

# Impacts of trout predation on fitness of sympatric sticklebacks and their hybrids

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Predation may be a significant factor in the divergence of sympatric species although its role has been largely overlooked. This study examines the consequences of predation on the fitness of a pair of lacustrine stickleback species (*Gasterosteus aculeatus* complex) and their F<sub>1</sub> hybrids. Benthic sticklebacks are found in the littoral zone of lakes associated with vegetation and bare sediments, whereas limnetic sticklebacks spend most of their lives in the pelagic zone. The cutthroat trout (*Oncorhynchus clarki*) is a major predator of sticklebacks and the only other fish species native to lakes containing both benthic and limnetic species. In pond experiments we found that the addition of these predators primarily impacted the survival of limnetics. By contrast, benthic survival was unaffected by trout addition. The result was that relative survival of benthics and limnetics was reversed in the presence of trout. The presence of trout had no effect on the rank order of parent species growth rates, with benthics always growing faster than limnetics. F<sub>1</sub> hybrids survived poorly relative to benthics and limnetics and their growth rates were intermediate regardless of treatment. The results implicate predation by trout in the divergence of the species but not through increased vulnerability of F<sub>1</sub> hybrids.

**Keywords:** adaptive radiation; field experiment; *Gasterosteus*; hybrid fitness; predation; reproductive isolation

## 1. INTRODUCTION

Adaptive radiations are characterized by the 'more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different... adaptive zones' (Simpson 1953, p. 223). Adaptive zones can be thought of as divergent ways of obtaining food, avoiding encounters with predators or reducing the virulence of parasites. The idea that interspecific competition between consumer species can promote morphological divergence, potentially favouring subsequent speciation, in adaptive radiation has been addressed by numerous theories (Slatkin 1980; Milligan 1985; Taper & Case 1985; Abrams 1987*a,b*) and empirical studies (Brown & Wilson 1956; Grant 1975; Schluter *et al.* 1985; Schluter & McPhail 1992).

Predation may also be critical to the origin and maintenance of divergence in sympatry, yet it has received less attention than competition (Schluter 2000). When considered, it has primarily been viewed as an interaction that may alleviate the effects of competition (e.g. Paine 1966; Werner 1991). However, predation may influence divergence via a number of other mechanisms. First, if two or more consumer species share a predator, they may diverge as a result of 'competition for enemy-free space' (Ricklefs & O'Rourke 1975; Jeffries & Lawton 1984; Holt & Lawton 1994; Abrams 2000). Second, predation may favour further divergence after character displacement stemming from competition for food, if they encounter different suites of predators in the new habitats (Abrams 2000). Predation may even facilitate character

displacement by creating steeper fitness trade-offs between habitats. Finally, hybrids between two consumer species may suffer higher levels of predation if their intermediate defences are maladaptive in the habitats of their parents (Fryer 1959; Whitham 1989). The morphology and behaviour of the parent species may represent adaptive peaks between which hybrids may be more susceptible to predators. The empirical evidence, however, has been mixed on this issue. The view that hybrids are more susceptible to attack than their parent species has received support from a number of studies (Whitham 1989; Floate *et al.* 1993; Hjalten 1998; Cummings *et al.* 1999). However, other studies have found that hybrid fitness was not different from the mean fitness of the parent species (Aguilar & Boecklen 1992) or was similar to the fitness of the more susceptible parent species (Gange 1995; Hjalten 1998).

In this paper we study some of the effects of a major predator, the cutthroat trout (*Oncorhynchus clarki*), on the survival and growth of two sympatric stickleback species (*Gasterosteus aculeatus* complex) and their first generation (F<sub>1</sub>) hybrids. This study was prompted by two considerations. First, cutthroat trout are the only other fish species native to all lakes containing pairs of benthic and limnetic sticklebacks (Schluter & McPhail 1992). Interactions between cutthroat trout and sympatric sticklebacks, however, have not, to our knowledge, been addressed to date. This predator occurs in both littoral and pelagic habitats (Nilsson & Northcote 1981; Reimchen 1994) and potentially preys on both species. The well-developed defensive armour of limnetics (McPhail 1992; Vamosi 2002) and their exclusion from the littoral zone, a habitat that provides protection against predators for small fishes (Werner *et al.* 1983; Mittelbach 1984), suggest they have higher encounter rates with cutthroat trout. For this reason, we

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Table 1. Design of the pond experiments, showing the treatments and the number of sticklebacks retrieved from the pond replicates.

(The total number of sticklebacks introduced was 900 in low replicates and 2100 for high and trout replicates. The ratio of benthic, to F<sub>1</sub> hybrid, to limnetic sticklebacks at introduction was 1 : 1 : 1 in all replicates.)

pond	treatment		
	low density	trout	high density
1	228	395	—
2	291	385	—
3 <sup>a</sup>	—	440	471
4	576	—	534
5	—	738	808

<sup>a</sup> A trout was retrieved from the high-density treatment in pond 3 at the end of the experiment, thus this replicate is not included in the analyses.

predict similar survival of both species in the absence of predators and a reduction in limnetic survival in the presence of cutthroat trout. The alternative hypothesis is that the strategies adopted by limnetics and benthics (defensive armour and habitat refuge, respectively) are equally effective and the presence of trout will not affect the relative survival of the species. Growth rate of benthics is predicted to be higher than that of limnetics, as in previous experiments (Hatfield & Schluter 1999; Vamosi *et al.* 2000), and this difference is expected to either remain the same or increase in the presence of cutthroat trout.

