations and are usually divergent from those in oceanic populations. They are superficial bony armor structures that form a single row of zero to about 35 plates on each side of the body. Three major lateral plate morphs (LPM), completes, partials, and lows are recognized in western North America (Fig. 1). They are discrete (e.g., Hagen and Gilbertson 1972; Bell and Foster 1994b) and controlled by a few loci (reviewed by Bańbura and Bakker 1995; Bell 2001). Lateral plate morph frequencies in oceanic and freshwater populations vary regionally, but in Cook Inlet, Alaska, oceanic stickleback are monomorphic for the complete morph (14 populations, $N = 3341$; M.A. Bell, unpubl. data), and almost all freshwater populations are monomorphic for the low morph. Low and partial LPM have evolved in fresh waters around Cook Inlet from the complete morph within 22,000 years since deglaciation (Bell et al. 1993; see Reger and Pinney 1995).

Diversification of LP phenotypes is adaptive (reviewed in Reimchen 1994, 2000; Bell 2001). The posterior LPs of complete morphs reduce injury during capture by predatory fishes

and increase the probability of escape after capture (Reimchen 1992, 2000), but they may hinder escape before capture (Bergstrom 2002). Reimchen (2000) concluded that LPM frequencies depend on the relative survival values for evasion before capture versus escape and survival after capture by predatory fishes. Thus, selection should favor the low morph in littoral habitats with structural refuge and the complete morph in the ocean, where structural refuge is absent. Low morphs may also be favored in fresh water because lower ionic concentration may increase the cost of ion uptake to mineralize bone (Bertin 1925; Heuts 1947; Giles 1983; Bourgeois et al. 1994).

Plate number varies within each LPM, and differences in low-morph LP number influence the effectiveness of armor against predatory fishes (e.g., Moodie 1972; Hagen and Gilbertson 1972, 1973a; Reimchen 1994). Low morphs from sites with abundant predatory fishes have higher plate numbers, and lower plate number phenotypes occur where predatory fishes are absent (reviewed by Bell 1976, 1984, 2001; Reimchen 1994). Lateral plate phenotypes of *G. aculeatus* thus have excellent potential for the study of evolutionary mechanisms and patterns.

In this paper, we describe contemporary patterns of LP evolution in a recently founded threespine stickleback population from Loberg Lake, Cook Inlet, Alaska between 1990 and 2001. Like most neighboring stickleback populations, the original Loberg Lake population was monomorphic for the low LPM. It was exterminated using rotenone in October 1982 to improve the lake for recreational fishing. Threespine stickleback were not detected during inspections in conjunction with annual trout and salmon plants until 1990 (A.C. Havens, pers. comm. 1990). Appearance of adult, complete-morph stickleback in Loberg Lake in 1990 indicates that it was invaded by anadromous stickleback between 1983 and 1988. This study minimizes several common limitations of
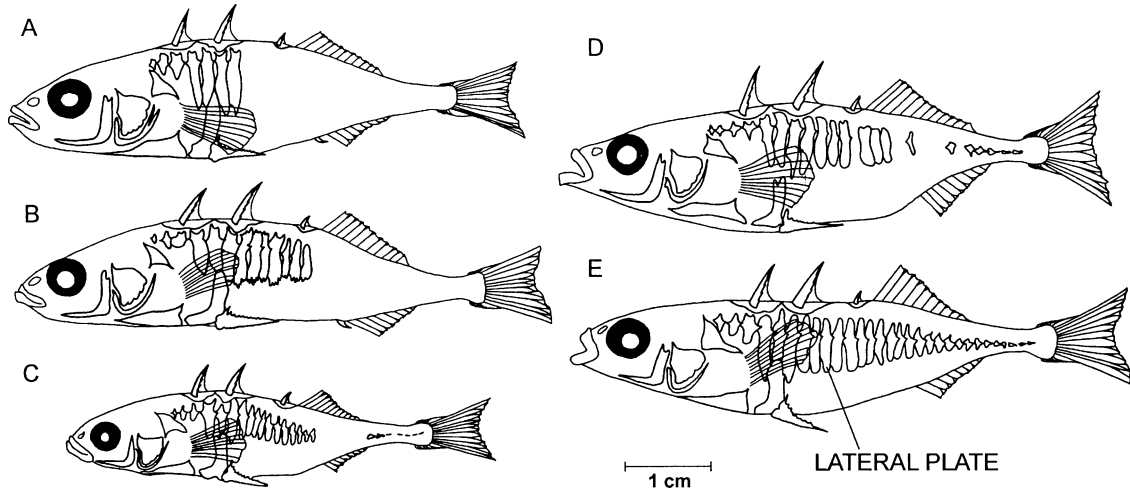
FIG. 1. Lateral plate morphs and major phenotypes of *Gasterosteus aculeatus* in Loberg Lake. A, low morph; B, intermediate low phenotype; C, partial morph; D, intermediate partial phenotype, and E, complete morph. Modified from Francis et al. (1985).

studies on contemporary evolution. Habitat conditions are relatively natural, the population's ancestry can be inferred, and large annual samples have been made most years since the population was founded. Extensive information on evolution of western North American *G. aculeatus* provides a context for interpretation of our results (see reviews in Bell 1976, 1984, 2001; Bell and Foster 1994b; Reimchen 1994).

