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Predictable Patterns of Disruptive Selection in Stickleback in Postglacial Lakes

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ABSTRACT: Disruptive selection is often assumed to be relatively rare, because it is dynamically unstable and hence should be transient. However, frequency-dependent interactions such as intraspecific competition may stabilize fitness minima and make disruptive selection more common. Such selection helps explain the maintenance of genetic variation and may even contribute to sympatric speciation. There is thus great interest in determining when and where disruptive selection is most likely. Here, we show that there is a general trend toward weak disruptive selection on trophic morphology in three-spine stickleback (*Gasterosteus aculeatus*) in 14 lakes on Vancouver Island. Selection is inferred from the observation that, within a lake, fish with intermediate gill raker morphology exhibited slower growth than phenotypically extreme individuals. Such selection has previously been shown to arise from intraspecific competition for alternate resources. However, not all environments are equally conducive to disruptive selection, which was strongest in intermediate-sized lakes where both littoral and pelagic prey are roughly balanced. Also, consistent with theory, we find that sexual dimorphism in trophic traits tends to mitigate disruptive selection. These results suggest that it may be possible to anticipate the kinds of environments and populations most likely to experience disruptive selection.

Keywords: frequency dependence, niche variation, sexual dimorphism, speciation.

Natural selection is generally thought to reduce genetic variation by eliminating less fit genotypes (Fisher 1930). This loss of genetic variation, in turn, reduces a population's capacity for further adaptive evolution, since variation is the raw material on which selection acts (Fisher 1930; Blows and Hoffmann 2005). Evolutionary biologists are thus faced with an important puzzle: what maintains genetic variation for ecologically important traits? Possible explanations include mutation-selection balance (Turelli 1984), migration-selection balance (Slatkin 1985), and temporally fluctuating selection (Ellner and Hairston 1994). Another often overlooked possibility is that natural selection itself maintains genetic variation. Specifically, variance increases under disruptive selection, which occurs when a population's mean phenotype is located in a valley of a fitness landscape, so that extreme phenotypes have higher fitness than average ones. This mode of selection has long been assumed to be relatively rare, because fitness landscape valleys represent unstable equilibria (Endler 1986). When a population's mean rests in a fitness valley, any perturbation away from this minimum results in net directional selection "uphill" toward a fitness peak. It was therefore surprising when a recent meta-analysis found that disruptive selection is as common, and as strong, as stabilizing selection (Kingsolver et al. 2001), suggesting that disruptive selection is more stable, and hence more widespread, than generally thought.

Stable disruptive selection can arise from negative frequency-dependent interactions, such as intraspecific competition for multiple resources (Abrams et al. 1993). Many apparently generalized populations are actually composed of relatively specialized individuals that use different subsets of the population's resource base (Bolnick et al. 2003). Competition is then more intense among ecologically similar individuals within a given population. Because competition tends to reduce fitness, relatively common phenotypes with many competitors may have lower fitness than rarer phenotypes with fewer competitors, resulting in persistent disruptive selection (Roughgarden 1972; Slatkin 1979; Wilson and Turelli 1986; Abrams et al. 1993; Bürger 2005).

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Both laboratory and field experiments have confirmed that intraspecific competition can be frequency dependent, favoring rare phenotypes in bacteria (Rainey and Travisano 1998), *Drosophila* (Fitzpatrick et al. 2007), crossbill finches (Benkman 1996), cichlid fishes (Swanson et al. 2003), and three-spine stickleback (Schluter 2003). This frequency dependence in turn has been found to drive disruptive selection in a few natural populations (Bolnick 2004a; Calsbeek and Smith 2007; Pfennig et al. 2007), niche shifts in laboratory populations of *Drosophila* (Bolnick 2001), and adaptive radiations in laboratory bacterial cultures (Rainey and Travisano 1998; Meyer and Kassen 2007).

Although it is now clear that intraspecific competition can drive disruptive selection, it is not known how common or how strong this selection will be. In particular, it would be valuable to be able to predict where and when disruptive selection is most likely. A number of forces have been hypothesized to influence the potential for disruptive selection. Theory suggests that disruptive selection is more likely to occur in populations that use a variety of resources, which permits frequency-dependent competition. Such niche variation may be strongest in populations that have been released from interspecific competition and have invaded novel niches (Van Valen 1965). Conversely, disruptive selection may be less likely if predation or density-independent population regulation lead to weaker intraspecific competition. Cyclic changes in population density may also limit disruptive selection to periods of high density (Svanbäck and Persson 2004). Finally, past episodes of disruptive selection may have already led to evolutionary responses that mitigate selection in modern populations. Disruptive selection may drive either sympatric speciation (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000; Bürger et al. 2006) or niche partitioning via polymorphism (Rueffler et al. 2006) or sexual dimorphism (Bolnick and Doebeli 2003). Once diversification occurs, the phenotype distribution is better matched to the resource spectrum, equalizing the effect of competition and eliminating disruptive selection (Bolnick and Doebeli 2003).