Second, F<sub>1</sub> hybrids are found in low frequencies in lakes with benthic and limnetic sticklebacks (McPhail 1992). Experiments conducted in the laboratory reveal no intrinsic inviability of F<sub>1</sub> hybrids (Hatfield & Schluter 1999). A component of reproductive isolation between the sympatric species, thus, may involve ecological selection pressures against hybrids (McMillan *et al.* 1997; Hatfield & Schluter 1999; Vamosi & Schluter 1999; Vamosi *et al.* 2000) and predation may play a part. Hybrid survival is predicted to be lower than the parental species in the absence of cutthroat trout and further reduced in their presence. In the absence of ecological selection, growth rate of hybrids is expected to be the same as that of benthics in the absence of trout, as in the laboratory environment (Hatfield & Schluter 1999), and reduced in their presence. If ecological selection is acting, hybrid growth rate is predicted to be intermediate in the absence of cutthroat trout, as in previous field experiments (Vamosi *et al.* 2000), and further reduced in their presence.

## 2. MATERIAL AND METHODS

### (a) *Sympatric sticklebacks*

Benthic and limnetic sticklebacks are found in Paxton Lake (49°42' N, 124°31' W) in the Strait of Georgia region of British Columbia, Canada. Paxton Lake is a small lake, with a surface area of 17 ha and a mean depth of 6 m. The populations are named for their morphological and habitat use differences: benthics are larger, deeper bodied fishes that forage on invertebrates associated with the vegetation and substrate, whereas limnetics are smaller, streamlined fishes that forage on zooplankton in the open-water zone (Larson 1976; McPhail 1992). F<sub>1</sub> hybrids tend to have trophic morphologies intermediate to those of benthics and limnetics, resulting in intermediate growth rates and the

consumption of both benthos and zooplankton in experimental ponds (Vamosi *et al.* 2000). A number of studies have provided evidence for pre-mating (Hatfield & Schluter 1996; Nagel & Schluter 1998; Vamosi & Schluter 1999; Rundle *et al.* 2000) and post-mating (Hatfield & Schluter 1999; Vamosi & Schluter 1999; Vamosi *et al.* 2000) isolation between benthics and limnetics in Paxton Lake. These populations meet the criteria of the biological species concept (McPhail 1992; Rundle *et al.* 2000), thus we follow previous studies in referring to them as species.

Wild benthic and limnetic individuals in reproductive condition were used as parents to make crosses. We made approximately 50 benthic, 35 limnetic and 80 reciprocal F<sub>1</sub> hybrid crosses for the experimental ponds. To supplement numbers of limnetics, owing to low trapping success and clutch sizes of limnetic females, we collected eggs from nests guarded by wild limnetic males. Because of the low number of limnetic eggs available for crosses, F<sub>1</sub> juveniles were *ca.* 90% (benthic female × limnetic male) and only *ca.* 10% (limnetic female × benthic male). The morphology, hatching success and growth rates of the reciprocal hybrid crosses do not differ in the laboratory (McPhail 1992; Hatfield & Schluter 1999). The procedure for making crosses followed Vamosi *et al.* (2000), with the exception that fishes were fed with infusoria cultures for the first 2, rather than 7 days before switching to a diet of brine shrimp (*Artemia*) nauplii.

### (b) *Cutthroat trout*

Cutthroat trout, and no other predatory fish species, are native to all lakes with both benthic and limnetic sticklebacks (Schluter & McPhail 1992). Cutthroat trout larger than 100 mm standard length (SL) are known to forage on sticklebacks in both littoral and pelagic zones (Nilsson & Northcote 1981; Reimchen 1990) and piscivory can reach high levels in trout larger than 180 mm (Moodie 1972). Sticklebacks of most size classes (10–80 mm) have been found in the diets of cutthroat trout (Moodie 1972; Reimchen 1990).

We obtained cutthroat trout (range in SL: 170–250 mm) by angling in Placid Lake (49°19' N, 122°34' W), a small (1.6 ha) lake in the University of British Columbia (UBC) Malcolm Knapp Research Forest in June and August 1997. Trout were transported to the UBC and held in flow-through holding tanks for 2 to 5 days prior to their introduction to the experimental ponds. Logistic considerations, especially the mortality associated with transport of live fishes from more distant lakes, dictated

Table 2. Meristic comparison of benthic, limnetic and F<sub>1</sub> hybrid sticklebacks recovered from the pond experiment. (Data for dorsal spines and pelvic girdle are given as proportions of individuals. Number of lateral plates (mean  $\pm$  s.e.) refers to counts on left side of the body.)

