

Predation sharpens the adaptive peaks: survival trade-offs in sympatric sticklebacks

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This study tests whether living in different lake habitats in benthic and limnetic sticklebacks (*Gasterosteus aculeatus* complex) has resulted in divergence of antipredator traits and habitat-associated survival trade-offs. Adult benthics were larger than limnetics, had poorly developed defensive armour and showed no tendency to school with conspecifics. Limnetics, in contrast, were smaller, had well developed defensive armour and demonstrated strong schooling behaviour. In littoral arenas, juvenile limnetics were significantly more vulnerable than juvenile benthics to predation by adult benthics and backswimmers (*Notonecta* sp.) but not dragonfly larvae (*Aeshna* sp.). This pattern was reversed in open water arenas when adult benthics and limnetics were exposed to diving avian predators, double-crested cormorants (*Phalacrocorax auritus*). These findings show that divergence in antipredator traits between benthic and limnetic sticklebacks has accompanied divergence in foraging traits, resulting in survival trade-offs in addition to those previously observed for foraging success and growth rates across habitats.

Introduction

Interspecific competition for resources has historically been the favoured explanation for the observation that closely related species tend to be more divergent when they are found together than when they occur alone (Lack 1947, Brown & Wilson 1956, Schluter 2000b). Numerous the-

oretical (Slatkin 1980, Milligan 1985, Abrams 1986) and empirical studies (e.g., Schluter *et al.* 1985, Schluter & McPhail 1992, Dayan & Simberloff 1994; for review, *see* Schluter 2000b) confirm its role in divergence of morphology, behaviour and habitat use. More recently, the role of other interactions, such as predation (Holt 1977, Brown & Vincent 1992, Abrams 2000)

and parasitism (Hudson & Greenman 1998), in the evolution of divergence has started to receive attention. Despite the wealth of empirical studies addressing character displacement, no study has considered whether divergence due to interspecific competition for resources has had any consequences for interactions between the consumer species and their predators or parasites.

One frequently observed consequence of competition for shared resources, particularly in aquatic systems, is habitat segregation (Werner *et al.* 1977, Schluter & McPhail 1992, Robinson & Wilson 1994, Kawano 1995, Chiba 1999). Different habitats often present different prey types for consumers, and divergence of consumers may involve adaptations to feeding on these alternate types (Schluter 2000a, 2000b). These adaptations can be accompanied by trade-offs in foraging efficiency (Schluter 1993) and growth rates (Schluter 1995), such that each species outperforms the other in its native habitat. However, habitats may also contain different predators (Mittelbach 1984, Reimchen 1994, Gilbert *et al.* 1999, Pitt 1999), a fact that has been largely overlooked by studies of character displacement. These predators, in turn, may have different modes of detecting or capturing prey (e.g., Reimchen 1994, DeWitt *et al.* 2000). Analogous to the case of resources, a diversity of predator types can drive the divergence of anti-predator traits in the consumer species inhabiting differing habitats. The result is a trade-off in survival when one consumer species encounters predators associated with the habitat of the competitor species. The purposes of this

study were to explore whether: (1) divergence in behavioural and morphological antipredator traits accompanies divergence in trophic traits in a pair of sympatric species and (2) trade-offs in survival exist, such that a consumer species has higher relative survival in its preferred habitat when in the presence of predators associated with the preferred habitat but lower survival in the other habitat when presented with predators from the other habitat.

To address these questions, I studied benthic and limnetic sticklebacks (*Gasterosteus aculeatus* complex) from Paxton Lake, Texada Island, British Columbia. These two species are divergent in their habitat use, preferred prey and trophic traits. Benthics are larger fish with fewer, shorter gill rakers that feed on macroinvertebrate prey in the shallower, vegetated waters of the littoral zone, whereas limnetics are smaller fish with many, long gill rakers and forage predominantly on zooplankton in the pelagic zone (Larson 1976, McPhail 1984, 1992, Schluter & McPhail 1992). The divergence in morphology is thought to have arisen in part as a result of competition for shared resources (Schluter & McPhail 1992, McPhail 1993, Schluter 1994) and is associated with trade-offs in foraging performance (Schluter 1993) and growth rates (Schluter 1995) between habitats.