MATERIALS AND METHODS

Habitat, Sampling Procedures, and Phenotypic Scoring

Loberg Lake is in the Matanuska-Susitna Valley, Cook Inlet, Alaska (61°33′35″N, 149°15′30″W; Fig. 2A). It discharges into a short (<50 m) channel that ends blindly and apparently flows through porous glacial till into the Palmer
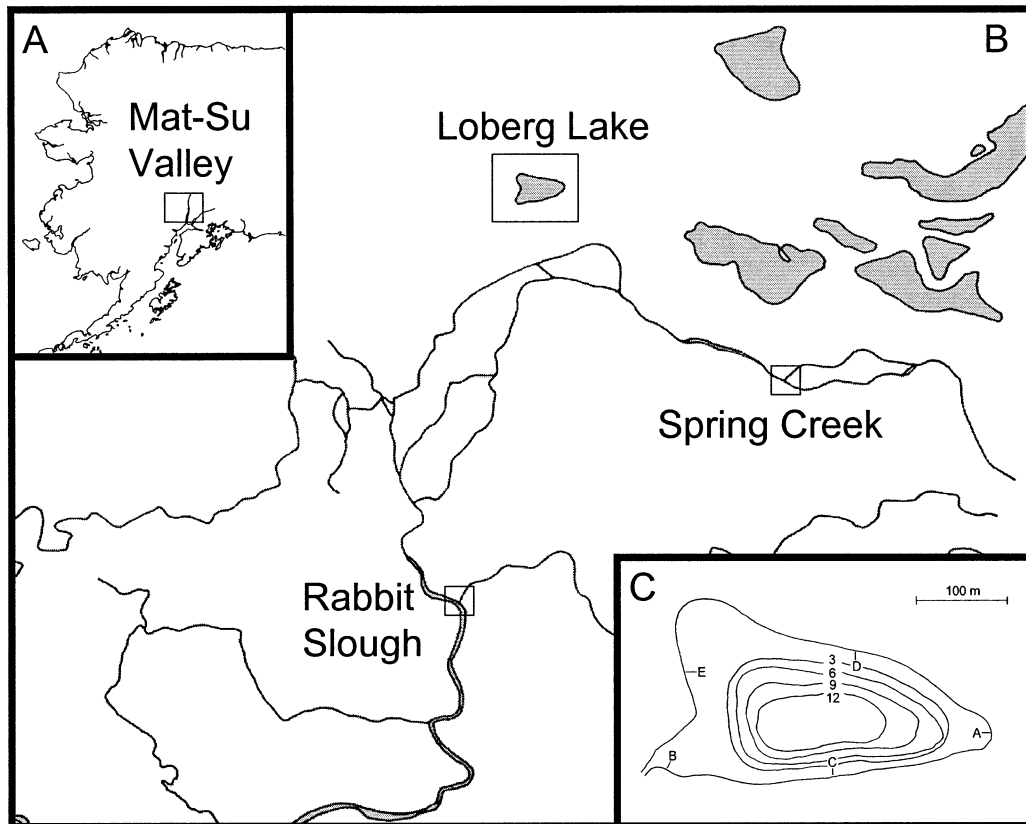

FIG. 2. Locations of sampling sites, showing A, the position of the Matanuska-Susitna Valley in Alaska; B, three habitats from which stickleback were sampled in the Matanuska-Susitna Valley; and C, sampling sites (A–E) and isobaths (m) within Loberg Lake.

TABLE 1. Sample size, mean standard length (SL), and lateral plate morph (LPM) frequencies for *Gasterosteus aculeatus* in Loberg Lake from 1990 to 2001. Mean standard length is based on samples of 100 specimens from site A, except for 1990 when there were 59 specimens. LPM frequencies are based on samples of size *n* for site A from 1990 to 1993 and weighted averages of all sites for 1994 to 2001.

			LPM frequency				
Year	*n*	SL	Complete	Intermediate partial	Partial	Intermediate low	Low
1990	59	49.68	0.959	0.041	0.000	0.000	0.000
1991	100	34.56	0.760	0.040	0.040	0.000	0.160
1992	621	38.11	0.781	0.019	0.050	0.000	0.150
1993	334	43.82	0.389	0.009	0.240	0.051	0.311
1994	3240	42.78	0.396	0.020	0.113	0.010	0.461
1995	2287	48.11	0.369	0.012	0.106	0.011	0.502
1996	1948	45.51	0.368	0.012	0.108	0.032	0.480
1997	1113	47.18	0.278	0.043	0.084	0.036	0.560
1998	770	38.67	0.261	0.032	0.108	0.017	0.582
1999	6582	36.12	0.198	0.029	0.103	0.006	0.664
2000	3348	37.15	0.171	0.030	0.092	0.013	0.694
2001	3304	37.61	0.112	0.036	0.085	0.014	0.752

Slough drainage, where both stream resident and anadromous *G. aculeatus* occur within about 2.5 km (Fig. 2B). It has a mean depth of 5.4 m, a surface area of 4.45 ha, and an elevation of 23 m. It is alkaline (pH 8.2), turbid (71.7 mg L^{-1} nephelometric turbidity units), and slightly stained by tannins, and has a high specific conductance (276 mhos/cm). Stonewort (*Chara* sp.) covers much of the littoral zone, but about three-quarters of the lake bottom is below euphotic zone depth. Rainbow trout (*Oncorhynchus mykiss*) and silver salmon (*O. kisutch*), which both eat stickleback (Reimchen 1994), are planted annually for sport fishing, but most are caught before they become large enough to eat stickleback (see Moyle 1976; Morrow 1980; Havens 1983).

Gasterosteus aculeatus were sampled from five sites around the perimeter of Loberg Lake (Fig. 2C). Only site A was sampled from 1990 to 1993, and sampling since 1994 has included all five sites (sites A–E). Most Loberg Lake samples were collected with six to 10 minnow traps (chamber 44.45 cm long, 22.86 cm diameter; openings 2 cm diameter; mesh 0.635 or 0.318 cm) per site in late spring or early summer. The 1990 sample was collected with a seine (3.05 m long, 1.2 m wide, mesh 3.18 mm) in July, and the 1991 sample was trapped through the ice in November. Traps were unbaited and set overnight on the bottom near shore in 1–2 m of water. Stickleback were anesthetized with MS-222 (tricaine methanesulfonate), fixed in 10% buffered formalin, preserved in 50% isopropyl alcohol, and stained with an alkaline aqueous solution (<1% KOH wt/wt) of alizarin red to visualize LP (e.g., see Bell 1981, 1984).