phenotype	<i>n</i>	number of dorsal spines		number of lateral plates	pelvic girdle	
		2	3		present	absent
benthic	382	0.678	0.322	0.64 $\pm$ 0.05	0.016	0.984
hybrid	239	0.113	0.887	3.85 $\pm$ 0.06	0.921	0.079
limnetic	382	0.005	0.995	5.22 $\pm$ 0.05	1.000	0.000

Table 3. Effects of treatment (low-density, trout, high-density) and pond (block) on survival and growth of benthics, survival and growth of limnetics, and the difference between benthic and limnetic survival and growth. (Abbreviation: MS, mean square.)

source	d.f.	benthic			limnetic			benthic–limnetic		
		MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
survival										
treatment	2	129.84	6.40	0.14	180.14	3.52	0.22	1015.69	40.17	0.02
pond	3	208.11	10.26	0.09	102.38	2.00	0.35	106.94	4.23	0.20
error	2	20.29	—	—	51.13	—	—	25.29	—	—
growth										
treatment	2	1.32 $\times 10^{-3}$	38.51	0.03	1.07 $\times 10^{-3}$	54.95	0.02	6.05 $\times 10^{-5}$	0.40	0.70
pond	3	1.27 $\times 10^{-4}$	3.70	0.22	1.59 $\times 10^{-4}$	8.14	0.11	4.37 $\times 10^{-5}$	0.30	0.80
error	2	3.40 $\times 10^{-5}$	—	—	2.00 $\times 10^{-5}$	—	—	1.56 $\times 10^{-4}$	—	—

our choice of Placid Lake as the source for cutthroat trout. Sticklebacks do not occur in Placid Lake, and the diet of resident cutthroat trout consists of insects gleaned from the surface, large zooplankton from deeper offshore areas and benthic invertebrates from the littoral zone (Nilsson & Northcote 1981). Nevertheless, cutthroat trout readily consumed sticklebacks in holding tanks and sticklebacks were recorded in the stomach contents of 25% of trout retrieved at the end of the experiment. We feel that the absence of sticklebacks from the source lake, while preventing the coevolution of cutthroat trout with sticklebacks, ensures that the results of our study would not be solely the result of prior experience with a specific phenotype.

### (c) Experimental design

The experiment was conducted in 1997 at the UBC experimental pond facility. We used an incomplete block design having three treatments, with two treatments per divided pond. The design was unbalanced because only five ponds, rather than six, were available for the experiment (table 1). In the trout treatment, we introduced high densities of sticklebacks and added cutthroat trout. The high-density treatment, paired with the trout treatment in two ponds, was included as a control for the presence of trout. The low-density treatment, paired with the trout treatment in two ponds, was a control for the effects of lower density, proposed to occur as a consequence of predation by trout, on the growth of sticklebacks. We paired the low- and high-density treatments in a fifth pond.

### (d) Pond experiment

Five ponds (23 m  $\times$  23 m, 3 m maximum depth) were each divided into two with UV-resistant polyethylene plastic barriers to prevent the movement of fishes. From 20–22 June 1997, juvenile sticklebacks were introduced to each side of every pond.

Fishes from each cross type were added in batches of 100 sampled haphazardly from a larger pool, which was created by combining fishes from all aquaria. Batches were assigned randomly to a specific pond and side. We added 700 individuals of each cross type to randomly assigned trout and high-density pond-sides, and 300 were added to low-density pond-sides (table 1).

At the time of counting fishes for introduction, 100 randomly selected individuals of each cross type were preserved to provide an estimate of the starting size of individuals of each cross type. These fishes were narcotized with tricaine methanesulfonate (MS-222; Syndel Laboratories), fixed in 10% formalin for one week, stained in Alizarin red S and then preserved in 37% isopropyl alcohol. Additionally, at least 400 fishes of each cross type were raised in the laboratory for the duration of the experiment. A random sample of these fishes was later used to discriminate between benthics, limnetics and F<sub>1</sub> hybrids retrieved from the ponds using the methods detailed in Vamosi *et al.* (2000).

Trout were stocked as they became available: two individuals were added to each trout pond side one week after the introduction of sticklebacks and an additional individual was introduced three weeks after the introduction of sticklebacks. Because the viability of cutthroat trout in the experimental ponds had not previously been assessed, we placed gill nets into the ponds at eight weeks to confirm that trout were still present in trout pond-sides and absent from other pond-sides. Gill nets were removed after we had retrieved two trout from each trout pond-side, after which we introduced two new trout from the holding tanks. Cutthroat trout were retrieved from only trout-pond sides at this time; however, at the end of the experiment, we retrieved a single trout from the high-density pond-side of pond 3 (table 1). We assume it leapt the barrier between pond-sides, since the

barrier itself was still intact and without holes. This pond was excluded from statistical analyses, although we include the trout pond-side in the figures for comparison.