Previous studies (Foster *et al.* 1988, Foster & Ploch 1990, Reimchen 1994) and field observations (Table 1) suggest that different predators of sticklebacks are associated with the two habitats. Sticklebacks in the littoral zone are expected to encounter primarily invertebrate predators (Reimchen 1980, Foster *et al.* 1988) and can-

Table 1. Predators observed at Paxton Lake (1994–1997). Invertebrate predators in the littoral zone were collected with minnow traps or sweep nets; their absence from the pelagic zone was determined by snorkelling along transect lines. Observations of the other predators were made as follows: birds: spotting scope; snakes: from shore or boat; trout: from boat.

	Littoral zone	Pelagic zone
Invertebrate	various [back swimmers, belostomatids (<i>Belostoma</i> sp.), diving beetles (<i>Dytiscus</i> sp.), dragonfly larvae, water scorpions (<i>Ranatra</i> sp.)]	
Vertebrate	belted kingfisher (<i>Ceryle alcyon</i>) cutthroat trout garter snake (<i>Thamnophis</i> sp.) great blue heron (<i>Ardea herodias</i>)	common loon cutthroat trout

nibalistic adult sticklebacks (Foster *et al.* 1988), whereas sticklebacks in the pelagic zone are more likely to encounter diving birds and predatory fish (Reimchen 1994). I tested whether benthics and limnetics were divergent in defensive traits and whether this divergence was associated with trade-offs in survival between habitats, such that benthics are more vulnerable to pelagic zone predators, whereas limnetics are more vulnerable to littoral zone predators. I used insects and large benthics as predators in the littoral treatment and diving birds in the pelagic treatment. Cutthroat trout, which may prey on sticklebacks in both habitats, were examined in another study (S. M. Vamosi & D. Schluter, unpubl.).

Materials and methods

Defensive armour

Adult fish used for morphometric measurements were taken from collections made at Paxton Lake by Schluter and McPhail (1992). These fish had been fixed in 10% formalin for a week, stained in Alizarin red S dye, and preserved in 37% isopropyl alcohol. Standard length (SL) and five defensive armour traits were measured on the left side of 40 benthic and 40 limnetic sticklebacks following the methods of Lavin and McPhail (1985): length of the first dorsal spine, length of the second dorsal spine, number of lateral plates, pelvic girdle length, and pelvic spine length. The five traits were chosen because previous studies (Hagen & Gilbertson 1972, 1973, Reimchen 1994, Vamosi 2001) have demonstrated that their degree of expression is correlated with predation pressure. Lateral plates provide protection for the epidermis against attacks by toothed predators (Reimchen 1992, 2000). When erect, pelvic spines, in conjunction with dorsal spines, increase the effective diameter of an individual when they are locked erect, reducing vulnerability to gape-limited predators (Reimchen 1991). The pelvic girdle buttresses the pelvic spines and helps create a protective bony “ring” around the stickleback (Reimchen 1983).

I adjusted all defensive armour traits, other than number of lateral plates, of each population

to a universal standard length of 47.5 mm using the equation:

$$Y_i = X_i - \beta(SL_i - 47.5) \quad (1)$$

where Y_i is the size-adjusted trait value at 47.5 mm, X_i is the original value for the trait in individual i ($i = 1$ to 40 for each species), β is the regression coefficient of the original trait values on standard length, and $(SL_i - 47.5)$ is the standard length of the individual minus the universal standard length (Hagen and Gilbertson 1972). The choice of universal standard length is somewhat arbitrary (Hagen and Gilbertson 1972), but I chose 47.5 mm because it was approximately the mean length of sticklebacks measured (mean = 47.59 mm).

