Declining interspecific competition during character displacement: Summoning the ghost of competition past

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ABSTRACT

Prevailing theories of biotic diversification incorporate resource competition as a leading cause of divergence between new species. In support of this, many cases of divergent character displacement between close relatives (congeners) are known. Yet, experimental tests of underlying mechanisms are uncommon. In a pond experiment with threespine sticklebacks (*Gasterosteus* spp.), we tested the prediction that competition between species should decline as character divergence proceeds, yielding descendants whose present-day interaction is a 'ghost' of its former strength. Competition's impact on the marine threespine stickleback (*G. aculeatus*) was contrasted between two treatments simulating early and late stages of a hypothesized character displacement series that began at the end of the last ice age when marine sticklebacks colonized lakes containing an earlier descendant. Growth rate and niche specialization of marine sticklebacks were higher in the 'post-displacement' treatment than in the 'pre-displacement' treatment, suggesting a decline in competition strength through time. The result supports the idea that interspecific competition favoured divergence between sympatric sticklebacks, with reduced competition the outcome. The influence of other interactions on divergence between sympatric species may be tested with analogous experimental designs.

Keywords: adaptive radiation, character displacement, competition, sticklebacks.

INTRODUCTION

Observational evidence for ecological character displacement is abundant. Over 70 cases have now been described, many of them increasingly solid as alternative hypotheses become tested and rejected (Schluter, 2000). Most cases (85%) are between closely related species (congeners) and many of the rest include congeners as well as more distant relatives, a pattern consistent with the classical (yet often controversial) view that interspecific competition plays an important role in the origin of ecological diversity (Huxley, 1942; Lack, 1947; Simpson, 1951; Mayr, 1963; Schluter and Grant, 1984; Grant, 1986).

Although the many examples are persuasive, the evidence is incomplete in several ways, justifying a complementary, experimental approach. First, in most cases confirmation is

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lacking that resource competition even occurs and hence is a candidate mechanism driving divergence (but see Martin and Harding, 1981; Brown and Munger, 1985; Pacala and Roughgarden, 1985; Abramsky *et al.*, 1990; Schluter, 1994; Gorbushin, 1996; Pfennig and Murphy, 2000). Second, most evidence is based on comparisons of species differences between sites of sympatry (where species occur together) and allopatry (where species occur alone). The approach assumes that consistent differences in resource distribution between sites of sympatry and allopatry are absent, an assumption that has been tested in only two cases (Schluter, 2000). Experiments allow the possibility of measuring interaction strength in a common setting (e.g. Martin and Harding, 1981). Finally, the hypothesis of character displacement makes predictions about how interaction strength and the intensity of selection should change through time (Slatkin, 1980; Abrams, 1986; Taper and Case, 1992; Doebeli, 1996) that are difficult, perhaps impossible, to test with observational methods alone.

   We used a pond experiment with threespine sticklebacks to test a simple prediction of character displacement: that competition intensity should decline with time. The stickle-backs of interest inhabit small post-Pleistocene lakes of coastal southwestern British Columbia, Canada, and exhibit a pattern of morphology and ecology consistent with character displacement. Where two species are present in a lake, one is a 'limnetic' and the other is a 'benthic'. Limnetics are small and slender, have many long gill rakers and a narrow gape, and forage mainly on zooplankton in open water (McPhail, 1984, 1992, 1994; Schluter and McPhail, 1992). Benthics are larger and more robust, have fewer, shorter gill rakers and a wider gape, and forage on invertebrates living on littoral vegetation or in the sediments. Several limnetic–benthic pairs are known, with those in different drainages having separate origins (Taylor, *et al.*, 1997; Taylor and McPhail, 1999, in press). Solitary stickleback species inhabiting lakes similar in size to those containing pairs tend to be intermediate in morphology and consume both zooplankton and benthic invertebrates (Schluter and McPhail, 1992). Morphological differences between populations and species persist in the laboratory and have a polygenic basis (McPhail, 1984, 1992; Hatfield, 1997).