The experiment was terminated after three months following the methods of previous experiments conducted at the pond facility (Schluter 1994; Vamosi *et al.* 2000; Pritchard & Schluter 2001). We added 0.5 kg of 5% rotenone ( $C_{23}H_{22}O_6$ ; Syndel Laboratories) to each pond-side and retrieved fishes with large dip nets as they swam to the surface. Sticklebacks were narcotized with MS-222 and fixed with 10% formalin. Trout were narcotized with MS-222 before their stomachs were dissected, fixed with 10% formalin for at least a week and transferred to 37% isopropyl alcohol. The following day, we searched the bottom of each pond-side for dead sticklebacks overlooked on the first day. These fishes were also fixed with formalin but were used only to calculate the total number of fishes retrieved from each pond-side. Fishes were removed from formalin after one week, stained with Alizarin red S and preserved in 37% isopropyl alcohol. All fishes recovered from ponds were counted and survival and growth rates of the cross types were determined in a random sample of 100 fishes from each pond-side. A total of 1000 fishes were measured (table 2).

### (e) *Statistical analyses*

We analysed results from the incomplete block design (blocks = ponds) using multiple regression. This is the recommended approach when designs are unbalanced (Hicks 1964; Lindman 1992) as in the present experiment. With this analysis, the effect of treatment is calculated simultaneously with block effects. The significance of treatment effects is tested after block effects are accounted for. The whole pond-side, rather than the individual fish, was the unit of replication. For this reason the interaction between block and treatment was not included in the regression model.

Because all three cross types were stocked together, their separate survival and growth rates are not independent (Werner & McPeck 1994). Thus, we analysed the mean response of each cross type separately or we analysed differences between the mean of types in their responses. We were interested in two differences: that between mean benthic and limnetic responses; and that between mean hybrid and the mean of the two parent species' responses. Survival is the number of individuals retrieved from a pond-side divided by the number introduced at the start of the experiment. Survival proportions were arcsine transformed prior to analysis. Growth rates ( $\text{mm day}^{-1}$ ) were calculated as  $(L_e - L_s)D^{-1}$ , where  $L_e$  is the standard length of an individual at the end of the experiment,  $L_s$  is the mean standard length of its cross type at the start of the experiment, and  $D$  is the duration of the experiment in days ( $D = 45$  days). We applied a logarithmic transformation (base  $e$ ) to growth rates prior to analysis.

## 3. RESULTS

### (a) *Limnetics and benthics*

Survival of benthics and limnetics was highly variable among replicates and did not vary significantly with treatment (table 3). There was, however, a significant treatment effect on the difference between benthic and limnetic survival (table 3). Tukey's HSD-test revealed significant differences between trout and low-density treatments and between trout and high-density treatments. The relative survival of limnetics was higher than that of benthics in

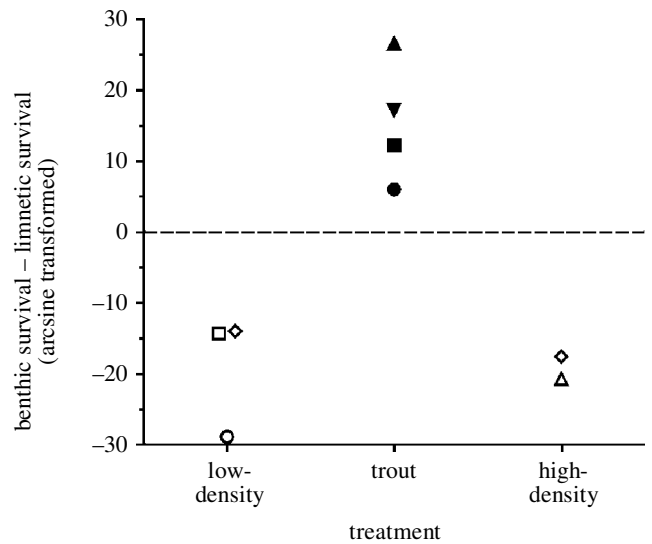


Figure 1. Differences in the absolute survival of benthic and limnetic sticklebacks in ponds. Relative survival of benthics was higher in trout pond-sides (black symbols) whereas relative survival of limnetics was higher in low- and high-density pond-sides (white symbols). Symbols indicate individual ponds: 1, square; 2, circle; 3, inverted triangle; 4, diamond; 5, triangle.

low-density and high-density treatments and lower in trout treatments (figure 1). Pond effects were absent in all three cases (table 3). We wished to determine which of the two species was most affected by the addition of trout, thus contributing to the observed pattern in relative survival. To do this, we analysed benthic and limnetic survival using a one-way ANOVA, ignoring block effects (which were not significant; table 3). The results of this *post hoc* analysis suggest that limnetics ( $F_{1,7} = 5.85$ ,  $p = 0.05$ ) contributed more strongly to the observed pattern in relative survival than did benthics ( $F_{1,7} = 0.13$ ,  $p = 0.73$ ).

We detected a significant treatment effect on growth of both benthics and limnetics and no effect on the difference in mean growth between benthics and limnetics (table 3). Tukey's HSD-tests revealed that growth rates of both species were higher in the low-density treatment than in trout and high-density treatments (figure 2). Significant pond effects were absent in all cases (table 3).