To determine whether benthics and limnetics were divergent in defensive armour, I first conducted an exploratory principal components analysis using the correlation matrix of ln-transformed body-size corrected traits and ln-transformed number of lateral plates. Restricting my attention to principal components with eigenvalues greater than one, I then considered individual traits with significant component loadings (≥ 0.40) and compared means among benthics and limnetics using a two-sample t -test.

Schooling behaviour

Schooling is an antipredator behavioural trait (Magurran 1990, Pitcher & Parrish 1993, Svensson *et al.* 2000) which may differ between benthics and limnetics because of the different habitats with which the two species are associated. If schooling behaviour differs between the species it should differ in the following way. Limnetics, which live mostly in open waters, are predicted to display strong schooling behaviour (Bertram 1978, Pitcher 1986). Benthics, conversely, which live in a more structured environment where aggregations may be hard to maintain, are predicted not to display strong schooling behaviour (Lima & Dill 1990, Aboul Hosn & Downing 1994, Rangeley & Kramer 1998).

Schooling behaviour was measured in an experimental arena, a large (200 l) aquarium divided into three sections by inserting two

panels of window screen mesh 30 cm from either end. This created two end sections (each 30 cm × 30 cm × 50 cm) and a central section (75 cm × 30 cm × 50 cm). In the central section, I drew nine equally spaced vertical lines on the front of the aquarium with a Sharpie® pen to create ten equally sized “compartments” for observation.

Ten conspecifics were introduced to a randomly chosen end section and one conspecific was introduced to the other end section. The compartment nearest the single conspecific was assigned a score of one, the second nearest compartment a two, etc., and the compartment closest to the group of ten conspecifics was assigned a score of 10. These fish were acclimated for 1 hr and then a single fish (= focal individual) was introduced into the central section. I recorded from behind a blind which compartment the focal individual was in at 30 s intervals for 30 min. If the body of the focal individual spanned two compartments, I recorded which compartment the head was in.

I calculated the mean position of each fish and compared the mean position for each species to a random expectation with a one-sample *t*-test. If the mean position for a species was significantly greater than 5.5, the random expectation, I would consider this evidence for schooling behaviour. Mean position significantly lower than 5.5 would indicate avoidance of schools, and a lack of a significant difference would indicate no preference. I compared means of the two species with a two-sample *t*-test.

Predation experiments — design

To determine whether survival trade-offs have accompanied the divergence of benthics and limnetics, I measured the relative predation rates on benthics and limnetics by predators from the two habitats. Two special features of the design of the predation experiments require explanation. First, my design modifies the typical reciprocal transplant experiment (e.g., McPeck 1990) by using individuals of different age in different habitats. In the typical design, individuals of the same age from the two species are assigned at random to one of two habitats that differ only in

one way (e.g., presence or absence of a predator). In my experiment, the arena representing the pelagic habitat is larger and the individuals are older (and larger) than in the littoral habitat. A larger arena was chosen because of the larger size of diving birds in relation to invertebrate and fish predators. Older individuals were used because diving birds do not tend to feed on juvenile sticklebacks (Reimchen 1995).

Second, logistic constraints prevented the use of common loons (*Gavia immer*), which have been observed at Paxton Lake in summer (Table 1), in the pelagic arena experiments. Double-crested cormorants (*Phalacrocorax auritus*), which I have not observed at Paxton Lake but may be present in winter, were available for experiments (see Acknowledgments) and were used as a surrogate open water predator. Both species are common in the Strait of Georgia region, forage for sticklebacks predominantly in the pelagic zone of lakes (Reimchen 1994, 1995), and dive under water to pursue and capture prey.

Predation experiments were conducted at the University of British Columbia Animal Care Facility after consulting with staff about issues concerning experimental design. Special considerations included providing vegetation as refuge to subjects from predators in littoral experiments (e.g., Foster *et al.* 1988, Kruuk & Gilchrist 1997), keeping pelagic experiments as short as possible (most trials were < 10 min in duration), using the minimum number of subjects needed to ensure sufficient statistical power ($n = 10$ of each cross type for littoral trials, $n = 8$ for pelagic trials), while minimizing the effects of isolation on subjects. Cormorants were kept in pairs and used for multiple trials to minimize isolation and disturbance.