Given the important role that disruptive selection may play in maintaining genetic variation and possibly speciation, it is important to determine the incidence of disruptive selection in natural populations. We therefore surveyed the fitness landscapes in 14 lacustrine populations of three-spine stickleback (*Gasterosteus aculeatus*) and tested whether selection varies in a predictable manner.

Study System

Three-spine stickleback in north-temperate lakes are excellent candidates for disruptive selection due to intraspecific competition. Stickleback exhibit high levels

of diet variation within populations, permitting frequency-dependent competition (Bolnick et al. 2003; Svanbäck and Bolnick 2007; Araújo et al. 2008). Stickleback use invertebrate prey in littoral and/or pelagic habitats (also called benthic and limnetic habitats). These alternative habitats support distinct species of stickleback in a handful of lakes (benthic and limnetic species pairs; Schluter and McPhail 1992). More often, lakes contain a single panmictic population of stickleback that use both types of resources. Within a given single-species lake, individuals tend to specialize on a subset of the available resources, with some individuals eating primarily pelagic prey and others eating primarily littoral prey (Araújo et al. 2008). Stomach content variation is correlated with stable isotope signatures, indicating that diet variation is consistent over time (Bolnick et al. 2008). This diet variation is not simply an effect of coarse-grained spatial structure of prey, since individuals continue to specialize on subsets of the available prey in small artificial enclosures (Svanbäck and Bolnick 2007).

Diet variation in stickleback is tied to variation in trophic morphology, providing measurable traits on which selection might act. Fish with larger gapes, deeper bodies, and fewer, shorter gill rakers are more effective at using littoral prey, whereas pelagic prey are preferred by fish with smaller gapes, narrower body depths, and more, longer gill rakers (Schluter 1995; Robinson 2000). Accordingly, the benthic/limnetic species pairs exhibit highly divergent morphology (Bentzen and McPhail 1984). In contrast, single-species lakes contain phenotypically intermediate populations, reflecting an adaptive compromise between littoral and pelagic resources. Mean phenotypes are shifted toward benthic-like traits in small lakes dominated by littoral habitat and toward limnetic-like traits in large lakes dominated by pelagic habitat (Lavin and McPhail 1986). However, the morphological distribution remains unimodal within a given lake because of continuing gene flow and recombination between fish using the different resources.

As a result of this dietary and morphological variation within populations, competition is expected to be most intense between morphologically similar individuals. Phenotypically intermediate individuals are most abundant, so this frequency-dependent competition leads to disruptive selection. Supporting this claim, a survey of one lake on Vancouver Island revealed that stickleback with long or short gill rakers were larger than phenotypically average individuals and had relatively more gonad mass given their size (Bolnick 2004a). Experimental manipulation of competition in large field enclosures showed that this disruptive selection was stronger at high population density, confirming a causal role of intraspecific competition (Bolnick 2004a).

An important next step is to determine the frequency

and strength of this disruptive selection in unmanipulated natural populations. In particular, does selection vary in a predictable manner across lakes? We predicted that disruptive selection would be restricted to intermediate-sized lakes (comparable to those with species pairs) in which littoral and pelagic habitats are about equally productive. Disruptive selection may be less likely in small shallow ponds that are almost exclusively littoral or in large pelagic lakes, because there is less potential for diet variation and frequency-dependent competition. In addition, theory suggests that sexual dimorphism in trophic traits may mitigate the effects of intraspecific competition (Bolnick and Doebeli 2003). Because stickleback exhibit varying levels of sexual dimorphism in trophic traits (Reimchen and Nosil 2001; Reimchen and Nosil 2004; Kitano et al. 2007), we predicted that disruptive selection would be negatively correlated with dimorphism.

Methods

Collection

In 2005 and 2006, we collected between 300 and 530 stickleback from each of 14 lakes (table 1). One lake (Roberts Lake) was sampled in two successive years as part of an ongoing long-term study. All lakes are from a set of adjacent watersheds on northern Vancouver Island and share a similar history of recent glaciation. Lakes were selected to span a wide range of sizes (table 1).

In each lake, stickleback were collected using >50 unbaited minnow traps placed in a variety of microhabitats along <0.5 km of shoreline and from 0.1 to 20 m deep. Traps were left to collect fish for ≤ 12 h. This sampling scheme is intended to capture as wide a diversity of phenotypes as possible. Because both benthic and limnetic

stickleback nest close to shore, we expect to be able to capture a representative sample, though there is the potential for sampling bias due to differences in the propensity to approach unfamiliar objects. Such sampling biases may skew our estimated mean traits or variances but should not have a substantial impact on our estimated correlations between growth rate and trait values.

Collected specimens were euthanized in MS-222 and preserved in 10% neutral buffered formalin after preserving ~ 5 mg of caudal muscle tissue in 0.75 mL of RNAlater (Ambion). The RNAlater-preserved sample was stored in a 4°C refrigerator in the field for <6 weeks and at -80°C thereafter. Specimens were later rinsed and stained with alizarin red solution and stored in isopropanol. Collection and euthanasia were carried out in accordance with University of Texas institutional guidelines for the care of vertebrate animals (Institutional Animal Care and Use Committee 03120501).