### (b) *F<sub>1</sub> hybrids*

$F_1$  hybrids survived poorly overall (figure 3). Their survival was significantly below the average survival of limnetics and benthics (paired-sample  $t$ -test;  $t_7 = 5.56$ ,  $p < 0.001$ ).  $F_1$  hybrids constituted  $23.7\% \pm 1.5$  of the fishes retrieved at the end of the experiment, which is 9.6% lower than their frequency at introduction. However, there was no treatment effect on the survival of  $F_1$  hybrids (table 4). Neither was there a treatment effect on the difference between the survival of  $F_1$  hybrids and the mean of benthic and limnetic survival (table 4). Adding trout did not reduce relative  $F_1$  hybrid survival below the low value observed in their absence. No significant pond effects were detected on hybrid survival (table 4).

We detected a highly significant effect of treatment and pond on the growth of  $F_1$  hybrids (table 4). Tukey's HSD-

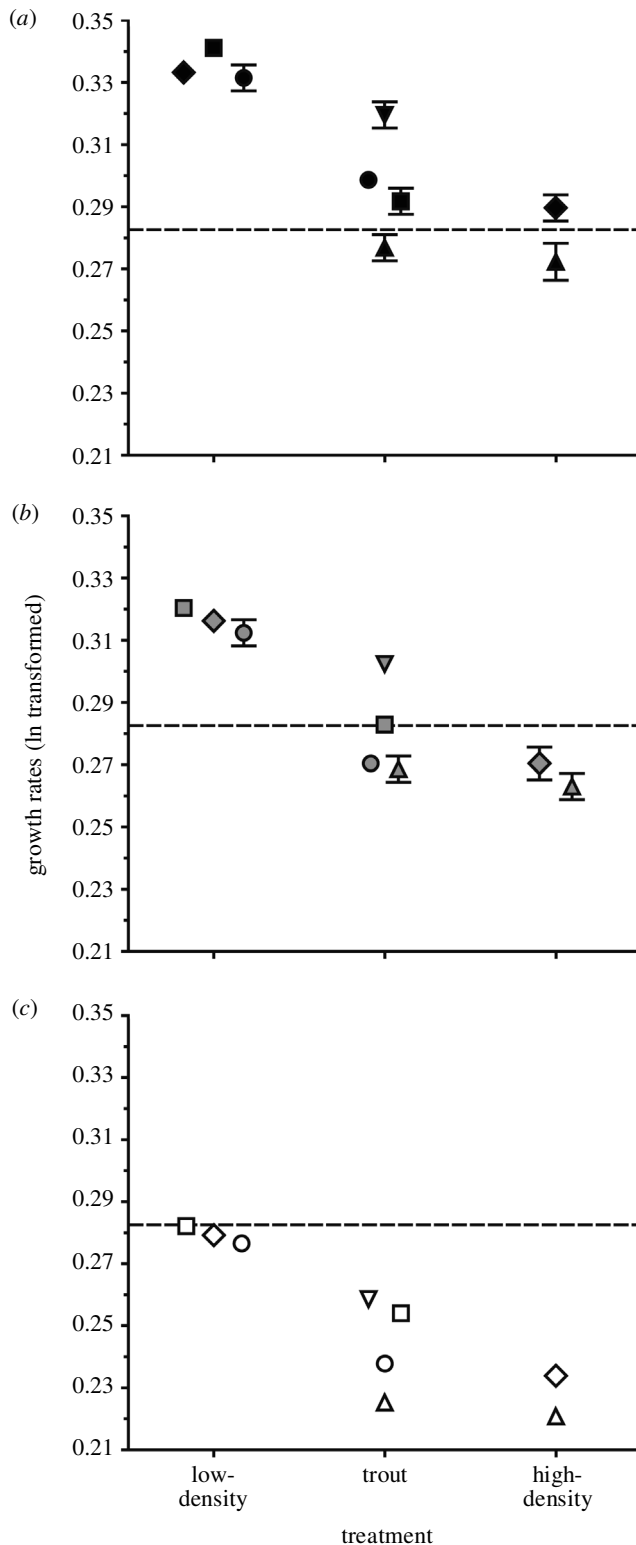


Figure 2. Mean ( $\pm$  s.e.) growth rates of (a) benthic, (b)  $F_1$  hybrid and (c) limnetic sticklebacks in ponds. Dashed lines indicate overall mean growth rate (all cross types combined). Relative growth of hybrids was not different from the mean of the parent species, regardless of treatment. Symbols indicate individual ponds, as in figure 1.

test revealed that their growth rates were higher in the low-density treatment than in the trout and high-density treatments (figure 2). There was, however, no treatment effect on the difference between hybrid growth rates and the