Predation experiments — experimental fish

Fish for experimental studies of predation were obtained by making crosses in May of the year of study for littoral arena trials and the year before for pelagic arena trials. Adults for crosses were collected from Paxton Lake using minnow traps. Crosses were made by stripping eggs

from gravid females into Petri dishes using gentle abdominal pressure and adding water and macerated testes from males. A single male was used per five female clutches. After two hours had elapsed, fertilized eggs were transferred to plastic hatching containers (175 ml) with mesh bottoms suspended in 100 L aquaria above air stones. Air stones provided oxygen to the eggs through the mesh. Eggs that became infected with fungus were removed daily. After hatching, fish were transferred from the hatching containers to the aquaria. A minimum of 25 benthic and 40 limnetic crosses were made in each year.

Juveniles were fed with infusoria cultures for the first two days, then switched to diets consisting of live brine shrimp (*Artemia*) nauplii fed once or twice daily. After three months, diets of fish to be raised to adulthood were supplemented with frozen bloodworms and brine shrimp.

Predation experiments — littoral arena

To assess the relative predation rates of juvenile benthics and limnetics, I conducted laboratory experiments based on the design of Foster *et al.* (1988). The littoral zone treatment involved placing juvenile sticklebacks into arenas containing three types of predators: dragonfly nymphs (*Aeshna* sp.), backswimmers (*Notonecta* sp.), and large adult benthics. Littoral trials were conducted in July of 1995, 1996, and 1998. Invertebrate predators were obtained from Paxton Lake, Texada Island (1995) or the Experimental Research Ponds, University of British Columbia (1996 and 1998) using dip nets. Adult benthic sticklebacks were caught with minnow traps from Paxton Lake (1995) or were taken from a lab population of fish obtained from Paxton Lake as juveniles the previous year (1996 and 1998). All predators were collected one to three days prior to trials, and maintained in an unfed state in vegetated aquaria.

Experimental containers were circular wading pools (0.75 m diameter $\times$ 0.2 m deep). Pools were filled with freshwater 24 hr before each trial. Substrate consisted of a thin layer (5–10 mm) of coarse granular beach sand, instead of lake sediment, to allow accurate enumeration of individuals during observation periods. Each pool

contained two clumps of an aquatic macrophyte (*Chara* sp.), two lily pads, and a cattail stalk for cover.

To start a trial, ten juvenile benthics and ten juvenile limnetics were haphazardly selected from stock aquaria, added to each pool and acclimated for at least 30 min before three predators (either adult benthics or backswimmers or dragonfly larvae) were added. Predators and prey were used only once. Number of predators was chosen to match the predator densities used by Foster *et al.* (1988). Pools with sticklebacks but no predators served as controls. After addition of insect predators, pools were censused every 24 hours. Pools with adult benthics were censused eight hours after trials began because the results of Foster *et al.* (1988) indicated that the rates of predation by adult sticklebacks are relatively high compared to those of insect predators. Pools were observed from behind mesh screens to minimize disturbances to juvenile sticklebacks. Dead or missing predators were replaced at each census, and dead fish were removed. Trials were terminated after four days in 1995, seven days in 1996 and 1998, or earlier if fewer than five juvenile individuals of one or both stickleback species remained.

Predator feeding bias was quantified with Manly's preference index:

$$\alpha = \frac{\ln(p_b)}{\ln(p_b p_l)} \quad (2)$$

where p_b is the proportion of benthics surviving out of the initial ten and p_l is the proportion of limnetics surviving (Manly 1974, Chesson 1978). Values for α range from 0 to 1, with $\alpha = 0.5$ representing even prey selection by the predator, $\alpha = 0$ representing only limnetics being consumed and $\alpha = 1$ only benthics.