   If character displacement is partly responsible for divergence between sympatric species, then reduced competition should be its legacy. We tested this expectation in an experiment whose treatments conformed as closely as possible to stages in the presumed histories of stickleback species pairs. McPhail (1994; Schluter and McPhail, 1992) proposed that each pair was formed by a process of double colonization and divergence (Fig. 1A). In his scenario, marine sticklebacks colonized newly formed lakes as sea levels dropped following retreat of the glaciers (first invasion). The colonists evolved an intermediate phenotype adapted to exploiting both zooplankton and benthic invertebrates, as is seen today in single-species lakes. Some thousands of years later, the marine species colonized several lakes a second time (second invasion). Competition for food then caused a shift of the intermediate species towards a more benthic lifestyle, whereas the second invader remained a zooplanktivore similar (but not identical) in shape to the present-day marine species (Schluter and McPhail, 1992; Pritchard, 1998). Although many details of the double invasion scenario remain to be confirmed, including the timing of invasions, its broad outlines are supported by studies of nuclear molecular markers (allozymes and microsatellites; McPhail, 1984, 1992; Taylor and McPhail, in press) and measurement of the salinity tolerance of fresh-water populations (Kassen *et al.*, 1995). In contrast, mtDNA measurements support a scenario of sympatric speciation following only a single colonization per lake, but this discrepancy appears to be an artifact of mtDNA flow across the species boundary after the
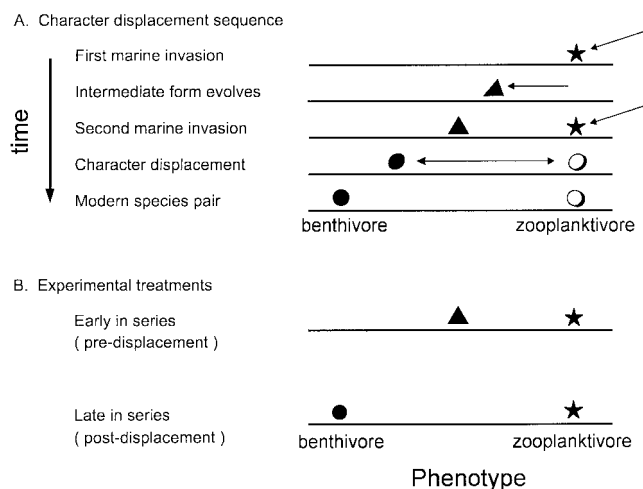
Fig. 1. (A) Hypothesized character displacement sequence assuming double invasion with allopatric speciation. Sloping arrows on the right indicate invasion events by marine sticklebacks. Symbols indicate the mean position of a population along a resource-based morphological continuum: marine (ancestral) (★), intermediate (▲), benthic (●) and limnetic (○) species. (B) Experimental treatments simulate stages in (A) before and after character displacement. Modified from Taylor *et al.* (1997).

second invasion (Taylor *et al.*, 1997; Taylor and McPhail, 1999, in press). The expectation that resource competition should be reduced after divergence is nevertheless general and would apply even had speciation occurred sympatrically.

In the present experiment, we simulated past and contemporary stages of this postulated sequence, taking advantage of the availability in the ocean of the ancestral marine phenotype. We put marine sticklebacks together with intermediate sticklebacks ('pre-character displacement') and benthic sticklebacks ('post-character displacement') in experimental ponds, and measured the intensity of competition (Fig. 1B). This design holds the phenotype of the zooplanktivore constant between treatments to ensure that treatment effects are attributable to changes in the first invader, the form that departs the most from the ancestral condition according to both standard morphological comparison (Schluter and McPhail, 1992) and landmark-based geomorphometric analysis (Pritchard, 1998). Marine sticklebacks are similar to present-day limnetic species in shape and size when both are raised in freshwater (Pritchard, 1998). As in the wild, benthic sticklebacks in the ponds consume less plankton and more benthic invertebrates than intermediate sticklebacks (Schluter and McPhail, 1992; Schluter, 1993, 1995, personal observation), whereas limnetics and marines consume mainly zooplankton (Schluter, 1994, personal observation).