Morphometrics

Specimens were blotted dry and weighed to 0.001 g. Following Bolnick (2004b), we measured standard length, head length, snout length, eye width, first dorsal spine length, head depth, body depth, opercular width, gape width, and lower jaw length on each specimen, using digital calipers accurate to 0.01 mm. We also counted gill raker number under a dissecting microscope and measured the length of the longest three gill rakers using an ocular micrometer. Specimens were sexed by inspecting gonads. Of the morphometric traits, gill raker length generally has the strongest association with stomach contents and stable isotopes in wild-caught fish (Bolnick et al. 2008) and was subject to disruptive selection in a previous study (Bolnick

Table 1: Information on the lakes surveyed in this study, including coordinate location, perimeter, area, number of stickleback sampled, and year sampled

Lake	Latitude	Longitude	Perimeter (m)	Area (ha)	Sample size	Year sampled
Big Mud	50°12'1"N	125°33'59"W	4,750	37.5	398	2006
Blackwater	50°10'40"N	125°35'20"W	5,750	37.2	498	2005
Cecil	50°14'13"N	125°32'35"W	2,041	12.0	400	2006
Farewell	50°12'1"N	125°35'14"W	3,413	20.7	300	2005
First	50°3'7"N	125°47'9"W	1,447	8.4	497	2005
Gosling	50°2'43"N	125°30'41"W	6,608	73.2	400	2006
Gray	50°3'27"N	125°35'40"W	5,239	54.7	400	2006
Little Mud	50°12'23"N	125°33'0"W	1,037	4.5	400	2006
Little Woss	50°10'51"N	126°36'39"W	2,074	9.2	300	2005
McNair	50°13'40"N	125°34'31"W	3,299	19.1	400	2006
Mohun	50°9'47"N	125°29'18"W	31,207	573.7	399	2006
Ormond	50°10'49"N	125°31'30"W	1,870	7.1	400	2006
Roberts	50°12'58"N	125°32'30"W	8,345	161.7	530	2005
Roberts	50°12'45"N	125°32'3"W	8,345	161.7	400	2006
Second	50°03'28"N	125°47'3"W	1,334	5.8	400	2006

2004b). Gill raker number can also be associated with diet and isotope signatures in natural populations (L. Snowberg and D. I. Bolnick, unpublished manuscript). Hence, these traits are the main focus of this study.

Fitness Proxy Measurements

Survivorship and lifetime reproduction are difficult to evaluate in natural populations of stickleback because of large population sizes. Furthermore, survivorship and reproductive success represent total fitness variation (including predation effects and sexual selection), whereas we were specifically interested in evaluating fitness variation arising from differential foraging success (competition). We therefore used growth rates as a fitness proxy to measure the partial selection gradients arising from frequency-dependent competition. Parasitism, predation, and sexual selection may all impose additional partial selection gradients not detected here. Furthermore, by measuring adult growth rates, we are not able to measure selection acting on larval or juvenile stickleback.

Growth rate has been used extensively as a proxy for fitness in studies of three-spine stickleback (Schluter 1994; Rundle et al. 2003; Schluter 2003), because larger fish tend to have higher survivorship and reproductive success (Wootton 1973, 1977). To measure relative growth rate, we took advantage of a biochemical index of growth, the ratio of RNA to DNA concentrations in muscle tissue (R/D). More successful foragers tend to grow more quickly, which is reflected in higher RNA concentrations due to increased ribosomal titer, whereas DNA concentration per cell remains constant. The ratio R/D is tightly correlated with growth rate in laboratory studies of stickleback ($r = 0.92$; Ali and Wootton 2003) and other fishes (McLaughlin et al. 1999; Caldaroni et al. 2001; Dahlhoff 2004). In a field competition experiment, fish held at high density showed lower R/D than low-density controls, because elevated fish density reduced prey availability (Svanbäck and Bolnick 2007). Muscle samples stored in RNA-later preservative were blotted dry, rinsed with distilled water, and trimmed to 2–5 mg wet weight. The R/D quantitation protocol is described in appendix A in the online edition of the *American Naturalist*.

Statistical Analyses

Selection gradients can be estimated by quadratic regression of a fitness measure (R/D) against a phenotypic trait (Lande and Arnold 1983; Blows and Brooks 2003). Linear coefficients (β) measure directional selection. A positive quadratic coefficient (γ) indicates disruptive selection, whereas negative γ reflects stabilizing selection. When the fitness landscape is more complex, the linear and quadratic

terms represent net selection for changes to the trait mean and variance, respectively.

To obtain measures of size-independent trophic morphology, we first conducted a principal component analysis (PCA) on log-transformed morphometric characters. A PCA was carried out separately for each population (table B1 in the online edition of the *American Naturalist*). The second and third PC axes (PC2 and PC3) are heavily associated with gill raker length and number, respectively (PC1 represents size). These size-corrected traits are frequently correlated with stomach contents (Bolnick 2004a; Bolnick et al. 2008), stable isotope signatures (Bolnick et al. 2008), and foraging efficiency on alternate prey (Ibrahim and Huntingford 1988; Robinson 2000; Schluter 2003).