Predation experiments — pelagic arena

Experiments designed to assess the relative predation rates of adult benthic and limnetic sticklebacks were conducted in July–September 1998. The experimental arena was a large (9 m $\times$ 3 m $\times$ 1 m deep) unvegetated indoor pool. An aviary

was built above the pool and two perches were provided for the birds.

Predators were lab-reared adult double crested cormorants (2.0–2.5 kg). Their regular diet consisted of a daily ration of four herring and 14–18 smelt. Three to five days before conducting a set of trials, I introduced a pair of cormorants to the experimental arena. During their acclimation, I released 4–5 adult benthics and 4–5 adult limnetics into the experimental arena prior to their daily feeding. I considered a pair of cormorants to be acclimatised when they: (1) entered the water within 30 min to forage on sticklebacks after I stepped behind a blind, (2) left the water and flew to their perches after I stepped out from behind the blind and (3) repeated these behaviours two days in a row. Each pair was used for ten replicates, and a total of three pairs were used.

Adult sticklebacks used in each trial were haphazardly selected from the stock aquaria. Eight adult benthics and eight adult limnetics were added to the experimental arena in each trial. Benthics and limnetics were introduced simultaneously at the end of the arena furthest from the perch of the cormorants. After introduction, I would stand in full view of the cormorants for 5 min before stepping behind the blind. This acclimation period was chosen to minimize disturbance to the cormorants. Sticklebacks often swam the entire length of the pool more than once during this time.

Trials were terminated after approximately half of the fish were consumed. The remaining fish were then counted and identified. Obser-

vations from a pilot experiment indicated that entering the aviary to collect the surviving fish with a dip net would alter the behaviour of the birds in subsequent trials, so this method was not used in subsequent trials. Instead, my assistant and I would count and identify remaining fish separately from the edge of the pool, after which we could compare counts. Once detected, fish were easily identified to species because of the considerable length (Table 2), weight (Table 2), and shape (Schluter and McPhail 1992) differences that exist between adult benthics and limnetics. After we finished counting, cormorants returned to the pool to consume the remaining sticklebacks. In this way, individual sticklebacks were used for only a single trial. Cormorant feeding bias was calculated using Manly's preference index (Eq. 2), adjusted to reflect the lower numbers of benthics and limnetics at the start of pelagic trials compared to littoral trials, as detailed for the littoral arena experiment.

Results

Defensive armour

Exploratory principal components analysis suggests that adult limnetics have more defensive armour than adult benthics. The first principal component (PC1), which had an eigenvalue of 3.82 and accounted for 76.44% of the total variance, represented significant variation in four of the armour traits considered, and marginal variation in a fifth, second dorsal spine length. Pelvic spine length had the highest loading (loading = 0.49), followed by number of lateral plates (0.48), pelvic girdle length (0.48), first dorsal spine length (0.40), and second dorsal spine length (0.36). PC1 was the only principal component with an eigenvalue greater than one, so PC2 to PC5 are not considered further. There was no overlap between benthics and limnetics, and limnetics had higher PC1 scores than benthics (Fig. 1).

Analysis of the individual traits identified by the principal components analysis confirms that adult limnetics have more defensive armour than adult benthics (Table 3). Limnetics had longer size-corrected pelvic spines ($t_{78} = 38.88$,

Table 2. Mean (± 1 SE) standard length and mass (for pelagic experiment only) of benthics and limnetics used in predation experiments. Standard length of fish reported for the littoral experiment based on individuals retrieved from control pools only, whereas standard length and wet mass of all fish in the pelagic experiment were recorded before their introduction to the pool.