In a previous experiment, we showed that, after the addition of a zooplanktivore, selection favoured the more benthic-like phenotypes within an intermediate species (Schluter, 1994). The present study targeted competition's impact on the zooplanktivore and measured overall changes in the effect of competition between populations at the extremes of the postulated character displacement sequence. The hypothesis of character displacement predicts that the marine species should experience weaker competition from the benthic species (post-displacement) than from the intermediate sticklebacks (pre-displacement). Weaker competition should be manifested as faster growth, a narrower diet

and higher survival. A narrower diet is expected in the presence of benthic sticklebacks because depletion of zooplankton should then be less, and depletion of benthic resources more, than in the presence of intermediates. Failure to verify these predictions would indicate that the character displacement hypothesis is wrong or at best incomplete. For example, in the laboratory, benthics are more aggressive than intermediates (D. Schluter, personal observation), behaviour that may result in a strong impact on fitness of marines despite greater ecological divergence. Such an outcome would point to mechanisms other than merely resource competition driving divergence. In the Discussion, we consider other possible mechanisms favouring divergence.

MATERIALS AND METHODS

Fish populations

Marine sticklebacks were collected from the Little Campbell River, White Rock, British Columbia. This population was chosen because its breeding season overlaps that of the two lake populations, but its morphology and ecology are otherwise similar to other marine populations of the eastern Pacific Ocean (Schluter and McPhail, 1992; Saimoto, 1993; Bell and Foster, 1994; D. Schluter, personal observation). (Populations of the western Pacific are larger in size than those of our coast but they are similar in body shape and plankti-vorous habit; J. McKinnon, S. Mori and D. Schluter, unpublished manuscript.) Benthic sticklebacks came from Paxton Lake, Texada Island, British Columbia. The ecology and morphology of this population is similar to that of benthic populations in other lakes, although it exhibits the greatest reduction in body armour (McPhail, 1992). Our solitary sticklebacks came from Cranby Lake, Texada Island. Solitary populations are variable, with some more limnetic-like and others more benthic-like, depending on lake size and topography (Lavin and McPhail, 1986; Walker, 1997). We used the Cranby Lake population because the lake is very similar to Paxton Lake in size, vegetation characteristics and prey types available. Both lakes are productive spring-fed lakes on limestone substrates. They lie within a few hundred metres of one another but in different drainages. The Cranby Lake population has a low salinity tolerance, like the present-day benthics, suggesting that it formed around the time of the first invasion to lakes presently containing two species (Kassen *et al.*, 1995).

Experimental fish were obtained by stripping eggs from wild-caught females, fertilizing them with the minced testes of conspecific males, and then transporting the eggs to the University of British Columbia. Forty-five batches of 500 eggs each were randomly assigned to separate 100-litre aquaria. After hatching, young fish were reared on liquid and flake food, then switched to *Artemia nauplii* after 3 days. The fish were added to experimental ponds about 1 month after hatching.

Experimental design

The experiment was carried out in the summer of 1995 in three experimental ponds on the campus of the University of British Columbia. We use ponds rather than large lake enclosures to avoid the risk of new species introductions to lakes. Each pond is 23 × 23 m and its depth slopes gradually to 3 m in the centre. The ponds were constructed in 1991 and seeded with plants and invertebrates from Paxton Lake. The ponds are sand-lined and

bordered with limestone extracted from surface mines near Paxton Lake. Although we dug the holes and initialized the ponds in 1991, they are otherwise unmanipulated environments. They differ from the native lakes mainly by their youth and smaller size. All invertebrates found in the diets of experimental fish were characteristic of the species in the wild. Insect predators are common in the ponds, but fish predators are absent (their effects will be investigated in future studies). Predation by piscivorous birds is present, albeit sporadic. The ponds have sustained thousands of sticklebacks over multiple generations in other experiments, their life-cycles being similar to those in the wild (D. Schluter, personal observation). Measured growth rates of individual fish in the ponds are no less than rates in native lakes (see below).