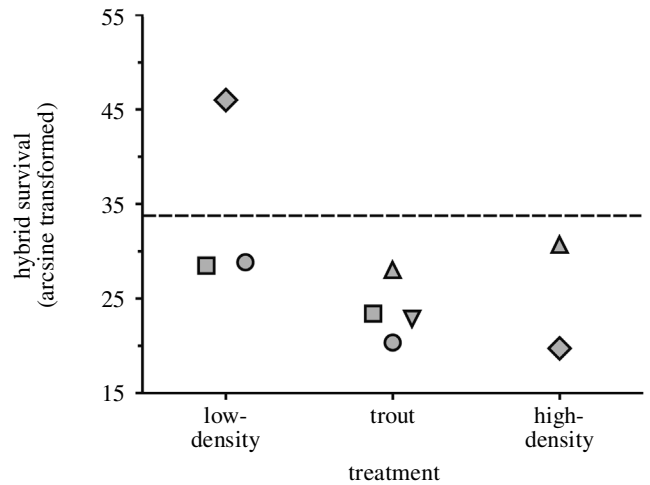


Figure 3. Survival of  $F_1$  hybrid sticklebacks in ponds. Dashed lines indicate overall mean survival (all cross types combined). Hybrid survival tended to be lower than the mean survival for all cross types. Symbols indicate individual ponds, as in figure 1.

mean of benthic and limnetic growth rates (table 4). Furthermore, a weak pond effect on this difference was detected (table 4).

#### 4. DISCUSSION

Limnetics and benthics were differentially affected by the presence of trout. Limnetics survived better than benthics in the absence of trout, whereas benthics survived better than limnetics in the presence of trout. This pattern in relative survival appeared to be driven primarily by a reduction in the survival of limnetics in the presence of trout. Two factors possibly contributed to this pattern. First, limnetics have shorter body lengths and narrower body depths than benthics (Schluter & McPhail 1992), which may make them more vulnerable to gape-limited predators (e.g. Brönmark & Miner 1992). This size handicap should be mitigated at least partially, however, by their increased amounts of defensive armour (table 2; McPhail 1992; Vamosi 2002). Reimchen (1994, 2000) has demonstrated that spines and lateral plates increase the probability of post-capture escape of sticklebacks from cutthroat trout. Second, and possibly more important, is the habitat use of limnetics compared with benthics. Based on stomach analyses of sticklebacks recovered at the end of the experiment (S. Vamosi, unpublished observations), limnetics foraged on zooplankton in the open water habitat even in the presence of trout. Benthics, by contrast, foraged in the littoral habitat, regardless of treatment. These different patterns of habitat use may have resulted in relatively high encounter rates between cutthroat trout and limnetics and low encounter rates between cutthroat trout and benthics (cf. Werner *et al.* 1983; Mittelbach 1984; L'Abée-Lund *et al.* 1993).

Previous hypotheses to explain the origin and maintenance of morphological and habitat differences between the sympatric stickleback species have concentrated on interspecific competition (Schluter & McPhail 1992; Schluter 1994). Our results on survival of benthics and limnetics suggest that predation by cutthroat trout may

Table 4. Effects of treatment (low-density, trout, high-density) and pond (block) on survival and growth of hybrids and the difference between the survival and growth of hybrids and the mean survival and growth of the parent species. (Abbreviation: MS, mean square.)

source	d.f.	hybrid			average of parent species-hybrid		
		MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
<b>survival</b>							
treatment	2	148.64	2.94	0.25	0.51	0.11	0.90
pond	3	63.17	1.25	0.47	65.63	14.19	0.07
error	2	50.64	—	—	4.63	—	—
<b>growth</b>							
treatment	2	$1.56 \times 10^{-3}$	519.77	0.002	$8.00 \times 10^{-6}$	0.54	0.65
pond	3	$6.87 \times 10^{-5}$	22.89	0.04	$7.60 \times 10^{-5}$	5.41	0.16
error	2	$3.00 \times 10^{-6}$	—	—	$1.40 \times 10^{-5}$	—	—

have contributed to this divergence. Differential vulnerability of limnetics to trout predation may indicate that littoral and open-water habitats differ more greatly in their selection pressures than is generated by food and competition alone. In this way contrasting predation pressures could promote further divergence than would otherwise be expected. Alternatively, higher trout predation in open water could reduce the value of exploiting this habitat, a process that could hinder divergence. Further experiments would be necessary to distinguish these alternatives.

Survival of  $F_1$  hybrids was low overall but, contrary to our predictions, not significantly affected by the presence of trout. Divergence between sympatric benthics and limnetics thus does not appear to be maintained by increased vulnerability of  $F_1$  hybrids to cutthroat trout. Despite the lack of a treatment effect on hybrid survival, ecological factors are nevertheless implicated in their poor performance because reduced survival is not seen in the laboratory environment (Hatfield & Schluter 1999). One possibility is that invertebrate predators (e.g. backswimmers, dragonfly larvae, and dytiscid beetles), which are present in the ponds and prey on young-of-the-year sticklebacks in the wild (Reimchen 1980; Foster *et al.* 1988), may have reduced hybrid survival. These invertebrates are found in shallow, vegetated waters (Foster *et al.* 1988; Vamosi 2002) where hybrids and benthics concentrate their foraging activities, as inferred from gut content analyses (Vamosi *et al.* 2000; S. Vamosi, unpublished observations). Evidence that invertebrates selectively prey on smaller and (or) more armoured (Foster *et al.* 1988; Vamosi 2002) sticklebacks suggests that hybrids may be more susceptible than benthics. Alternatively, reduced hybrid fitness may stem from other ecological mechanisms unrelated to predation.