Habitat	Species	SL (mm)	Mass (g)
Littoral	benthic	11.86 $\pm$ 0.28	–
	limnetic	11.26 $\pm$ 0.30	–
Pelagic	benthic	55.80 $\pm$ 0.31	2.54 $\pm$ 0.04
	limnetic	48.13 $\pm$ 0.19	1.42 $\pm$ 0.02

$P < 0.001$) and pelvic girdles ($t_{78} = 20.10$, $P < 0.001$) than benthics. Similarly, limnetics had longer size-corrected first dorsal spines than benthics ($t_{78} = 8.44$, $P < 0.001$). Finally, limnetics had more lateral plates than benthics ($t_{78} = 28.40$, $P < 0.001$).

Schooling behaviour

Benthics and limnetics differed in their distributions in the schooling trials (Fig. 2); limnetics spent more time near the group of ten conspecifics than did benthics. The mean position of benthics in the aquarium was not significantly different from a random expectation ($t_{10} = 0.87$, $P = 0.41$). Mean limnetic position, conversely, was highly significantly different from random ($t_{10} = 10.44$, $P < 0.001$) and from the mean position of benthics ($t_{20} = 3.70$, $P = 0.001$).

Predation experiments

Limnetics tended to be more vulnerable than benthics to predators in the littoral arenas (Table 4). Relative survival of limnetics was significantly lower in the presence of adult benthics and backswimmers and tended to be lower, albeit not significantly, in the presence of dragonfly larvae. The pattern of vulnerability was reversed in the open water arena (Table 4), where benthics were more vulnerable than limnetics to double-crested cormorants. The results

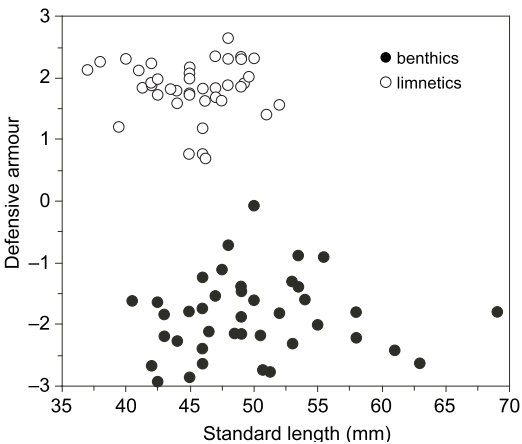


Fig. 1. Plot of the relationship between standard length and defensive armour (PC1) in adult benthic and limnetic sticklebacks. Symbols indicate individuals. PC1 accounted for 76.44% of the total morphological variance. $n = 40$ for each species.

from the two experiments provide support for the prediction that a survival trade-off is associated with adaptations to predators from the two habitats. Illustrating this with a fitness set (Levins 1962) reveals a negative relationship between performance in the two experiments (Fig. 3): each species is more vulnerable to predators from the habitat of the other species.

Discussion

An old observation in biology is exaggerated differences between closely related species when

Table 3. Summary statistics for the five defensive armour traits of adult benthic ($n = 40$) and limnetic ($n = 40$) sticklebacks. Values for traits, with the exception of number of lateral plates, are adjusted to a body length of 47.5 mm.

Trait	Species	Mean	Range
First dorsal spine length	benthic	0.90	(0–2.28)
	limnetic	2.39	(1.34–3.09)
Second dorsal spine length	benthic	2.50	(1.69–3.43)
	limnetic	3.14	(2.16–4.02)
Pelvic spine length	benthic	0.10	(0–3.21)
	limnetic	4.52	(2.91–5.75)
Pelvic girdle length	benthic	0.69	(0–4.97)
	limnetic	7.87	(6.13–9.49)
Number of lateral plates	benthic	0.30	(0–3)
	limnetic	5.58	(4–7)