A paired design was used. Each pond was divided down the middle with an impermeable plastic barrier (4-mm UV-resistant polyethylene) the day before the experiment. The top edge of each barrier was kept afloat with polystyrene foam planks slipped into a sleeve. The lower edge was held on the bottom with a 30.5-m steel chain and concrete flagstones placed at 0.5-m intervals by a scuba diver. We detected no contamination of treatments by movement of fish between sides.

On 19 June, 1000 marine sticklebacks were added to each side of every pond. We also added 2000 intermediate sticklebacks to one side, chosen at random, and 2000 benthic sticklebacks to the other side. Fish were added in batches of 500 sampled from a larger pool created by combining conspecific fish from all rearing aquaria. Batches were assigned randomly to a specific pond and side. The mortality rate of very young sticklebacks was high. Observation suggests that aquatic insect predators are the main cause.

We checked whether growth of surviving fish was realistic by comparing it with an estimate of mean growth rate in the wild. We took samples of juveniles from Cranby Lake on 10 June 1997 (near the end of the breeding season) and 8 August 1997 (well into the non-breeding season). Young of the year were easily identified by their small size. Their mean standard length changed from 10.4 to 21.8 mm over this period, a growth rate of 0.19 ± 0.003 mm·day^{-1} (mean ± standard error). In contrast, the mean standard length of Cranby Lake sticklebacks in the ponds increased from 10.0 to 36.6 mm over the 51 days, a rate of 0.52 ± 0.008 mm·day^{-1}. Therefore, growth rates were not lower in the ponds than in the wild, making it unlikely that the levels of food depletion were unrealistic.

The experiment ran for 7 weeks, after which fish were harvested by adding 0.5 kg of 5% rotenone (Syndel Laboratories, Vancouver, BC) to each half pond. We used dipnets to collect fish as they swam to the surface. Captured fish were anaesthetized with tricaine methanesulphonate (MS-222, Syndel Laboratories) and then fixed in labelled jars of 10% formalin. These fish were used for morphological and diet analyses. On the day after adding rotenone, we used boats to search the bottom of each pond for dead sticklebacks overlooked the first day. These fish were also preserved but were used only to calculate the final number of fish in each experimental unit. Fish were removed from formalin after 2 weeks, sorted and counted, stained in a 2% KOH and alizarin red solution for 12 h and then preserved in 38% isopropyl alcohol.

Data acquisition and analysis

We used final size (standard length to within 0.01 mm) to measure growth of marine fish using a digital calliper connected to a computer. We measured all fish from each half-

pond when less than 100 were retrieved on the first harvest day. We measured a random sample of 100 fish if harvested numbers exceeded 100. Pond and treatment were unknown to the measurer to minimize unconscious bias. The digital display on the callipers was also covered to prevent the measurer from seeing the result. Repeatability of measurements was 0.99, determined by measuring 10 marine fish 10 times in random order (Krebs, 1992).

The survival of marine sticklebacks was measured in each half-pond in two ways. Absolute survival was measured as the number of marine sticklebacks retrieved at the end of the experiment divided by 1000, the number stocked. This measure was underestimated because an unknown number of fish killed on harvesting day were not recovered. Relative survival was measured as the number of marines retrieved divided by the total number of fish retrieved. This measure compensates for differences between pond sides in recovery rates of fish. Standard errors of relative survival were calculated using a bootstrap procedure (Sokal and Rohlf, 1995).

Stomach contents were measured in 10 randomly sampled marine fish from each pond side (sample sizes may be less if any stomachs were empty). To avoid unconscious bias, species, pond and treatment were unknown to the measurer. Whole prey items were identified and grouped into two broad categories: zooplankton (calanoid copepods and cladocerans: *Bosmina*, *Diaphanosoma*, *Ceriodaphnia* and *Simocephalus*) and benthic prey (amphipods, snails, cyclopoid and harpactacoid copepods, and insect larvae) (Pennak, 1978). Ostracods and chydorids were excluded because they move between the water column and the substrate (Pennak, 1978; W.E. Neill, personal communication). The results did not change when ostracods and chydorids were included and classified as either plankton or benthic prey items. Diet was estimated for each fish as the plankton proportion of total dry mass of prey in the stomach. Mean dry mass of each prey type was estimated from mean length measurements (Hopcroft, 1991).