Mean growth rates of  $F_1$  hybrids were intermediate between the parent species, with benthics having the highest growth rates. Reduced growth rates of  $F_1$  hybrids compared with benthics has been observed in previous field experiments (Hatfield & Schluter 1999; Vamosi *et al.* 2000) but not in the laboratory (Hatfield & Schluter 1999). What might be causing the different patterns observed in laboratory and field experiments? One possibility is that the field setting allows competition between hybrids and the parent species, whereas isolation of cross types prevents such competition in the laboratory. In the field there is significant diet overlap between hybrids and

parent species (Vamosi *et al.* 2000). On the other hand, this hypothesis would predict higher growth of  $F_1$  hybrids in the low-density treatment relative to that of the parent species than in the high-density treatment, whereas no such differences were observed. Another possibility is that growth rates in the benthic species are suppressed in the laboratory by crowding.

Generalizations have yet to emerge on the effects of predation on the relative fitness of parent species and their hybrids. This is partially due to the paucity of studies considering predation on hybrids and partially to the diversity of results obtained in the few studies conducted to date. Semlitsch (1993), for example, measured the survival of hybridogenetic *Rana esculenta* and one of the parent species (*R. lessonae*) and demonstrated higher survival of the hybrid in the presence of dragonfly larvae, but no difference between the two taxa in the presence of fish and newt predators. Spaak & Hoekstra (1997) showed that *Daphnia cucullata* × *D. galeata* hybrids were less vulnerable to fish predation than *D. galeata* but more vulnerable than *D. cucullata*. Finally, Wahl & Stein (1989) demonstrated that *Esox masquinongy* × *E. lucius* hybrids were more vulnerable to predation by largemouth bass (*Micropterus salmoides*) than either of the parent species. Continued interest in the role of ecology in evolution (Schluter 2000; Schneider 2000; Reznick & Ghalambor 2001) may eventually enable us to resolve the relative importance of predation in the origin and maintenance of divergence in sympatry.

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## REFERENCES

- Abrams, P. A. 1987a Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution* **41**, 651–661.