Next, we compared our fitness proxy (ln-transformed R/D values) with the morphological traits of interest (PC2 and PC3) to test for disruptive selection in each surveyed population. We used cubic spline to visualize the shape of the fitness landscape to evaluate the applicability of quadratic fitness functions (Schluter 1988). We then ran quadratic regression of ln(R/D) on PC2 and on PC3. Including PC1 and/or sex as factors in the quadratic regressions had no qualitative impact on our results, so these terms are omitted here. Statistical significance of linear and quadratic terms was evaluated to test for directional, disruptive, or stabilizing selection within each lake (all tests reported here are two tailed). To address concerns over multiple comparisons (15 independent statistical tests each for PC2 and PC3), we used the *qvalue* package in R to estimate the overall false discovery rate, the fraction of tests for which the null hypothesis is true (π_0), and *q* values for each lake (Storey 2002).

Because statistical power is notoriously poor for quadratic regression (Kingsolver et al. 2001), we also adopted a meta-analytic approach. To evaluate whether there is a general across-lake trend toward disruptive selection, we used one-sample two-tailed *t*-tests on the 14 estimated selection gradients for each trait (PC2 and PC3), averaging the gradients for 2005 and 2006 samples from Roberts Lake. The null hypothesis, $\bar{\gamma} = 0$, can be interpreted either as no significant selection gradients or as equally common stabilizing and disruptive selection. The advantage of this approach is that one can detect a general trend toward disruptive selection (i.e., γ consistently exceeds 0) even if quadratic regression coefficients are not statistically significant within any one lake individually.

Very small and very large lakes will be dominated by a single habitat (littoral and pelagic, respectively), reducing the opportunity for frequency-dependent intraspecific competition. At some intermediate size, lakes presumably contain a rough balance between littoral and pelagic prey (perhaps 20–40 ha, as with the lakes supporting species

pairs; Schluter and McPhail 1992). We therefore tested whether disruptive selection is strongest in intermediate-sized lakes. We obtained measures of lake area and perimeter from digital analyses of satellite photographs of each lake. The relative abundance of littoral and pelagic habitat (L/P) was calculated by dividing lake perimeter (m) by surface area (ha). All large lakes are also quite deep, so large surface area corresponds to a large pelagic habitat volume. To test for a maximum, we used quadratic regression of the strength of disruptive selection γ against L/P (or surface area alone).

We also used quadratic regression to test whether dimorphism is maximized for intermediate values of L/P or surface areas. We quantified dimorphism as the difference between male and female mean PC scores. Because the PC axes are already in units of standard deviations, this difference provides a standardized measure of dimorphism. Statistical support for dimorphism was evaluated with a t -test for each lake. Finally, we tested for a negative correlation between dimorphism and disruptive selection, using the residuals from regressions of each trait on L/P to control for lake geomorphology.

Results

Size-adjusted trophic morphology was represented by the second and third principal component axes (PC2 and PC3). In all lakes, PC2 and PC3 were heavily weighted toward gill raker length and gill raker number, respectively (table B1).

Cubic spline analysis confirmed that in nearly all lakes, linear or quadratic curves are sufficient to describe the fitness surface for both gill raker length and number (figs. A1, A2 in the online edition of the *American Naturalist*). Quadratic regression of relative growth rates ($\ln[R/D]$) on each of these PC axes revealed only a few instances of statistically significant disruptive selection (table 2). Size-adjusted gill raker length (PC2) exhibited significant disruptive selection in only one population (Little Mud Lake; $P = .008$) and marginal support for disruptive selection in three others (Gosling, Second, and Farewell lakes; $P < .1$). Gill raker number (PC3) exhibited significant disruptive selection in four populations (McNair, Big Mud, Gosling, and First lakes). In most cases where $\gamma > 0$, the predicted fitness minimum was within the range of phenotypic variation, as indicated by both the minimum of the quadratic regression line (Mitchell-Olds and Shaw 1987) and cubic spline (Schluter 1988). Selection gradients were similar for males and females (e.g., fig. 1), so we pooled the sexes to obtain a single selection gradient for each lake.

To correct for possible Type II error due to multiple comparisons, we determined the false discovery rate (FDR)

for PC2 and for PC3 separately. The FDR is the proportion of significant tests ($P < .05$) that are likely to be false positives (Storey 2002). Gill raker length (PC2) had one significant test and an FDR of 0.072. Gill raker number (PC3) had four significant tests and an FDR of 0.112. The FDR analysis also estimates π_0 , the proportion of tests for which the null hypothesis ($\gamma = 0$) is likely to be true ($\pi_0 = 0.606$ for PC2 and 0.627 for PC3). We can therefore tentatively conclude that disruptive selection might occur in as much as 40% of the lakes surveyed, although only 7% and 29% of populations (for PC2 and PC3, respectively) were statistically significant individually. This discrepancy arises because selection may be present even when it is too weak to be reliably detected at $\alpha = 0.05$ with the available statistical power. Sample sizes more than 500 may be often required to reliably detect quadratic selection (Kingsolver et al. 2001).