Treatment effects were tested using one-tailed paired *t*-tests with 2 degrees of freedom (based on $n = 3$ ponds). Survival and diet proportions were first transformed using arcsine square root. Additional tests were carried out to compare ponds in the magnitude of differences seen between treatment sides in growth and diet (analysis of variance) and survival (generalized linear models). These secondary tests treat 'pond' as a fixed effect and base significance levels on the number of fish sampled rather than the number of ponds. For this reason, they do not test treatment effects *per se*.

RESULTS

Growth

Marine sticklebacks grew significantly larger in the presence of benthic sticklebacks (post-displacement treatment) than in the presence of intermediate sticklebacks (Fig. 2; $t_2 = 3.297$, $P = 0.04$). Within ponds, the difference in growth between treatments was highly significant ($F_{1,411} = 45.7$, $P < 0.0001$); little heterogeneity was detected among ponds in the magnitude of this difference (treatment-side × pond interaction, $F_{2,411} = 2.63$, $P = 0.073$). Observed differences in growth were not accounted for by differences in total fish density because final densities were highest in the benthic (post-displacement) treatment in two of the three ponds (Table 1).
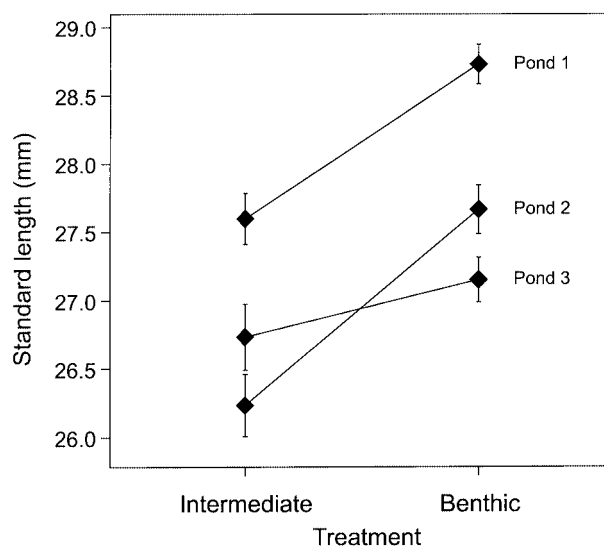
Fig. 2. Growth of marine sticklebacks (mean ± standard error). Sample sizes: $n_1 = 101$, $n_2 = 44$, $n_3 = 31$ (intermediate treatments), and $n_1 = 100$, $n_2 = 72$, $n_3 = 69$ (benthic treatments).

Survival

We detected no difference between treatments in either absolute survival of marine stickle-backs ($t_2 = -0.29$, $P = 0.60$) or relative survival ($t_2 = -0.31$, $P = 0.61$). Differences between pond sides were in the predicted direction in two of the three ponds but not in the third (Table 1). Overall, marine survival did not differ between the treatment and control sides of ponds ($\chi^2_1 = 0.49$, $P = 0.48$). There was significant heterogeneity among ponds in mean survival ($\chi^2_2 = 64.4$, $P < 0.001$) and in the magnitude of the difference between treatments ($\chi^2_2 = 43.9$, $P < 0.001$). Similar patterns were observed in relative survival.

Diet shifts

Marine sticklebacks consumed mainly zooplankton in both treatments (Table 2), especially the cladocerans *Diaphanosoma* and *Bosmina*. The proportion of zooplankton in their diet was higher in the benthic treatment than in the intermediate treatment ($t_2 = -3.26$, $P = 0.041$).