Lateral plate morph and LP number were scored in specimens ≥32 mm standard length (SL; i.e., tip of the upper jaw to end of the last vertebra), by which size all plates have ossified in most populations (reviewed by Bell 2001). Complete morphs in Loberg Lake have a continuous row of 27 (usually ≥30) to 35 plates extending from the shoulder to the caudal fin, where it forms a keel (Fig. 1E). The partial morph has a row of anterior plates separated by a gap of two or more consecutive unplated body segments from a posterior row of plates, where a keel may be present (Fig. 1C). Low morphs have four to 10 anterior plates (Fig. 1A). However, the Loberg Lake population also includes atypical specimens

that cannot be assigned to a morph, so two additional plate phenotypes were recognized. The ''intermediate low'' phenotype has 10 or more abdominal plates but lacks posterior plates (Fig. 1B). The ''intermediate partial'' phenotype resembles the partial morph but has isolated plates in the gap between the continuous anterior and posterior plate rows, from which they are separated by unplated body segments (Fig. 1D). All specimens from sites A–E were assigned to a morph or major plate phenotype based on maximal plate expression on either side. Plate morph frequencies reported after 1993 are weighted means from the five sites.

Annual sample sizes summed for all sites from the extant Loberg Lake population ranged from 59 (1990) to more than 6500 (1999), and usually exceeded 1000 (Table 1). All LP on the left side were counted in a random subsample of 100 specimens from site A every year except 1990, when all 59 specimens were used. Lateral plate counts for complete morphs in these subsamples were used to calculate rates of complete-morph plate number evolution. However, there were too few complete morphs in random subsamples after 1997, so LP counts from additional complete-morph specimens were used to increase the sample size to ≥20 thereafter. Sample sizes for complete-morph plate counts thus ranged from 20 to 77 and averaged 38.6. Plates were counted on all low morphs from site A in 1992 and 1993 and from a subsample of 200 low morphs in 1994 to 2001.

Analysis of Temporal Trends

Temporal trends for arcsine-transformed frequencies of complete and low morphs at all sites were evaluated from 1994 to 2001, the years in which five sites were sampled. Residuals for the regression of LPM frequencies were tested for serial autocorrelation with the Durbin-Watson test (Durbin and Watson 1951; test executed with JMP software ver. 4.0.4; SAS Institute 2000), and serial autocorrelation was not detected (low-morph $d_{40} = 1.536$, $P = 0.0948$; complete-morph $d_{40} = 1.868$, $P = 0.5546$). *G*-tests with Williams's correction were used to test for spatial heterogeneity of LPM frequencies (Sokal and Rohlf 1995).

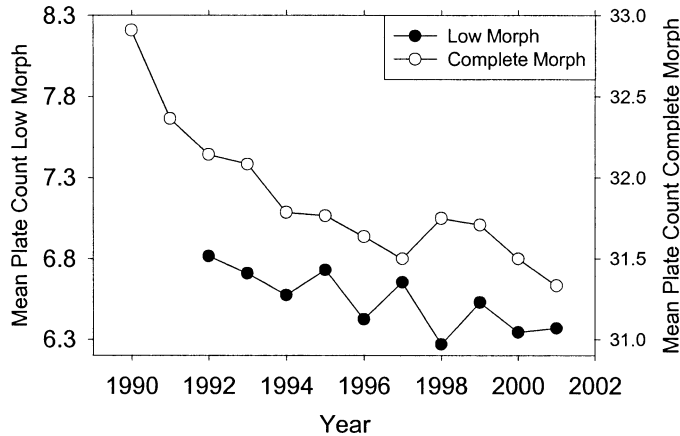Linear regression could not be used to analyze temporal

FIG. 3. Temporal variation of mean left lateral plate number of low and complete morphs of *Gasterosteus aculeatus* from site A in Loberg Lake.

trends in mean LP counts without dividing the observations into even-year and odd-year cohorts because residuals for the complete morph were positively autocorrelated (Durbin-Watson statistic: $d_{12} = 0.859$, $P = 0.0062$), and residuals for the low morph were negatively autocorrelated (Durbin-Watson statistic: $d_{10} = 3.644$, $P = 0.0016$). Negative temporal autocorrelation of low-morph LP number reflects zig-zag temporal variation (Fig. 3). Since Cook Inlet *G. aculeatus*, including the exterminated Loberg Lake population, usually have a two-year generation time (Havens et al. 1984; Baker 1994), negative autocorrelation of the residuals may reflect the existence of odd- and even-year cohorts. Regression analysis of odd- and even-year low- and complete-morph data separately substantially reduced the residual autocorrelation (low-morph odd-year cohort $d_5 = 1.461$, even-year cohort $d_5 = 1.765$; complete-morph odd-year cohort $d_6 = 2.165$, even-year cohort $d_6 = 1.320$).

Evolutionary Rate and Selection Estimates

Rates of low- (during 10 years) and complete-morph (during 12 years) plate number evolution were calculated in haldanes and darwins using first and last years' data only (endpoints) and complete time series, following Hendry and Kinnison (1999). Endpoint rates were similar to time-series rates so they are not reported. Time-series rates and pooled standard deviations for haldanes were calculated separately for odd- and even-year cohorts as the slopes of the regression of x/s_p and $\ln(x)$ on the number of generations and years for haldanes and darwins, respectively. Standard errors of the rates and confidence intervals were obtained using univariate methods for slopes (Sokal and Rohlf 1995). Low-morph LP number heritability (h^2) was estimated to be 0.879 for Loberg Lake stickleback based on 11 low × low-morph crosses performed in 2000 (Aguirre et al. 2004), and used to estimate selection intensities and selection differentials for low-morph LP. Previous estimates of LP number heritability (h^2) vary, but two methodologically comparable estimates are $h^2 = 0.34$ (Hermida et al. 2002) and $h^2 = 0.84$ (Hagen 1973). Selection intensity was calculated as the rate of evolution in haldanes divided by the heritability, and the selection differential was

calculated as the selection intensity multiplied by the pooled standard deviation (Hendry and Kinnison 1999). Heritabilities should change during evolution, and our use of this high value is conservative to estimate selection. We could not estimate selection intensities or differentials for complete-morph plate number because there are no h^2 estimates for this trait.