- Abrams, P. A. 1987b Alternative models of character displacement and niche shift. 2. Displacement when there is competition for a single resource. *Am. Nat.* **130**, 271–282.
- Abrams, P. A. 2000 Character shifts of prey species that share predators. *Am. Nat.* **156**, S45–S61.
- Aguilar, J. M. & Boecklen, W. J. 1992 Patterns of herbivory in the *Quercus grisea* × *Quercus gambelii* species complex. *Oikos* **64**, 498–504.
- Brönmark, C. & Miner, J. G. 1992 Predator-induced phenotypic change in body morphology in crucian carp. *Science* **258**, 1348–1350.
- Brown Jr, W. L. & Wilson, E. O. 1956 Character displacement. *Syst. Zool.* **5**, 49–64.
- Cummings, C. L., Alexander, H. M. & Snow, A. A. 1999 Increased pre-dispersal seed predation in sunflower crop-wild hybrids. *Oecologia* **121**, 330–338.
- Floate, K. D., Kearsley, M. J. C. & Whitham, T. G. 1993 Elevated herbivory in plant hybrid zones: *Chrysomela confluenta*, *Populus* and phenological sinks. *Ecology* **74**, 2056–2065.
- Foster, S. A., Garcia, V. B. & Town, M. Y. 1988 Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. *Oecologia* **74**, 577–585.
- Fryer, G. 1959 Some aspects of evolution in Lake Nyasa. *Evolution* **13**, 440–451.
- Gange, A. C. 1995 Aphid performance in an alder (*Alnus*) hybrid zone. *Ecology* **76**, 2074–2083.
- Grant, P. R. 1975 The classical case of character displacement. *Evol. Biol.* **8**, 237–337.
- Hatfield, T. & Schluter, D. 1996 A test for sexual selection on hybrids of two sympatric sticklebacks. *Evolution* **50**, 2429–2434.
- Hatfield, T. & Schluter, D. 1999 Ecological speciation in sticklebacks: environment-dependent hybrid fitness. *Evolution* **53**, 866–873.
- Hicks, C. R. 1964 *Fundamental concepts in the design of experiments*. New York: Holt, Rinehart & Winston.
- Hjalten, J. 1998 An experimental test of hybrid resistance to insects and pathogens using *Salix caprea*, *S. repens* and their F<sub>1</sub> hybrids. *Oecologia* **117**, 127–132.
- Holt, R. D. & Lawton, J. H. 1994 The ecological consequences of shared natural enemies. *A. Rev. Ecol. Syst.* **25**, 495–520.
- Jeffries, M. J. & Lawton, J. H. 1984 Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.* **23**, 269–286.
- L'Abée-Lund, J. H., Langeland, A., Jonsson, B. & Ugedal, O. 1993 Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. *J. Anim. Ecol.* **62**, 160–168.
- Larson, G. L. 1976 Social behavior and feeding ability of two phenotypes of *Gasterosteus aculeatus* in relation to their spatial and trophic segregation in a temperate lake. *Can. J. Zool.* **54**, 107–121.
- Lindman, H. R. 1992 *Analysis of variance in experimental design*. New York: Springer.
- McMillan, W. O., Jiggins, C. D. & Mallet, J. 1997 What initiates speciation in passion-vine butterflies? *Proc. Natl Acad. Sci. USA* **94**, 8628–8633.
- McPhail, J. D. 1992 Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): evidence for a species-pair in Paxton Lake, Texada Island, British Columbia. *Can. J. Zool.* **70**, 361–369.
- Milligan, B. G. 1985 Evolutionary divergence and character displacement in two phenotypically-variable, competing species. *Evolution* **39**, 1207–1222.
- Mittelbach, G. G. 1984 Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**, 499–513.
- Moodie, G. E. E. 1972 Predation, natural selection and adaptation in an unusual threespine stickleback. *Heredity* **28**, 155–167.
- Nagel, L. & Schluter, D. 1998 Body size, natural selection, and speciation in sticklebacks. *Evolution* **52**, 209–218.
- Nilsson, N.-A. & Northcote, T. G. 1981 Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. *Can. J. Fish. Aquat. Sci.* **38**, 1228–1246.
- Paine, R. T. 1966 Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.
- Pritchard, J. R. & Schluter, D. 2001 Declining interspecific competition during character displacement: summoning the ghost of competition past. *Evol. Ecol. Res.* **3**, 209–220.
- Reimchen, T. E. 1980 Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus*: an adaptation to predation? *Can. J. Zool.* **58**, 1232–1244.
- Reimchen, T. E. 1990 Size-structured mortality in a threespine stickleback (*Gasterosteus aculeatus*)—cutthroat trout (*Oncorhynchus clarki*) community. *Can. J. Fish. Aquat. Sci.* **47**, 1194–1205.
- Reimchen, T. E. 1994 Predators and morphological evolution in threespine stickleback. In *Evolutionary biology of the threespine stickleback* (ed. M. A. Bell & S. A. Foster), pp. 240–276. Oxford University Press.
- Reimchen, T. E. 2000 Predator handling failures of lateral plate morphs in *Gasterosteus aculeatus*: functional implications for the ancestral plate condition. *Behaviour* **137**, 1081–1096.
- Reznick, D. N. & Ghalambor, C. K. 2001 The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112**, 183–198.
- Ricklefs, R. E. & O'Rourke, K. 1975 Aspect diversity in moths: a temperate-tropical comparison. *Evolution* **29**, 313–324.
- Rundle, H. D., Nagel, L., Boughman, J. W. & Schluter, D. 2000 Natural selection and parallel speciation in sympatric sticklebacks. *Science* **287**, 306–308.
- Schluter, D. 1994 Experimental evidence that competition promotes divergence in adaptive radiation. *Science* **266**, 798–801.
- Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford University Press.
- Schluter, D. & McPhail, J. D. 1992 Ecological character displacement and speciation in sticklebacks. *Am. Nat.* **140**, 85–108.
- Schluter, D., Price, T. D. & Grant, P. R. 1985 Ecological character displacement in Darwin's finches. *Science* **227**, 1056–1059.
- Schneider, C. J. 2000 Natural selection and speciation. *Proc. Natl Acad. Sci. USA* **97**, 12 398–12 399.
- Semlitsch, R. D. 1993 Effects of different predators on the survival and development of tadpoles from the hybridogenetic *Rana esculenta* complex. *Oikos* **67**, 40–46.
- Simpson, G. G. 1953 *The major features of evolution*. New York: Columbia University Press.
- Slatkin, M. 1980 Ecological character displacement. *Ecology* **61**, 163–177.
- Spaak, P. & Hoekstra, J. R. 1997 Fish predation on a *Daphnia* hybrid species complex: a factor explaining species coexistence? *Limnol. Oceanogr.* **42**, 753–762.
- Taper, M. L. & Case, T. J. 1985 Quantitative genetic models for the coevolution of character displacement. *Ecology* **66**, 355–371.
- Vamosi, S. M. 2002 Predation sharpens the adaptive peaks: survival trade-offs in sympatric sticklebacks. *Ann. Zool. Fenn.* (In the press.)
- Vamosi, S. M. & Schluter, D. 1999 Sexual selection against hybrids between sympatric stickleback species: evidence from a field experiment. *Evolution* **53**, 874–879.

- Vamosi, S. M., Hatfield, T. & Schluter, D. 2000 A test of ecological selection against young-of-the-year hybrids of sympatric sticklebacks. *J. Fish Biol.* **57**, 109–121.
- Wahl, D. H. & Stein, R. A. 1989 Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* **46**, 2095–2103.
- Werner, E. E. 1991 Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* **72**, 1709–1720.
- Werner, E. E. & McPeck, M. A. 1994 Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology* **75**, 1368–1382.
- Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. 1983 An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540–1548.
- Whitham, T. G. 1989 Plant hybrid zones as sinks for pests. *Science* **244**, 1490–1493.

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