DISCUSSION

We simulated historical and contemporary stages of a postulated invasion sequence in sticklebacks to test the prediction from character displacement that intensity of com-petition between species should decline as they diverge. The target of our experiment was the marine threespine stickleback, the ancestor of all the freshwater populations. It is similar in phenotype and diet to the present-day limnetic species when both are raised in freshwater. Our results show that its mean growth rate was higher in the treatment mimicking the late stage of the proposed character displacement series (benthic treatment)

Table 1. Numbers of fish at the end of the experiment and survival of marine sticklebacks (mean ± standard error) in each pond-side

Pond	Treatment	Marine sticklebacks retrieved	Total sticklebacks retrieved	Marine absolute survival	Marine relative survival
1	Intermediate	253	868	0.25 ± 0.014	0.29 ± 0.013
1	Benthic	169	639	0.17 ± 0.012	0.26 ± 0.016
2	Intermediate	94	564	0.09 ± 0.009	0.17 ± 0.015
2	Benthic	142	756	0.14 ± 0.011	0.19 ± 0.013
3	Intermediate	128	752	0.13 ± 0.011	0.17 ± 0.013
2	Benthic	184	950	0.18 ± 0.012	0.19 ± 0.011

Note: Initial number of marines in each pond-side was 1000.

Table 2. Proportion zooplankton consumed by marine sticklebacks in each pond-side (mean ± standard error)

Pond	Treatment	
	Intermediate	Benthic
1	0.818 ± 0.027 ($n = 8$)	0.855 ± 0.022 ($n = 8$)
2	0.810 ± 0.032 ($n = 9$)	0.915 ± 0.024 ($n = 9$)
3	0.654 ± 0.055 ($n = 7$)	0.809 ± 0.032 ($n = 9$)

than that at an early stage, prior to sympatric divergence in morphology and resource use (intermediate treatment). The diet of the marine species was also more specialized post-displacement than pre-displacement. These results suggest that strength of competition between sympatric species declined through time, and that present-day differences between them are a 'ghost' of competition past (Rosenzweig, 1976, cited in Grossman *et al.*, 1982; see Connell, 1980). Survival differences were in the predicted direction in two of the three ponds but not overall. Although this was unexpected, consistent survival effects of competition are not typically detected in pond experiments of this duration (e.g. Schluter, 1994).

The predicted decline in strength of competition with increasing divergence has rarely been tested. Pacala and Roughgarden (1985) showed that competition was stronger between the two sympatric species of *Anolis* on the Caribbean island of St. Maarten, where differences between the species in body size and perch use are small, than between the two species on the island of St. Eustatius, which exhibit greater differences in body size and perch use. Their comparison was meant to test whether competition and niche overlap are correlated, not whether competition declined between early and late stages of a character displacement sequence, but the two treatments might indeed represent such stages. Experiments were also used to show that competition between the two salamander species, *Plethodon jordani* and *P. glutinosus*, was greater in the Great Smoky mountains where their altitudinal ranges abut without overlapping, than in the Balsam mountains

where their altitudinal ranges overlap extensively (Hairston, 1980). Whether high and low altitudinal range overlap represent stages of a character displacement sequence is not known. In these two experiments, different treatments were carried out in enclosures on different islands or mountain ranges; therefore, neither experiment controls for effects of local environment on competition intensity. Nevertheless, the results were in the predicted direction.

The present study differs from a previous experimental test of character displacement in threespine sticklebacks, and we regard it as independent evidence in support of the hypothesis. That experiment tested whether adding a zooplanktivore (limnetic species) altered natural selection pressures on an intermediate species with experimentally inflated phenotypic variance, favouring divergence (Schluter, 1994). The impact of adding the zooplanktivore, measured as change in growth rates of individuals, was indeed greatest on those phenotypes within the intermediate species that were most similar to the added competitor in morphology and resource use. In the present experiment, the target was instead a zooplanktivore. Competitive impacts were measured using the extremes of the proposed character displacement sequence representing thousands of generations of evolution. Also unlike the previous experiment, which controlled only the density of the target species, in the present study total density of fish was controlled at the outset. Our findings, therefore, suggest that competition between stickleback phenotypes is not just density-dependent but is also frequency-dependent (Schluter, 1994).