Interpopulation Comparisons

We compared mean low-morph LP and gillraker numbers (GR) of the extant Loberg Lake population to those of other Cook Inlet stickleback populations to infer potential ancestors of the extant Loberg Lake population. All comparisons involving the extant Loberg population were carried out with specimens from site A because samples were available from only this site before 1994. Samples from site A should give reliable estimates for the entire population because there was no evidence of spatial heterogeneity of either trait in 1994, the first year they could be assessed (Kruskal-Wallis test, LP: $H_{adj} = 0.8470$, df = 4, $P = 0.932$; GR: $H_{adj} = 3.3035$, df = 4, $P = 0.5084$). Both LP and GR are heritable (Hagen and Gilbertson 1973b; Hermida et al. 2002; Aguirre et al. 2004) and vary among populations, making them useful to infer source populations. The native Loberg Lake stickleback population was sampled in 1982 by the Alaska Department of Fish and Game using unknown methods just before the lake was poisoned. Spring Creek is the closest potential allopatric source for low-morph stickleback, and the closest site with anadromous, complete-morph stickleback is Rabbit Slough (Fig. 2B). Spring Creek was sampled in 1992, and Rabbit Slough was sampled several times between 1992 and 2001 using minnow traps, as described above. Lateral plates were counted in 100 specimens from the extinct Loberg Lake and Spring Creek samples. Gillrakers were counted in 50 specimens from the extinct Loberg Lake and Spring Creek samples and in 202 specimens of the 1992 Rabbit Slough sample. Finally, a database containing mean low-morph LP numbers for a subsample of 102 nearby lakes listed in Bell and Ortí (1994) was also evaluated.

RESULTS

Temporal Variation of Lateral Plate Morph Frequencies

Of the specimens in the 1990 sample, 96% were complete morphs, and the remainder were intermediate partials (Table 1; Fig. 4). Complete-morph frequency declined rapidly from 1990 to 1993 (to 39%) and more slowly thereafter (to 11% in 2001). Low morphs first appeared at 16% in 1991, doubled between 1992 and 1993, and increased gradually to 75% by 2001. Partial morphs and intermediate low and intermediate partial plate phenotypes were generally rare (Table 1; Fig. 4), comprising 10–15% of the individuals most years, and peaking at about 30% in 1993, when complete and low morphs were about equally frequent (Fig. 4). Lateral plate morph frequencies varied significantly among sites for five of the eight years in which five sites were sampled (G-tests, $P < 0.05$; Fig. 5). There was no significant spatial variation in 1998 ($G = 15.4$, $P = 0.498$), 2000 ($G = 21.1$, $P = 0.174$), or 2001 ($G = 24.9$, $P = 0.0716$). The cause of spatial het-
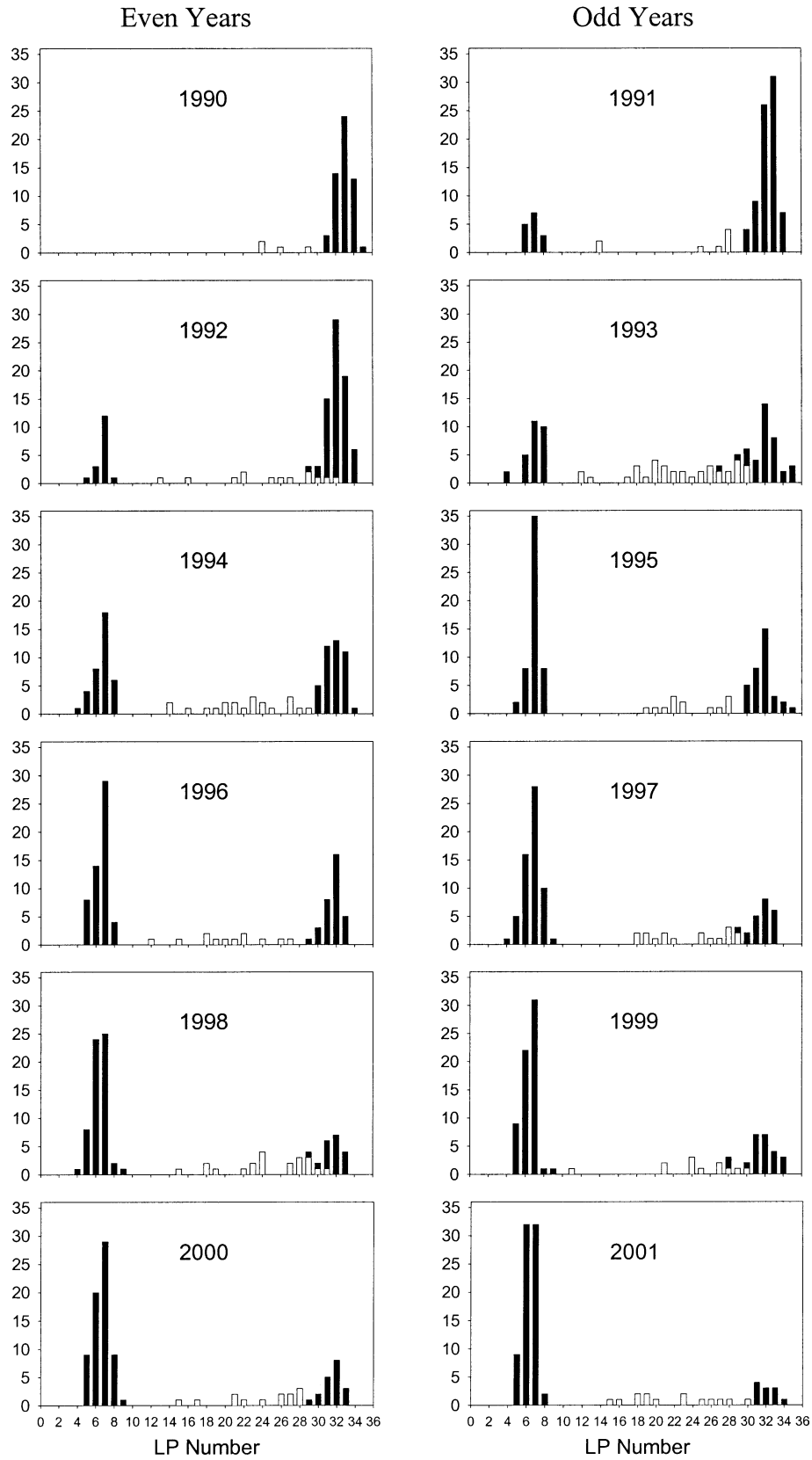
FIG. 4. Frequency of left lateral plate number phenotypes of *Gasterosteus aculeatus* samples at site A in Loberg Lake, Alaska, from 1990 to 2001. Closed bars on the left in each panel are low morphs, closed bars on the right are complete morphs, and open bars in the middle are partial morphs and intermediate low and intermediate partial phenotypes.
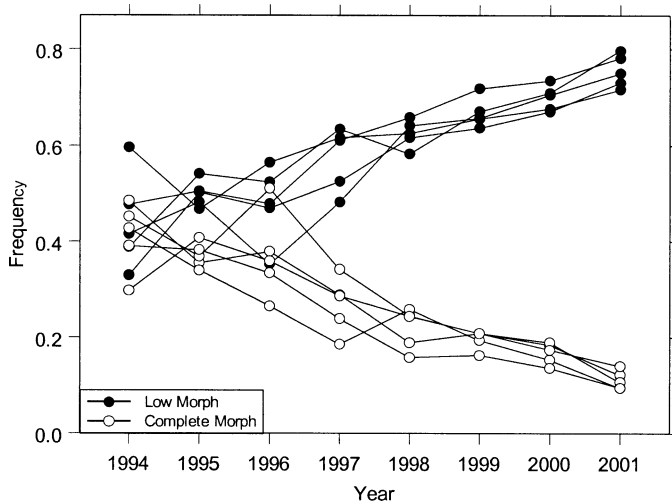
FIG. 5. Frequencies of low and complete morphs of *Gasterosteus aculeatus* from Loberg Lake during years in which five sites were sampled. Circles are morph frequencies at each site, and lines connect sites across years.

