Substrate discrimination and preference in foraging fish

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Increasing substrate structural complexity has been linked to higher densities of various refuge-seeking aquatic macroinvertebrates, many of which constitute major prey species in a variety of freshwater communities. We investigated (1) whether the three-spined stickleback, *Gasterosteus aculeatus*, a predator of such macroinvertebrates and an established model organism in studies of animal behaviour, is capable of discriminating between structurally complex and simple substrates, and (2) whether they show a substrate preference when foraging. Hunger-motivated sticklebacks presented with a choice of simple and complex substrate types preferentially foraged over complex substrates. This was seen when the prey density was equal on both substrate types, and when it was greater on the complex substrate. Where prey density was greater on the simple substrate, fish showed no preference for either. The preference for complex substrates existed in both the allocation of time spent foraging and in the direction and frequency of feeding strikes. No substrate preferences were seen in fish that were satiated, or when prey were absent from both substrates. This ruled out refuge as an explanation for the observed preference. We discuss the results in the context of the relative usefulness of substrate discrimination in effective patch foraging in fish.

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To maximize energy gains, a predator must select a foraging ground in which the potential prey encounter rate is optimal (Krebs et al. 1981). The rate of prey encounters will be affected by the density of the prey organisms and the detection rate, factors that are influenced by the physical structure of the habitat (Eklöv & Diehl 1994; Merilaita 2003).

For many predatory fish species, increasing habitat structural complexity directly, and usually negatively, influences the rate at which prey items are located and consumed (Savino & Stein 1982; Russo 1987; Diehl 1988; Tatrai & Herzig 1995; Mayer et al. 2001). This trend is not applicable to all fish predator–prey relationships, however, nor should one expect it to be. Patches of high structural complexity at the microhabitat level are associated with localized increases in macroinvertebrate density and diversity. Such habitat complexity can be caused by the presence of subaquatic vegetation cover (Rabe & Gibson 1984; Gregg & Rose 1985; Lodge 1985; Chick & McIvor 1994; Kurashov et al. 1996) or related to substrate form and characteristics (Rempel et al. 2000; Cole et al. 2003; Macia et al. 2003). The observed increases in macro-invertebrate density are due in part to the increased provision of refugia, and, in the case of vegetation patches, availability of a locally abundant primary food resource. Some populations of predatory fish species have to an extent overcome the problem of foraging in structurally complex habitats to capitalize on these spatially focused aggregations (e.g. Diehl 1988; Dudgeon 1993).

We investigated the role of substrate structural complexity on the foraging preferences of the three-spined stickleback, *Gasterosteus aculeatus*, a generalist predator of macroinvertebrates, and a well-established model organism in studies of behavioural ecology (Bell & Foster 1994). We used individuals from a reach of a small, slow-moving stream, with little mid-channel vegetation. As such, differences in habitat structural complexity occurred through variation in the nature and form of the substrate: patches of well-sorted silt and fine sand deposits, and more complex, poorly sorted deposits of larger gravels and fragments of woody debris (personal observations). Stomach content analysis has shown that this population consumes primarily benthic prey, of which chironomid larvae are most important for the size category of fish used in this study (H. Chambers, unpublished data).

The microhabitat preferences of chironomid larvae, which are important prey organisms in many freshwater stream communities (Poepperl 2003), have been well

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studied. They occur at the highest densities in unvegetated, poorly sorted sediment deposits where interparticle voids (used as refugia) are most prevalent (Sagova-Mareckova 2002; De Bisthoven & Gerhardt 2003; Gayraud & Philippe 2003; Johnson & Kennedy 2003; Tolonen et al. 2003).

Given that the more complex deposits, which are poorly sorted and rich in refugia, have higher potential prey densities, it is conceivable that three-spined sticklebacks discriminate between substrates of differing structural complexity when foraging. In this study we examined this possibility, and explored the hypothesis that foraging sticklebacks will preferentially select foraging areas with greater structural complexity. The influence of internal state, as defined by hunger, and prey density on foraging ground choice was also investigated.

METHODS

Collection, Housing and Welfare

Several hundred three-spined sticklebacks were collected from Stonton Brook, a small tributary of the river Welland, Leicestershire, U.K., using hand nets in October 2003. We have no data on the size of the population at this location; however, personal observations indicate that the three-spined stickleback is very abundant here, and the number removed and transferred to the laboratory represents only a small proportion of the local population. As such, the number of fish removed for this study was expected to have little impact on the ecology of the stream. They were transferred by road in 25-litre containers for approximately 30 min to laboratory holding tanks (water temperature: 11°C; photoperiod 12:12 h light:dark) and fed daily to satiation on commercially available frozen bloodworms (*Chironomus* spp. larvae). After 3 weeks, 12 experimental groups, each of 12 size-matched (mean standard length $\pm$ SD = 32.2 $\pm$ 0.35 mm) individuals, were removed and transferred to tanks (40 × 25 cm and 28 cm deep, water depth 25 cm), where each group was in visual and olfactory isolation from the other groups for 7 further days before the trials.