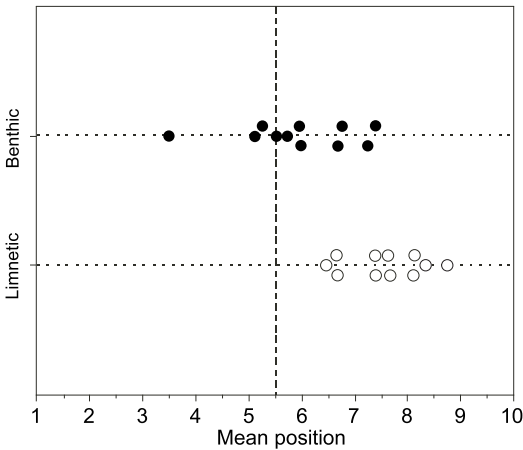


Fig. 2. Mean position of adult benthic and limnetic sticklebacks in the schooling behaviour experiment. A value of 1 represents the focal fish being beside the single individual during all observations, a value of 10 beside the group of 10 individuals, and 5.5 (vertical dashed line) is the random expectation. *n* = 11 for each species.

they occur together. Competition for food has been, and continues to be, the most widely studied mechanism as a cause of behavioural and morphological differences between sympatric species (Schluter 2000b). Predation is an important ecological phenomenon, yet we remain largely ignorant of the evolutionary consequences of the interactions between coexisting species and their predators (Abrams 2000). In this study, I documented differences in anti-predator traits and predator-mediated survival of two sympatric stickleback species.

Limnetics had longer mean size-corrected first dorsal spines, pelvic spines, and pelvic girdles and more lateral plates than benthics. Furthermore, benthics tended to lack these struc-

tures. These results agree with, and extend, the findings of McPhail (1992), who found differences between benthics and limnetics in number of lateral plates and size-corrected length of pelvic spines. Interestingly, the amount of armour in these sympatric species parallels the association between number of lateral plates and habitat use in a solitary population of three-spined sticklebacks polymorphic for number of dorsal and pelvic spines (Reimchen 1980). Reimchen (1980) found that, in Boulton Lake, individuals having higher spine number tended to be found in the pelagic zone whereas individuals with fewer spines were found in the littoral zone.

Based on studies of solitary populations that vary in their predator communities, both among habitats within a lake (Reimchen 1980, Reimchen 1994) and between lakes (e.g., Hagen & Gilbertson 1972, Bell *et al.* 1993, Walker 1997), limnetics appear to be adapted to a predation regime dominated by cutthroat trout and diving birds whereas benthics have adapted to increased invertebrate predation on juveniles and (or) a release from vertebrate predation on adults. The marked reduction in the defensive armour of benthics is not likely due to low calcium levels, as has been suggested for some cases of armour reduction (Giles 1983), because of the levels of defensive armour observed in limnetics and the presence of calcium-rich marl deposits in Paxton Lake (Larson 1976; S. M. Vamosi, pers. obs). A comparison of benthics and limnetics from lakes in independent drainages revealed a similar, although less marked, reduction of the defensive armour of benthics (Vamosi 2001), implying adaptive divergence.

Limnetics displayed a stronger tendency than benthics to associate with a larger group of

Table 4. Selective predation on benthic and limnetic sticklebacks. Values given for Manly's index are means (± 1 SE) of trials for each predator. *n* is the number of replicates for each predator.

Arena	<i>n</i>	Predator	Manly's index (α)*	<i>P</i> -value
Littoral	14	adult benthic	0.34 $\pm$ 0.06	0.007
	16	backswimmer	0.16 $\pm$ 0.06	< 0.001
	12	dragonfly larva	0.46 $\pm$ 0.08	0.61
Pelagic	29	cormorant	0.62 $\pm$ 0.03	< 0.001

* α > 0.5: higher relative survival of limnetics; α < 0.5: higher relative survival of benthics

conspecifics. Aggregating with conspecifics has been associated with animals living in open habitats (Bertram 1978) and avoidance of conspecifics with those living in structurally complex habitats (Sih 1987, Lima & Dill 1990, Rangeley & Kramer 1998). Limnetics may school to dilute predation risk and to increase vigilance. In contrast, benthics may avoid large groups to avoid detection by ambush predators. These differences in tendency to school are in addition to differences between the two species in their fast-start responses (Law & Blake 1996), which were also interpreted as adaptations to escaping predators in different habitats.