TABLE 2. Time-series rates of evolution in haldanes and darwins for low- and complete-morph left lateral plate number in *Gasterosteus aculeatus* from Loberg Lake, Alaska. Rates were calculated separately for odd- and even-year cohorts. CI, confidence interval.

	Even year	Odd year
Low morph		
haldanes	-0.137 ± 0.036	-0.104 ± 0.024
95% CI	-0.251 to -0.024	-0.180 to -0.027
darwins	-9525 ± 2464.1	-6700 ± 1571.7
95% CI	-17367 to -1683	-11702 to -1698
Complete morph		
haldanes	-0.237 ± 0.067	-0.142 ± 0.029
95% CI	-0.423 to -0.050	-0.223 to -0.061
darwins	-3716 ± 1046	-2929 ± 602.3
95% CI	-6619 to -812.5	-4601 to -1256

erogeneity is unclear, but the rank of LPM frequencies among sites varied from year to year (Fig. 5), indicating that the heterogeneity is not due to persistent genetic population structure or habitat differences. This heterogeneity decreased through time probably because most individuals in later samples are low morphs. Despite the spatial heterogeneity, changes in low- and complete-morph frequencies among years were much greater than variation among sites within years (Fig. 5). Using the individual frequencies from all sites, there is a highly significant increasing temporal trend for low morphs from 1994 to 2001 (least-squares regression, $b = 2.70$, $t_{38} = 12.06$, $P < 0.001$) and a corresponding decrease for complete morphs (least-squares regression, $b = -2.922$, $t_{38} = 13.4$, $P < 0.001$). Lateral plate morph frequencies for all 12 years at site A (Table 1) show similar temporal trends but fit a quadratic curve significantly better than a straight line because the rate of LPM frequency evolution was initially high and declined after 1993 (polynomial regression: low-morph fit: $F_{1,41} = 26.46$, $r^2 = 0.880$, $P < 0.001$; complete-morph fit: $F_{1,41} = 22.456$, $r^2 = 0.881$, $P < 0.001$).

Temporal Variation of Lateral Plate Number

Lateral plate number decreased significantly in both complete and low morphs, although it decreased at a higher rate in completes. The modal LP count for the complete morph was 33 per side in 1990 and 1991, and decreased to 32 in subsequent years with adequate sample sizes (Fig. 4). Mean complete-morph plate number decreased significantly for both odd- and even-year cohorts (Fig. 3; least-squares regression: odd-year cohort: $b = -0.093 \pm 0.019$, $t_4 = -4.822$, $P = 0.009$; even-year cohort: $b = -0.119 \pm 0.034$, $t_4 = -3.532$, $P = 0.024$), and the slopes and adjusted means did not differ significantly between cohorts (ANCOVA, slopes: $F_{1,8} = 0.439$, $P = 0.526$; adjusted means: $F_{1,9} = 1.573$, $P = 0.241$).

Low morphs exhibited a strong mode at seven plates per side most years (Fig. 4), but had a mode of six in 1998 and

2001. Mean low-morph plate number also decreased significantly for both odd- and even-year cohorts (least-squares regression: odd-year cohort: $b = -0.044 + 0.010$, $t_3 = -4234$, $P = 0.024$; even-year cohort: $b = -0.063 \pm 0.016$, $t_3 = -3.807$, $P = 0.032$). The slopes did not differ significantly between cohorts, but the adjusted means did (ANCOVA, slopes: $F_{1,6} = 0.920$, $P = 0.375$; adjusted means: $F_{1,7} = 9.213$, $P = 0.019$).

Evolutionary Rates and the Magnitude of Selection on Lateral Plate Number

Rates of evolution of LP number were generally comparable between cohorts and morphs given the broad confidence intervals of these estimates. Although the confidence intervals overlapped, the even-year cohort always had a higher rate than the odd-year cohort (Table 2). The selection intensity and selection differential for the low-morph odd-year cohort were -0.118 and -0.100, respectively, -0.156 and -0.142 for the even-year cohort, respectively.