A meta-analysis of all 14 lakes revealed a general tendency for the quadratic selection gradient (γ) to be positive (disruptive selection) instead of negative (stabilizing selection; table 2). The t -tests confirmed that quadratic selection coefficients tended to be significantly >0 for both morphological axes (PC2: mean $\gamma = 0.029$, $t = 2.83$, $df = 13$, $P = .014$; PC3: mean $\gamma = 0.028$, $t = 2.52$, $df = 13$, $P = .026$; fig. 2).

Lake geomorphology explained some of the variation in quadratic selection strength among lakes. Disruptive selection on gill raker number was strongest for lakes with intermediate ratios of littoral and pelagic habitat (L/P), resulting in a significant quadratic relationship between γ and L/P (fig. 2B; L/P effect: $P = .018$; $[L/P]^2$ effect: $P = .007$). Overall, L/P explained 60% of the variation in γ ($r^2 = 0.6$). This relationship did not hold for gill raker length (PC2; fig. 2A; L/P effect: $P = .440$; $[L/P]^2$ effect: $P = .482$). Lake area gave similar results as L/P (the two measures are highly correlated): PC3 but not PC2 exhibited a significant maximum γ for intermediate-sized lakes of about 50-ha surface area (PC3 area² effect: $P = .038$; $r^2 = 0.39$).

Lake geomorphology also explained some of the variation in sexual dimorphism in gill raker morphology. Gill raker length (PC2) exhibited consistent sexual dimorphism across nearly all lakes, with males having longer rakers than females (tables B2–B4 in the online edition of the *American Naturalist*). This PC2 dimorphism was maximized in lakes with intermediate L/P ratios (fig. 3A; L/P: $P = .008$; $[L/P]^2$: $P = .016$; $r^2 = 0.595$). In contrast, gill raker number (PC3) exhibited significant sexual dimorphism in only five of the fourteen populations, and the direction of dimorphism is variable. Males had more gill rakers in three of the five significantly dimorphic populations. Dimorphism in PC3 was unrelated to L/P ratio (fig. 3B; L/P: $P = .113$; $[L/P]^2$: $P = .168$).

Table 2: Linear and quadratic selection gradients (β and γ) for size-adjusted gill raker length (PC2) and gill raker number (PC3), by lake

Lake	β	SE (β)	t	P	γ	SE (γ)	t	P	q
PC2:									
Big Mud	.058	.052	1.119	.264	.004	.037	.129	.897	.560
Blackwater	.005	.047	.091	.928	.028	.035	.787	.432	.393
Cecil	.002	.053	.024	.981	.053	.033	1.621	.106	.193
Farewell	.138	.059	2.314	.021	.079	.044	1.784	.075	.193
First	.017	.049	.370	.711	.036	.033	1.108	.268	.379
Gosling	.070	.051	1.399	.163	.060	.036	1.686	.093	.193
Gray	-.089	.053	-1.657	.098	-.037	.034	-1.056	.292	.379
Little Mud	.110	.049	2.199	.028	.097	.037	2.673	.008	.073
Little Woss	.005	.060	.072	.942	.031	.048	.629	.530	.426
McNair	-.072	.062	-1.156	.249	-.005	.047	-.095	.924	.560
Mohun	.100	.052	1.942	.053	.031	.038	.799	.425	.393
Ordug	.066	.055	1.233	.218	-.035	.040	-.921	.358	.393
Roberts 2005	.090	.050	1.825	.069	-.002	.030	-.099	.921	.560
Roberts 2006	.002	.051	.037	.971	.018	.033	.580	.562	.426
Second	-.087	.050	-1.745	.082	.054	.031	1.725	.085	.193
PC3:									
Big Mud	.006	.052	.115	.909	.073	.032	2.178	.030	.110
Blackwater	-.041	.047	-.876	.382	.023	.030	.785	.433	.486
Cecil	-.008	.051	-.145	.885	-.020	.037	-.571	.568	.486
Farewell	-.056	.059	-.948	.344	.066	.042	1.565	.119	.168
First	-.122	.049	-2.487	.013	.066	.022	2.941	.003	.028
Gosling	-.007	.051	-.164	.870	.070	.034	1.984	.048	.113
Gray	.005	.049	.119	.906	.063	.041	1.560	.120	.168
Little Mud	-.041	.049	-.817	.415	-.024	.039	-.646	.518	.486
Little Woss	-.247	.058	-4.257	.000	.031	.046	.661	.509	.486
McNair	-.006	.052	-.120	.905	.074	.035	2.120	.035	.110
Mohun	-.072	.052	-1.415	.158	.019	.041	.447	.655	.514
Ordug	-.068	.053	-1.316	.189	-.055	.035	-1.536	.125	.168
Roberts 2005	.082	.046	1.741	.082	.014	.036	.367	.714	.517
Roberts 2006	-.025	.051	-.480	.631	.002	.031	.082	.934	.586
Second	.075	.050	1.476	.141	.004	.037	.125	.901	.586

Note: For each morphological trait in each lake, we provide the least squares slope estimate, its standard error, and statistical significance. Values in bold indicate regression terms that are significantly different from 0 at $\alpha = 0.05$. As an indication of the potential false discovery rate, we present q values (Storey 2002) for the quadratic selection gradients. The q values for linear gradients are not provided because we draw no inferences from them in this article.