The results of the predation experiments were consistent with the prediction of predator-mediated survival trade-offs across habitats. Both species tended to have higher relative survival when in their preferred habitat. These survival trade-offs are in addition to the ones in foraging efficiency and growth associated with divergence in foraging traits (Schluter 1993, 1995). Schluter (1995) argued that the sharp trade-offs in foraging performance and growth rates may be responsible for the diversification across the two habitats. Habitat-specific predation may, thus, "sharpen" the adaptive peaks and contribute to the observed divergence between benthic and limnetic sticklebacks.

What traits contributed to the differential predation observed across habitats and predators? Body size differences are likely an important factor contributing to differential predation. Smaller individuals tend to be most susceptible to adult sticklebacks (Foster *et al.* 1988) and invertebrate predators (Hay 1974, Foster *et al.* 1988), with the possible exception of dragonfly larvae (Foster *et al.* 1988), which would favour benthics in the littoral experiments. Conversely, cormorants and loons tend to prefer larger sticklebacks (≥ 50 mm; Reimchen 1995), which would favour limnetics in the pelagic experiments. The presence of well-developed defensive armour may have also contributed to the vulnerability of limnetics to backswimmers (Reimchen 1980, Reist 1980). Reimchen (1980) suggested that invertebrates, such as backswimmers, that grapple their prey might be better at capturing sticklebacks with defensive armour than those lacking such structures. Finally, in the pelagic

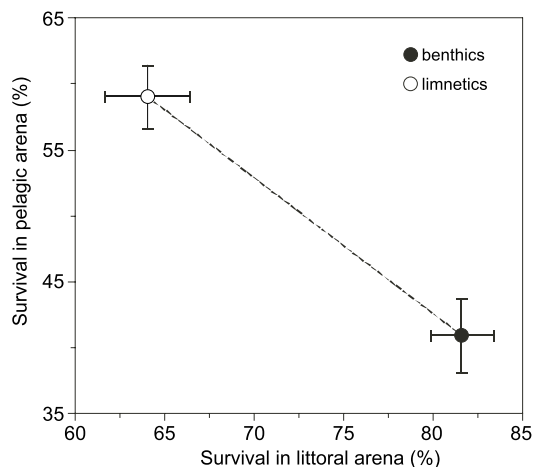


Fig. 3. Trade-off in survival between habitats. Symbols indicate means (± 1 SE) for benthics and limnetics. Survival in littoral arenas is averaged across three predators (adult benthics, back swimmers, and dragonfly larvae).

arena limnetics often formed tight schools (S. M. Vamosi, pers. obs.), which may be an adaptive response to the presence of avian piscivores (Rangeley & Kramer 1998).

A small, but growing, number of empirical studies suggest that differential predation may aid in the divergence of sister species. Kruuk and Gilchrist (1997), for example, studied the role of predation in the differentiation of hybridizing taxa of *Bombina*. Fire-bellied toads (*B. bombina*) tended to be found in semi-permanent ponds which had higher predator densities than the temporary puddles used by yellow-bellied toads (*Bombina variegata*). Yellow-bellied toads were more active and subsequently suffered higher mortality in laboratory predation experiments than did fire-bellied toads when presented with predators characteristic of *B. bombina* habitats. Continued interest in models of apparent competition (Holt 1977, Brown & Vincent 1992, Abrams 2000) and habitat-specific predation risk (Abrams 2000) will no doubt add to our understanding of the role of predators in divergence and speciation.

In conclusion, benthic and limnetic sticklebacks differ not only in trophic traits, but also in defensive armour and antipredator behaviours. These traits appear to be adaptations to different habitat-specific predation regimes and

are accompanied by survival trade-offs across habitats. The next challenge will be to elucidate whether habitat divergence in sympatric sticklebacks was initiated in response to competition for food with subsequent adaptation to different predators or to apparent competition via shared predators with subsequent adaptation to different prey.

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