Interpopulation Comparisons

Mean left LP numbers of stickleback populations from 102 Cook Inlet lakes range from 2.09 to 6.91 with a grand mean of 5.55 (M. A. Bell and W. E. Aguirre, unpubl. data). The 1982 Loberg Lake sample was monomorphic for the low morph, with a mode of 5 and a mean of 5.08 plates per side. Mean left plate number from site A in the extant Loberg Lake population ranged from 6.27 to 6.82 (Fig. 3), with means from the early years among the highest for Cook Inlet stickleback populations. Although mean low-morph plate number is decreasing in the extant Loberg Lake population, it was still significantly greater in 2001 (mean = 6.37) than the mean for the extinct population that occupied Loberg Lake until 1982 (Mann-Whitney U-test, $U = 16{,}620.5$, $t_\infty = 9.47$, $P < 0.001$). The Spring Creek sample included 48 low morphs (plus one partial morph and one intermediate partial morph), and their mean LP number was 6.54, which differed significantly from that of the earliest Loberg Lake sample with a reasonable number of low morphs (1992, low-morph mean = 6.82; Mann-Whitney U-test, $U = 2947.5$, $t_\infty = 2.0627$, $P = 0.0196$).

Gillraker comparisons were used to infer whether low

morphs in the extant Loberg population were phenotypically similar to low morphs from populations that could have served as a source of low morphs in Loberg Lake, as well as to assess whether Loberg Lake lows and completes differ for this heritable trait. Gillraker number in the 1990 Loberg Lake sample (mean = 22.34) did not differ significantly from the 1992 Rabbit Slough sample (mean = 22.36; Mann-Whitney U-test, $U = 5081.5$, $t_\infty = 0.070$, $P = 0.4721$) but differed significantly from those of both the 1982 Loberg Lake (mean = 20.82; Mann-Whitney U-test: $U = 1985$, $t_\infty = 5.163$, $P < 0.001$) and Spring Creek samples (mean = 18.08; Mann-Whitney U-test, $U = 2468.5$, $t_\infty = 8.474$, $P < 0.001$), which is consistent with the colonization of Loberg Lake by anadromous stickleback. The 1990 Loberg Lake mean GR number exceeded that of 37 of 40 Cook Inlet lake *G. aculeatus* populations reported by Walker (1997), indicating that it was probably not derived from another freshwater population. Moreover, a sample of 50 low morphs from the 1992 Loberg Lake sample (mean = 21.34) differed significantly in GR number from both the 1982 Loberg (Mann-Whitney U-test: $U = 1520$, $t_\infty = 1.916$, $P = 0.0277$) and Spring Creek (Mann-Whitney U-test: $U = 2429.5$, $t_\infty = 8.226$, $P < 0.001$) samples, suggesting that the low morphs in Loberg did not come from these potential source populations. Gillraker numbers of Loberg Lake 1992 lows and completes (mean = 21.5) did not differ significantly (Mann-Whitney U-test: $U = 1300.5$, $t_\infty = 0.358$, $P = 0.36$), which is consistent with the existence of a single interbreeding stickleback population in Loberg Lake that is polymorphic for LP phenotypes.

DISCUSSION

Origin of the Loberg Lake Population and Low-Morph Alleles

According to Alaska Department of Fish and Game records, the original Loberg Lake population was exterminated with rotenone in October 1982, and stickleback were not seen during annual inspections (A. C. Havens, pers. comm. 1990) until we observed them in May 1990. Stickleback probably could not have immigrated to Loberg Lake until spring 1983, because anadromous stickleback run to sea in late summer and do not return until spring. The lake lacks surface discharge, so it is not clear how it was colonized. However, allozyme polymorphism in Loberg Lake stickleback is comparable to that in adjacent lakes (J. E. Seeb and M. A. Bell, unpubl. data), suggesting that anadromous stickleback colonized it by natural means. Cook Inlet stickleback, including the original Loberg Lake population, usually have a two-year generation time (Havens et al. 1984; Baker 1994), so adult stickleback in the 1990 sample were probably born in spring 1988. Thus, the extant Loberg Lake population was probably founded some time within six years after the original population was poisoned.

The phenotype of the 1990 sample leaves little doubt that Loberg Lake was colonized by oceanic *G. aculeatus*. It had a high frequency of complete morphs, which do not occur in neighboring freshwater populations, and a higher mean GR number than most freshwater stickleback. Furthermore, specimens in the 1990 Loberg sample closely resemble local anadromous stickleback in size; body form; the size, placement,

and shape of fins; head shape; and spine lengths (W. E. Aguirre, unpubl. data). Anadromous *G. aculeatus* must have founded the extant population in Loberg Lake.

The phenotypic characteristics of low morphs in early samples from the extant Loberg Lake population are also inconsistent with massive gene flow from freshwater populations or the presence of separate complete and low-morph demes. The first low morphs that appeared in Loberg Lake do not appear to be derived from either the Spring Creek or the original Loberg Lake population. Low morphs were absent or rare ($n \leq 16$) before 1992, but the mean LP number of low morphs from the 1992 sample (6.82) was significantly greater than those of the extinct Loberg Lake (5.08) and Spring Creek (6.54) populations, as well as most lake populations in the area. Although the mean plate-number difference between the 1992 Loberg Lake and Spring Creek samples was small, GR means differ between them significantly (Loberg 1992 mean: 21.34, Spring Creek 1992 mean: 18.08), and their frequency distributions barely overlap. In addition, low and complete morphs in the extant Loberg Lake population do not differ for GR number or body shape (W. E. Aguirre, unpubl. data). Our phenotypic data imply that Loberg Lake lows and completes constitute one rapidly evolving deme rather than a pair of species, with the low-morph species replacing the complete-morph species.