As the sex of individuals cannot be determined outside the reproductive season, we could not divide experimental groups by sex. The laboratory conditions described above, however, are sufficient to ensure that the changes in physiology associated with commencement of the reproductive phase are inhibited (Guderley 1994).

Treatments

In each trial an individual was given the choice of moving and foraging for prey items over two substrate types, referred to as simple or complex. The simple substrate was composed of sieved sand particles (grain size ≤2 mm). This presented the fish with a homogeneous forage plane of sorted and well-packed sediment of uniform coloration and microtopography. The complex substrate comprised an assortment of angular mixed sandstone gravels (longest axis range of 5–20 mm), presenting

a heterogeneous bed of uneven topography and cryptic red–brown coloration containing many interparticle voids, which formed potential prey refugia that could be investigated by foraging fish. These substrate types are representative of the sediment deposits over which the fish forage in their natural habitat.

We used four different prey densities each with three experimental groups per treatment, with hunger level as the experimental variable. The densities were: (1) 0:0, no food was presented on either substrate type; (2) 1:1, simple:complex (1 item per 120 cm² on each substrate type); (3) 3:1 (1 item per 40 cm² on the simple substrate versus 1 item per 120 cm² on the complex substrate); and (4) 1:3 (1 item per 120 cm² on the simple substrate versus 1 item per 40 cm² on the complex substrate).

We presented 4-mm sections of thawed frozen bloodworm as prey items, with each delivered directly to a randomly determined point on the substrate tray, an approach that ensured prey items were well dispersed rather than aggregated. This was done before the introduction of the test fish. Fish were well accustomed to this prey as it was the sole constituent of their diet during the laboratory holding period. These food items were sufficiently small to ensure that stomach capacity was not rapidly reached and foraging motivation not lost during the trial (Gill & Hart 1994). Prey settled upon the surface of the simple substrate, whereas it was visually less obvious on the complex substrate, where it tended to lie within the interparticle voids.

Hunger is a motivational factor determining how much effort is directed towards foraging (Beukema 1968) and we also investigated this factor: within each of the four prey density treatments one group was fed to satiation 1 h before the trials, one group was fed to satiation before 24 h of food deprivation and one group was fed to satiation before 72 h of food deprivation.

Binary Choice Arena

The trials were run in a binary choice tank (54 × 25 cm and 30 cm deep; water depth 20 cm), covered at the sides with opaque plastic to eliminate outside disturbance. The tank contained two removable trays (24 × 24 cm and 4 cm deep) into which the substrate material was placed. These were separated by a 5-cm plastic divider strip on to the centre of which a 5-cm-diameter, 25-cm-tall mesh (mesh size 2 mm) cylinder was placed. We transferred each test fish to the cylinder before a trial, so that it could view both substrate types, but could not physically interact with either until the trial.

Fish were allowed a settling time of 5 min before we removed the cylinder from the tank, using a remote pulley mechanism, and the trial began. Each trial lasted 10 min during which we recorded the time spent directly over but less than 10 cm above each substrate (Hart 2003). Time spent above the divider was not included, unless more than half the body of the fish was directly over a substrate. We also recorded the number of feeding strikes made into the substrate type. These were recorded whether successful or not and multiple strikes made at a single food item as

part of the prey-handling process were recorded as single occurrences (Gill & Hart 1994). Finally, the number of food items consumed from each substrate type was recorded.

The position of the substrate trays within the tank was randomized for each trial to eliminate any tank end preferential bias. We replaced water and substrate materials after each trial so that any uneaten food items and faecal material did not carry over to contaminate subsequent trials. Fish were tested individually and were drawn at random from their respective treatment groups. No individual was used more than once throughout the study.

Ethical Note

Although unlikely, it is possible that fish conditioned in behavioural trials will behave differently thereafter, and this could have local population effects if the fish were returned to their point of capture. For this reason, after the study, those fish used were retained in the laboratory as breeding stock. Other fish captured but not used in this study were also retained for use in future studies, so as to minimize the number of collection trips subsequently required.

RESULTS

Substrate Preference

When deprived of food for 24 h and 72 h, test fish spent significantly more time over the complex substrate (Fig. 1). This was true when the prey item density was equal across both substrate types and when the prey item density was greater on the complex substrate. When the prey item density was greater on the simple substrate no significant preference for either substrate type was observed. Equal time was spent over substrate types when the fish were fed to satiation. This was true for all prey densities. No difference in time allocation between substrates existed when prey items were absent.