Consistent with a recent theoretical model (Bolnick and Doebeli 2003), we found that sexual dimorphism tends to mitigate the effects of disruptive selection. After adjusting for lake geomorphology (L/P ratio), we found a negative correlation between sexual dimorphism and disruptive selection for PC2 (fig. 4A; $r = -0.547$; $P = .043$) and a nonsignificant trend in the same direction for PC3 (fig. 4B; $r = -0.437$, $P = .118$).

Discussion

Disruptive selection seems to be fairly common in natural populations, perhaps even as common as stabilizing selection (Kingsolver et al. 2001). This observation undermines the long-held belief that fitness minima represent

unstable equilibria and should be rare (Endler 1986), a view predicated on the assumption that fitness landscapes are static. If instead we accept that fitness landscapes are frequency dependent and hence dynamic, it becomes easier to explain persistent disruptive selection. To illustrate this contrast, consider the fitness landscape in a lacustrine population of stickleback. Littoral and pelagic prey require different phenotypic adaptations, which we can envision as stabilizing selection for two different phenotypic optima. Phenotypically intermediate populations that use both resources are not optimally adapted to either habitat and so are subject to disruptive selection. If the fitness landscape is static, an intermediate population should eventually evolve away from the fitness minimum to specialize on one of the two resources. However, with a dy-

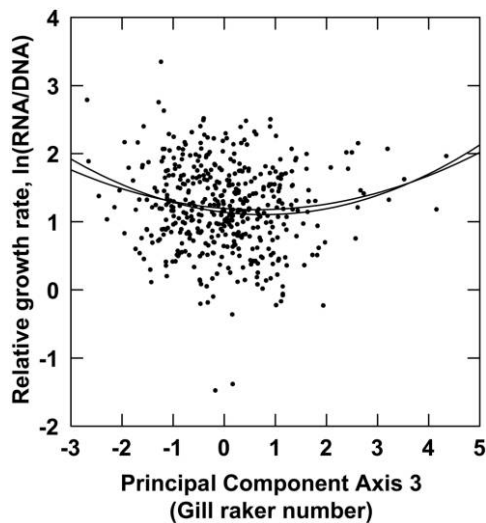


Figure 1: Quadratic regression of a fitness proxy, $\ln(\text{RNA}/\text{DNA})$, on trophic morphology (gill raker number, PC3) for one of the 14 lakes in this study (First Lake). Separate regression lines are provided for males and females to illustrate our finding that sexes could be pooled for the selection analyses. The quadratic regression coefficient ($\gamma = 0.066$) is statistically significant ($P = .003$), although morphology explains only a small fraction of the variation in growth rate ($r^2 = 0.032$).

dynamic fitness landscape, competition can depress the fitness of whichever phenotype is most abundant. Thus, if a population is adapted exclusively to the littoral resource, competition would drive directional selection (Bolnick 2001), favoring phenotypically divergent individuals that can efficiently subsist on underused pelagic prey. This directional selection drives the population toward an intermediate phenotype at which disruptive selection can occur.

A previous study confirmed that phenotypically intermediate populations of stickleback can be subject to disruptive selection on trophic morphology (gill raker length) and that this selection was driven by intraspecific competition (Bolnick 2004a). Here, we find that stickleback in north temperate glacial lakes exhibit a general trend toward disruptive selection. Although selection was weak within any given lake, there was a consistent tendency for quadratic selection coefficients to be positive, and our FDR analysis suggested that there is quadratic selection in $\sim 40\%$ of populations. This trend contrasts with a recent meta-analysis of selection gradients (Kingsolver et al. 2001) that found that quadratic selection was equally likely to be stabilizing ($\gamma < 0$) or disruptive ($\gamma > 0$). Stickleback in postglacial lakes on Vancouver Island thus appear to be unusually prone to disruptive selection.

Explaining Variation in Disruptive Selection

We posit that this disruptive selection arises from intra-specific competition for functionally disparate resources (Bolnick 2004a). This inference is supported by our finding that disruptive selection is weaker in lakes dominated by one habitat. Large lakes with a predominantly pelagic habitat (low L/P) and small lakes with a predominantly littoral habitat (high L/P) exhibited weaker disruptive selection than intermediate-sized lakes (fig. 2). Notably, disruptive selection was strongest in lakes of about 40–50-ha surface area, which is only slightly larger than Paxton lake, where benthic and limnetic species coexist (Schluter