Nonetheless, we cannot rule out limited gene flow of low-morph alleles from a freshwater source. If relatively few low-morphs introgressed the extant Loberg Lake population, then most lows in our samples would be hybrids or backcrosses whose LP and GR number phenotypes would not necessarily resemble those of the freshwater source population. If this is the case, the most likely sources of gene flow of low-morph alleles are stream-resident stickleback from Spring Creek, which runs close to Loberg Lake (Fig. 2B), or survivors from the 1982 poisoning.

We envision four possible scenarios for the source of low-morph alleles in the extant Loberg Lake population. The original Loberg Lake *G. aculeatus* survived the 1982 poisoning and persisted at low levels, or individuals from another deme (e.g., Spring Creek) entered Loberg Lake after it had been colonized by anadromous *G. aculeatus*, and these low morphs introgressed the new population. Second, anadromous *G. aculeatus* carry low-morph alleles acquired through gene flow elsewhere. This scenario requires inclusion of individuals carrying recessive low-morph alleles among the original founders of the Loberg Lake population. Anadromous and freshwater *G. aculeatus* frequently breed in sympatry (McPhail 1994), and alleles from anadromous *G. aculeatus* are largely dominant to those of lake fish (M. A. Bell and W. E. Aguirre, unpubl. data). Therefore, anadromous stickleback might be introgressed by freshwater populations but rarely express recessive alleles that would reduce fitness in the ocean. Both of these scenarios involve hybridization as a source of adaptive variation, which has been reported in other species (Arnold 1997; Grant 1998; Grant and Grant 2000, 2002). Third, alleles responsible for rapid divergence of plate phenotypes in the Loberg Lake population may be maintained by a mutation-selection balance in the anadromous ancestor. Selection depresses the frequency of alleles favored within freshwater habitats sufficiently to limit poly-

morphism in the anadromous ancestor. The last scenario is that anadromous *G. aculeatus* colonized Loberg Lake, and mutations for divergent LP phenotypes originated since colonization. In situ mutational origin of low-morph alleles is unlikely both because it would require very high mutation rates, and fixation of new recessive mutations is unlikely (see Orr and Betencourt 2001). The first three scenarios require that the low-morph allele is recessive, seemingly making it difficult for selection to act on it. However, Orr and Betancourt (2001) showed that the probability of fixation in response to favorable selection on previously deleterious recessive allele maintained by a selection-mutation balance is independent of dominance. This finding may also apply to a balance maintained largely by opposing effects of selection and gene flow (H. A. Orr 2003, pers. comm.). We cannot presently choose among these scenarios, and it will probably be necessary to study the genes for rapidly evolving phenotypic traits to identify the source of the adaptive genetic variation for radiation of postglacial, freshwater stickleback. Research to map LPM loci is well under way (see Peichel et al. 2001; Kingsley et al. 2004) and may soon allow empirical evaluation of these scenarios.

Selection on Lateral Plate Morph Frequency and Lateral Plate Number in Loberg Lake

We did not attempt to infer the selection agents responsible for LPM evolution in Loberg Lake, but the direction of evolution is consistent with evidence from studies reviewed in the introduction. The extant Loberg Lake population is evolving rapidly toward low-morph monomorphism, which was the condition in the original Loberg Lake population and predominates in Cook Inlet and other western North American lake populations (Hagen and Gilbertson 1972; Hagen and Moodie 1982). The similarity of LP reduction among isolated freshwater stickleback populations implies relatively uniform directional selection after colonization of different freshwater habitats. Reduced fish predation, increased access to cover, and reduced ionic concentration may all play a role in selection for low morphs in fresh water.

Lateral plate number also declined in both complete and low morphs. Low-morph LP number is converging with that of the original population and other nearby lake populations. Although there is abundant evidence that LP number is subject to strong selection based on predation (reviewed by Bell 1976, 1984, 2001; Reimchen 1994), it has been impossible to infer the ancestral number of plates for low morphs. When low morphs first appeared in Loberg Lake, they had a high mean of 6.82 per side and a mode at seven. Low morphs in the Knik Lake population, which may also have been derived recently from anadromous stickleback, also had a high mode (i.e., six per side; Francis et al. 1985). If high LP number is the ancestral condition for low morphs, lower mean plate numbers (≤5 per side) in low-morph populations (e.g., see Hagen and Gilbertson 1972; Moodie and Reimchen 1976; Reimchen 1994) represent a derived condition that has evolved repeatedly in fresh water. Furthermore, the advantages afforded by high plate number in low morphs for defense against fish predation must be an exaptation (sensu Gould and Vrba 1982), because the ancestral population from

which they were derived lacks low morphs in which high low-morph plate number could be selected.

The temporal pattern of partial morph and intermediate LP phenotype frequencies in Loberg Lake is difficult to interpret. Although partials were expected based on their common occurrence of trimorphic populations (reviewed in Bell 1984) and LPM genetics (see Bańbura and Bakker 1995), it is not clear why their frequency remained relatively constant at about 10% during the transition from numerical dominance by complete morphs to dominance by lows. In addition, substantial frequencies of atypical intermediate LP phenotypes have been reported previously only from Knik Lake, which was also poisoned to exterminate stickleback and probably recolonized by anadromous stickleback (Francis et al. 1985). Klepaker (1993) also reported divergence of LPM after a nearly monomorphic complete-morph marine population became landlocked. Partial morphs outnumbered lows, but his sample was too small to expect to see rare variants. The presence of unusual intermediate LP phenotypes in the young Loberg and Knik Lake populations may be due to novel allele combinations that destabilize developmental pathways, producing unusual LP phenotypes. Transient occurrence of intermediate LP phenotypes in such populations indicates that standing variation among older populations of an adaptive radiation may underestimate the phenotypic diversity generated during radiation.