Significantly more feeding strikes were made on the complex substrate when the prey densities were equal and where the density was greater on the complex substrate (Fig. 2a). As before, when the prey item density was greater on the simple substrate no significant preference was observed. Again, no significant preference for substrate type existed in the treatment where prey items were absent, or when the fish were fed to satiation. The number of prey items consumed did not differ between substrates (Fig. 2b).

Factors Influencing Time Allocation to Substrates

Time allocation data were normalized using an $(x + 1)$ log transformation and analysed using a two-way ANOVA, with prey density and hunger level as the main effects. Prey density had no effect upon substrate time allocation

($F_{3,36} = 1.942$, $P = 0.126$). Fish allocated more time to the complex substrate when hungry ($F_{2,48} = 3.693$, $P = 0.027$). Post hoc analysis revealed that the fish spent more time on the complex substrate when deprived food for 72 h than when satiated (Tukey HSD: $P = 0.036$).

Feeding Strike Rate

Feeding strike rate data were analysed using a two-way ANOVA, with prey density and hunger level as the main effects. The rate of feeding strikes was related to the degree of food deprivation, on both the simple ($F_{2,48} = 3.455$, $P = 0.034$) and the complex ($F_{2,48} = 3.519$, $P < 0.001$) substrates. Post hoc analyses revealed that on the simple substrate the fish had a greater feeding strike rate when deprived food for 72 h than when satiated (Tukey HSD: $P = 0.026$). On the complex substrate the rate of feeding strikes was higher after food deprivation than when the fish were satiated (Tukey HSD: 24 h: $P < 0.001$; 72 h; $P < 0.001$). More strikes occurred when fish were food deprived for 72 h than for 24 h (Tukey HSD: $P = 0.006$).

The feeding strike rate did not vary between prey density treatments on the simple substrate ($F_{2,36} = 0.606$, $P = 0.612$) but did on the complex substrate ($F_{2,36} = 9.632$, $P < 0.001$). Post hoc analyses revealed fewer feeding strikes in the trials where no prey was present than where prey density was equal on both substrates (Tukey HSD: $P < 0.001$), and where it was greater on the complex substrate ($P = 0.001$). There was no difference in feeding strike rates between trials without prey and those where prey density was greater on the simple substrate (Tukey HSD: $P = 0.350$). More strikes occurred in trials where prey was present in equal densities on both substrates than where it was greater on the simple substrate (Tukey HSD: $P = 0.009$), but not where density was greater on the complex substrate ($P = 0.756$). Finally, there was no difference in the feeding strike rate on the complex substrate when it held the greater prey density than when it was greater on the simple substrate (Tukey HSD: $P = 0.122$). The number of prey items detected and consumed by fish did not differ significantly with respect to hunger level ($F_{2,48} = 4.529$, $P = 0.548$) or prey density ($F_{2,36} = 2.873$, $P = 0.477$).

DISCUSSION

Fish showed a significant preference for the structurally complex substrate when hunger was a motivating factor, both when the prey density was constant across both substrate types, and when it was greater in the complex substrate. We interpret this substrate bias as a foraging preference because it existed not only in the form of time allocation, but also in the distribution of feeding strikes directed towards potential prey items, a well-defined element of the active foraging behavioural repertoire of the three-spined stickleback (Gill & Hart 1994).