Our findings shed light on the evolution of the zooplanktivore after the second invasion (Fig. 1). In particular, competition from the intermediate form helps to explain why the descendant of the second marine colonization remained specialized on zooplankton and failed to evolve a more generalist intermediate phenotype as apparently happened after the first invasion of sticklebacks into a lake.

Marine sticklebacks grew to a relatively small size in the freshwater ponds. For example, Cranby Lake fish (intermediates) from our first pond reached a size of 36.6 ± 0.40 mm by the end of the experiment, whereas marines from the same side of that pond reached only 27.6 ± 0.19 mm. The results were similar in the other two ponds. In contrast, wild marine sticklebacks are larger in mean size than most freshwater populations (Schluter and McPhail, 1992). This finding hints that the ancestral mean body size after invasion of freshwater may be small, not large. Although this is difficult to confirm without additional studies of more populations, it suggests that the present-day limnetic species, which is also small in size (Schluter and McPhail, 1992), has retained the ancestral condition, whereas large body size in the benthic species, which approaches that in the marine species, is secondarily derived. The proximate mechanism underlying size reduction of marines in freshwater is unknown.

Our results support the hypothesis of character displacement because they confirm one of its clearest predictions. This does not mean that all other hypotheses are thereby excluded, and continued testing of new predictions is warranted. Below we raise the possibility of three other antagonistic interactions. Each of these alternatives makes an analogous prediction to that tested here: that the strength of the interaction should lessen between the pre-divergent and post-divergent stages (otherwise no selection for divergence is expected). A fourth possibility not considered is that benthics are mutualists of zooplanktivores rather than just weaker competitors. However, other experiments have shown that adding benthics always reduces (never enhances) growth rates of other stickleback populations present (D. Schluter, personal observation).

- *Aggressive interference*. The marine species (like the present-day limnetic) is social in the non-breeding season and forages in open water in large schools. Benthics are more aggressive than intermediates (D. Schluter, personal observation); if this was the dominant interaction, we would have expected marine growth in the benthic treatment to have been lower than in the intermediate treatment. However, the opposite was observed.
- *Intra-guild predation*. Adult benthics are known to prey on juvenile sticklebacks, but only infrequently (Schluter and McPhail, 1992, personal observation). In any case, this interaction was prevented in our experiment, since our fish were the same age and relatively similar in size.
- *Apparent competition*. This is an antagonistic interaction that may arise between species that share predators (Holt, 1977) and under certain conditions it may favour trophic divergence between prey species (Brown and Vincent, 1987; Abrams, 2000). Perhaps in sticklebacks the second invasion to lakes by marines increased total predation on the prior inhabitant, an intermediate, and favoured its shift towards the littoral zone and away from open water. This hypothesis predicts that apparent competition should decline as divergence proceeds, an hypothesis that has never been tested. In our ponds, insects are the dominant predators in ponds and they probably caused most of the mortality of all three species. No consistent trend in marine survival was observed between treatments. Marine survival was worse in the post-displacement (benthic) treatment in two of the three ponds, against the expectation from apparent competition, whereas the opposite was true in the third pond (Table 1). This is not a strong test, however, as the short duration of the experiment would not allow the numerical changes in shared predators that are crucial to apparent competition. Also, one of the key predators, cutthroat trout, was not present. The possibility that apparent competition has contributed to divergence therefore requires further study.

Observational studies of character displacement suggest that the process is common in the early stages of diversification in many taxa (Schluter, 2000). However, tests of underlying mechanisms will require development of experimental approaches that go beyond simply testing whether species compete. In particular, experiments can address how the strength of interactions changes per increment of divergence. Such an approach will prove useful in testing the role of interactions in diversification, including those such as intra-guild predation and apparent competition, for which observational evidence is currently lacking.

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