Evolutionary Rates and Selection in Recent Isolates of Gasterosteus aculeatus

The rate of LPM frequency evolution is difficult to compare to previous studies because it is a Mendelian trait. However, it is similar to the highest rates reported by Kettlewell (1973) for industrial melanism in *Biston betularia*. The rate at which mean low-morph plate number evolved between 1992 and 2001 was -0.104 and -0.137 haldanes for the odd- and even-year cohorts, respectively. For complete morphs between 1990 and 2001, it was -0.142 and -0.237 haldanes for odd- and even-year cohorts, respectively. Hagen and Gilbertson (1973a) reported plate number evolution during three years in response to the onset of trout predation in Lake Wapato, Washington. Assuming that specimens with ≤10 plates per side were low morphs, and using mean values from the first and last years ($x_1 = 6.992$, $x_2 = 7.115$, $s_p = 0.830$) and two for the number of generations, the rate of evolution was 0.074 haldanes, which is slightly lower but comparable to our results. Rates computed by Hendry and Kinnison (1999) using Klepaker's (1993) data for eye diameter (0.043 haldanes) and first dorsal spine length (0.021 haldanes) in a recently founded pond population of threespine stickleback are lower. However, Kristjánsson et al. (2002) estimated much higher rates (0.16 to -0.80 haldanes) for five traits in a freshwater *G. aculeatus* population that had recently been isolated from its marine ancestor in Iceland. Rates in the Icelandic case are comparable to the highest rates reported by Hendry and Kinnison (1999) for Trinidadian guppies (0.267 to -0.742 haldanes) and Galapagos finches (-0.372 to 0.709 haldanes). The diversity of rates observed for the same traits in different stickleback populations may reflect differences among pop-

ulations in both their genetic constitution and environmental conditions.

Estimated selection intensities for low-morph plate number in Loberg Lake were −0.118 and −0.156 and selection differentials were −0.100 and −0.142 for odd- and even-year cohorts, respectively. Using our estimate of 0.074 haldanes for the Lake Wapato population and Hagen's (1973) heritability estimate of 0.83 for low-morph plate number, the intensity of selection was 0.089 and the selection differential was 0.074. Selection on low-morph plate number in both populations fell among the most common values at the lower end of the range reported by Endler (1986) and Kingsolver et al. (2001). These moderate estimates of selection may underestimate the true magnitude of directional selection because high heritability estimates were used. Nevertheless, within a few decades, even moderate selection could cause evolution of the range of low-morph plate number phenotypes observed among freshwater stickleback populations (e.g., see Hagen and Gilbertson 1972; Bell 1984; Reimchen 1994).

Other Implications of Contemporary Evolution in Threespine Stickleback

Contemporary evolution of Loberg Lake stickleback adds to our understanding of postglacial adaptive radiation in *G. aculeatus*. Presence of freshwater threespine stickleback in proglacial lakes (von Hippel, pers. comm. 2003) demonstrates that they can colonize lakes immediately after deglaciation. The speed with which the Loberg Lake and similar populations have diverged from oceanic ancestors (reviewed by Bell 2001; Kristjánsson et al. 2002) shows that adaptation after invasion of fresh water by oceanic stickleback can also be very fast. Thus, divergence of threespine stickleback in postglacial lakes may be substantially complete within decades after deglaciation.

Although the mean plate number in Loberg Lake low morphs has generally decreased, it has exhibited a zig-zag pattern since 1994 (Fig. 3). Given the common two-year generation time of Cook Inlet stickleback, including the extinct Loberg Lake population (Havens et al.1984; Baker 1994), this temporal pattern may reflect temporal reproductive isolation between odd- and even-year demes. Greater divergence (i.e., lower mean) in even-year samples than in the subsequent odd-year samples could have been caused by selection or drift. Although it seems likely that some Cook Inlet stickleback breed at one or three years of age, Cook Inlet lakes may contain pairs of temporally isolated odd- and even-year stickleback demes, between which gene flow is limited. This situation has been demonstrated in odd- and even-year runs of pink salmon (*Oncorhynchus gorbuscha*) from the same stream, between which genetic divergence (Aspinwall 1974; Churikov and Gharrett 2002) and hybrid breakdown (Gharrett and Smoker 1991; Gharrett et al. 1999) exist. Temporal isolation between odd- and even-year breeding classes of boreal fish species with two-year generation times may be common, providing excellent opportunities to study evolution of closely related but reproductively isolated populations in a common habitat.

The speed with which Loberg Lake was colonized and the extent to which the population has diverged indicate that phenotype-environment associations in postglacial populations of freshwater *G. aculeatus* can be used to identify selection agents in threespine stickleback (e.g., see Hagen and Gilbertson 1972; Bell et al. 1993; Reimchen 1994). This method assumes that similarities among populations are independent of ancestry (Martins 2000), which seems generally warranted for postglacial freshwater *G. aculeatus* (Bell 1995; but see Reusch et al. 2001). It also assumes that there has been enough time for postglacial populations to adapt to local conditions. Observed divergence within a few decades in recently founded threespine stickleback populations (Kristjánsson et al. 2002; see Bell 2001 for earlier studies) justify this assumption, as well.

Lateral plate morphs are controlled largely by one or two loci of major effect (Bańbura and Bakker 1995), and they evolved very rapidly. By 2001, low morphs constituted 75% of the population. Low-morph LP number, on the other hand, which is controlled by minor loci, declined from 6.82 only to 6.37 in 10 years. The rate of evolution for low-morph LP number is at the lower end of the published range, and, assuming that the mean for the extinct population (5.08) is optimal in Loberg Lake, only about a quarter of the expected evolutionary change has occurred. These results support Orr and Coyne's (1992; Orr 2003) contention that adaptation often involves genes of major effect, conflicting with the neo-Darwinian expectation that adaptation should depend mostly on additive variation.

The magnitude of contemporary LP evolution in Loberg Lake is comparable to diagnostic differences between now synonymized nominal species of *Gasterosteus* (Bell 1995) and differences between sympatric biological species within the *G. aculeatus* species complex (McPhail 1994; Vamosi 2002). Thus, the major morphological changes observed in this study are comparable to species differences and represent what Liem (1984) and West-Eberhard (2003) call ''intraspecific macroevolution.'' Despite claims that phenotypic divergence between and within species involve different mechanisms (e.g., see Erwin 2000), our results show that directional selection on common genetic variation within populations can produce evolutionary changes that often mark species differences.

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