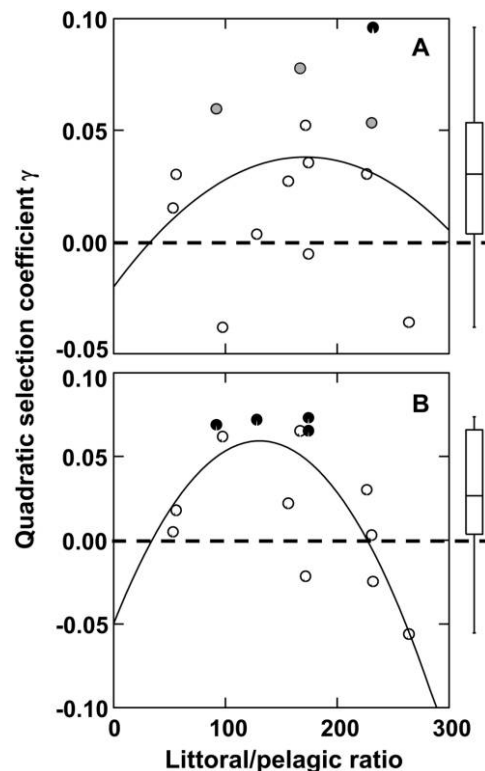


Figure 2: Estimated strength of disruptive selection on trophic morphology (γ , quadratic regression coefficient of growth rate [$\log \text{RNA}/\text{DNA}$] on morphology) as a function of the ratio of littoral to pelagic habitats (L/P, measured as meters of perimeter per hectare of surface area). Selection is estimated for two traits associated with foraging, size-adjusted gill raker length (PC2; A) and gill raker number (PC3; B). Quadratic selection gradients are shown for each lake sampled in this study. Disruptive selection on gill raker number (PC3) is significantly associated with lake area, as indicated by a best-fit regression line. Lakes with statistically significant disruptive selection ($P < .05$) are indicated by solid circles, and lakes with marginally significant selection ($P < .1$) are indicated by gray circles. The mean and distribution of these selection gradients are indicated by a box plot to the right of each panel. Across lakes, quadratic selection on both trophic traits tends to be significantly > 0 (dashed line).

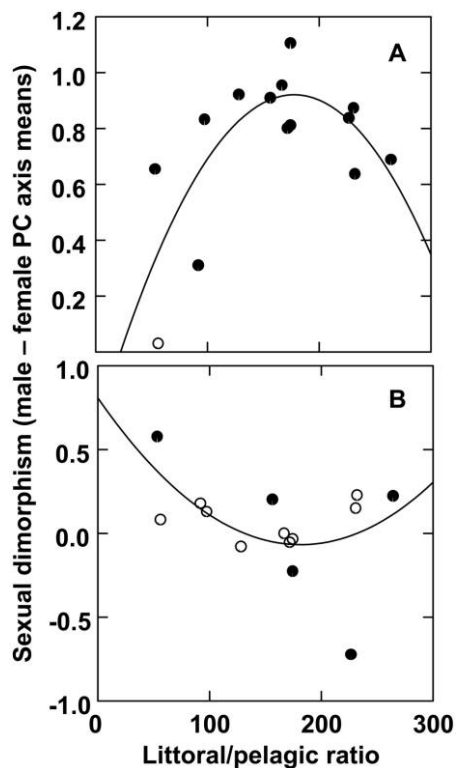


Figure 3: Sexual dimorphism in gill raker length (PC2; A) and gill raker number (PC3; B) as a function of the relative amounts of littoral and pelagic habitat (L/P ratio). Sexual dimorphism is measured as the difference in standard deviations between male and female trait means. Lakes with statistically significant sexual dimorphism are indicated by solid circles.

and McPhail 1992). It should be kept in mind that these results are correlative, and the association between selection and lake area could arise from mutual association with unmeasured factors such as predation regimes (Rundle et al. 2003) or genetic variation (Caldera and Bolnick 2008).

Curiously, the hump-shaped relationship between disruptive selection and lake size held for only one of the two trophic traits examined here (gill raker number, PC3). Why should disruptive selection on gill raker length (PC2) not show the same trend? One possibility is that past episodes of disruptive selection on raker length have already led to an evolutionary response. If past disruptive selection on gill raker length caused the evolution of greater dimorphism in intermediate-sized lakes (Bolnick and Doebeli 2003), the resulting weakening of selection may have negated the relationship between lake size and selection strength. Consistent with this hypothesis, we found that sexual dimorphism for gill raker length (PC2) is maximized for intermediate-sized lakes. The same was not ob-

served for gill raker number (PC3). Thus, for a given trait, intermediate-sized lakes have either stronger disruptive selection or greater dimorphism, but not both (figs. 2, 3). Furthermore, dimorphism is negatively correlated with the strength of disruptive selection after controlling for lake size effects (fig. 4). This provides the first empirical support for the theoretical prediction that sexual dimorphism can evolve in response to, and mitigate the effects of, disruptive selection (Bolnick and Doebeli 2003).

It is not immediately obvious why dimorphism should have arisen for gill raker length but not gill raker number. We hypothesize that stickleback gill raker length is genetically predisposed to be sexually dimorphic, since nearly all populations exhibited significant dimorphism and the direction of dimorphism is consistent across populations. In contrast, there may not have been a preexisting tendency toward dimorphism for raker number; relatively few populations exhibited dimorphism in raker number, and the direction of dimorphism was variable, with males having more rakers in two of the five dimorphic populations. Any preexisting dimorphism will accelerate ecological character displacement between the sexes. Another pos-

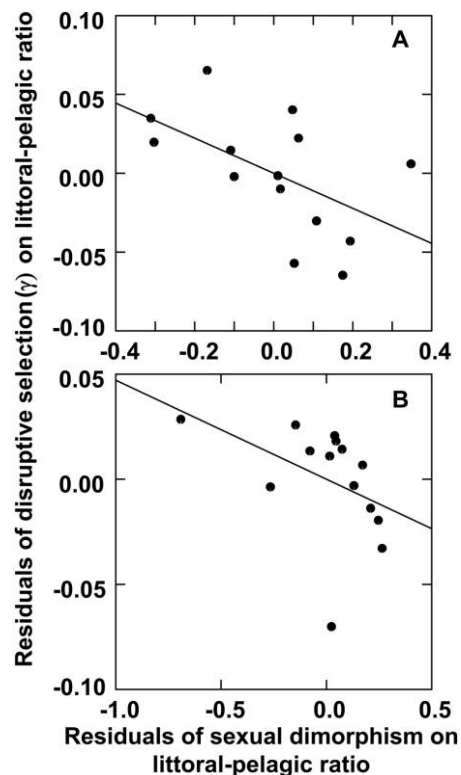


Figure 4: Correlation between disruptive selection and sexual dimorphism across the 14 lakes, adjusting for lake geomorphology by first taking the residuals of each variable on L/P before testing correlations. Results are shown for gill raker length (PC2; A) and gill raker number (PC3; B).

sibility is that historical disruptive selection was stronger on gill raker length, which often plays a greater role in determining individuals' diets (Bolnick et al. 2008). Stronger selection might cause raker length to evolve dimorphism faster than raker number.

Implications

The key findings of this study are that (1) there is a tendency toward disruptive selection in lake populations of stickleback and (2) the incidence of disruptive selection follows predictable patterns. This is noteworthy because disruptive selection can play an important role in maintaining or increasing quantitative genetic variation in natural populations. Hence, the within-population variation in trophic morphology and diet observed in stickleback may be maintained because of, not despite, natural selection. Just as importantly, not all populations are equally likely to exhibit disruptive selection: intermediate-sized lakes appear to be subject to stronger selection and so have greater opportunity for diversification.

Disruptive selection can drive a number of forms of diversification (Rueffler et al. 2006), including increased quantitative genetic variation (Bürger 2002), phenotypic plasticity (Parsons and Robinson 2006), discrete trophic polymorphisms (Levene 1953), sexual dimorphism (Bolnick and Doebeli 2003), and even speciation. Disruptive selection is invoked frequently in models of sympatric speciation, which rely on disruptive selection to drive the evolution of reproductive isolation (Udovic 1980; Dieckmann and Doebeli 1999; Bürger et al. 2006; Doebeli et al. 2007). However, despite ongoing disruptive selection, the populations studied here retain unimodal trait distributions and Hardy-Weinberg equilibrium for microsatellite loci (Caldera and Bolnick 2008). Given the long-standing controversy over sympatric speciation (Coyne and Orr 2004), it is interesting to speculate why sympatric speciation has not occurred. With the exception of a small number of species pair lakes (Schluter and McPhail 1992), diversification in lacustrine stickleback populations appears to be primarily via among-individual, or between-sex, niche partitioning.

We propose two possible explanations for the absence of widespread sympatric speciation despite widespread disruptive selection. First, disruptive selection is not a sufficient condition for sympatric speciation: populations must also exhibit strong assortative mating, preferably based on the trait under ecological selection (Bolnick 2004*b*; Gavrillets 2005; Polechova and Barton 2005; Waxman and Gavrillets 2005). Costs to mate choice, or limited genetic variation, may constrain this assortative mating and prevent speciation (Bolnick and Fitzpatrick 2007). Alternatively, the evolution of sexual dimorphism may have

reduced the strength of disruptive selection to the point where speciation is slow or impossible (Bolnick and Doebeli 2003; Bürger et al. 2006). This idea is supported by our current finding that sexual dimorphism is strongest in lakes where selection should have been strongest and that dimorphism and disruptive selection are negatively correlated (fig. 4).

Although this study only finds predictable patterns of disruptive selection in a single species, we believe that our results may apply far beyond stickleback. Many other fish species in low-diversity postglacial lakes also exhibit high levels of trophic polymorphism partitioning littoral and pelagic resources (Skulason et al. 1993; Smith and Skulason 1996; Wood and Foote 1996; Lu and Bernatchez 1999; Saint-Laurent et al. 2003; Jastrebski and Robinson 2004; Svanbäck and Persson 2004; Knudsen et al. 2006). More generally, many species exhibit among-individual niche variation necessary for frequency-dependent interactions to drive disruptive selection (Smith and Skulason 1996; Bolnick et al. 2003). If our results do extend to these other case studies, they may help to explain why disruptive selection is fairly common (Kingsolver et al. 2001). More importantly, it may be possible to predict where and when this disruptive selection will be strong, allowing us to better explain why some populations are more variable, or more prone to speciation, than others.

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