It is unlikely that this preference for complex substrates arose as a defence against predation. Although the cryptic coloration of the heterogeneous sediment of the complex
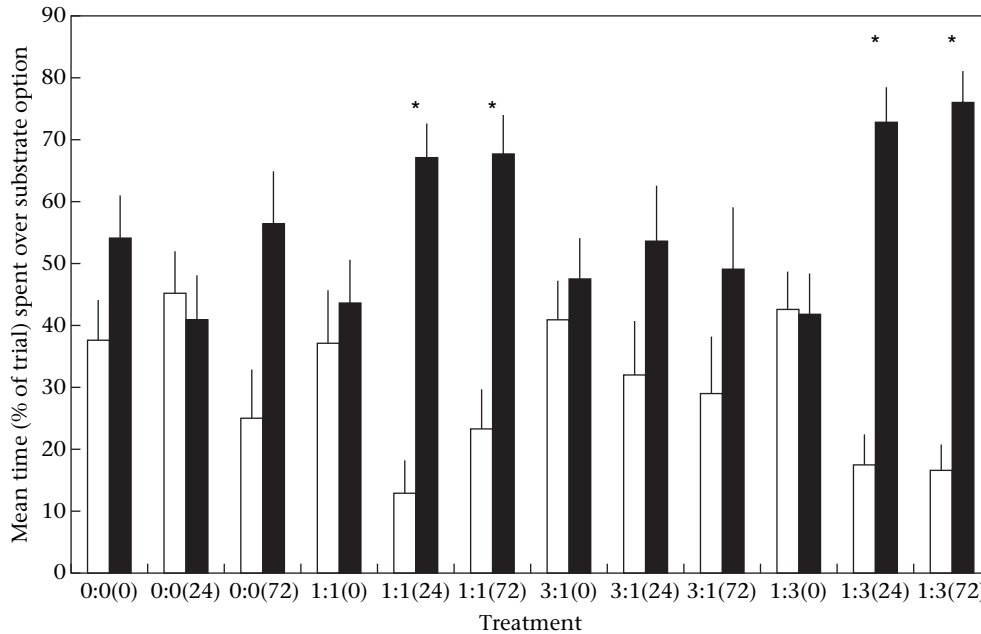
Figure 1. Mean time + SE spent by foraging three-spined sticklebacks on structurally simple (□) and complex (■) substrate types. The category ratios on the X axis refer to the experimental prey density ratio in each trial (simple:complex). 0, 24 and 72 refer to the period of food deprivation, either 0 h (satiated), 24 h or 72 h. Asterisks indicate a significant difference in time allocation to substrate types ($P < 0.05$). Data were normally distributed (Anderson–Darling test), and the proportion of time allocated to one substrate type was compared to an expected null value of 0.5 using a one-sample t test: 0:0(0): $t_{11} = 0.651$, $P = 0.529$; 0:0(24): $t_{11} = -1.213$, $P = 0.251$; 0:0(72): $t_{11} = 0.771$, $P = 0.457$; 1:1(0): $t_{11} = -0.853$, $P = 0.412$; 1:1(24): $t_{11} = 3.117$, $P = 0.010$; 1:1(72): $t_{11} = 2.852$, $P = 0.016$; 3:1(0): $t_{11} = -0.327$, $P = 0.750$; 3:1(24): $t_{11} = 0.435$, $P = 0.672$; 3:1(72): $t_{11} = -0.630$, $P = 0.951$; 1:3(0): $t_{11} = -0.414$, $P = 0.687$; 1:3(24): $t_{11} = 4.000$, $P = 0.002$; 1:3(72): $t_{11} = 5.150$, $P < 0.001$ ($N = 12$ repeats per trial).

substrate probably conferred a measure of visual protection from potential avian predation, it is possible that the topography of the substrate would have offered only limited elevated cover from piscivorous fish. Furthermore, the three-spined stickleback is a forager of open water microhabitats, relying more on spine and armour structure than on the proximity of cover to mediate the threat of predation (Godin & Clark 1997; Hart 2003). In addition, we found no preference in the absence of either reinforcing stimuli, provided by prey, or feeding motivation, in test fish that had been fed to satiation. These factors suggest that finding a refuge was not an influencing factor in the substrate selection process.

Actual prey density alone could not have influenced habitat selection either; if it had, a bias towards the structurally simple substrate should have existed when it held the higher prey density. A nonsignificant allocation of time and rate of striking by test fish between the two substrate options was seen, suggesting that prey density does have some effect, but that the densities examined in this study were not sufficient to bring about changes in foraging preference. Prey items on the simple substrate should have been more visually conspicuous as they tended to rest upon its level, planar surface, whereas those on the topographically uneven complex substrate had a tendency to settle among its constituent particles, where they were less visible. In spite of this, time allocation to the simple substrate did not differ between prey density ratio treatments either, indicating that fish showed no

significant preference for the simple substrate regardless of its prey density relative to other treatments, or to that of the complex substrate.

The increase in the rate of feeding strikes and time allocation seen on the complex substrate as the food deprivation period increased was expected, as previous studies have shown that the rate of prey consumption increases as a function of increasing hunger (Beukema 1968). When the prey density was greater on the complex substrate, when deprived of food for 72 h, and when the level of relative hunger was higher, the fish spent significantly less time on the simple substrate than they did when they were fed to satiation. Under higher hunger regimes feeding is prioritized over other behaviour types, for example shoaling (Krause 1993).

Because the preferences seen in this study did not alter to reflect prey density, it seems likely that they did not arise from either casual or active real-time sampling and appraisal of substrate prey density. Test fish had the opportunity to make a visual and olfactory assessment of the prey density of each substrate option, both while confined in the mesh holding cylinder close to both substrates, and also actively, over the trial. Optimal foraging theory predicts that in the absence of competition or predation risk a forager should select the foraging ground with the greatest prey density or detection rate, yet the three-spined sticklebacks in this study did not.

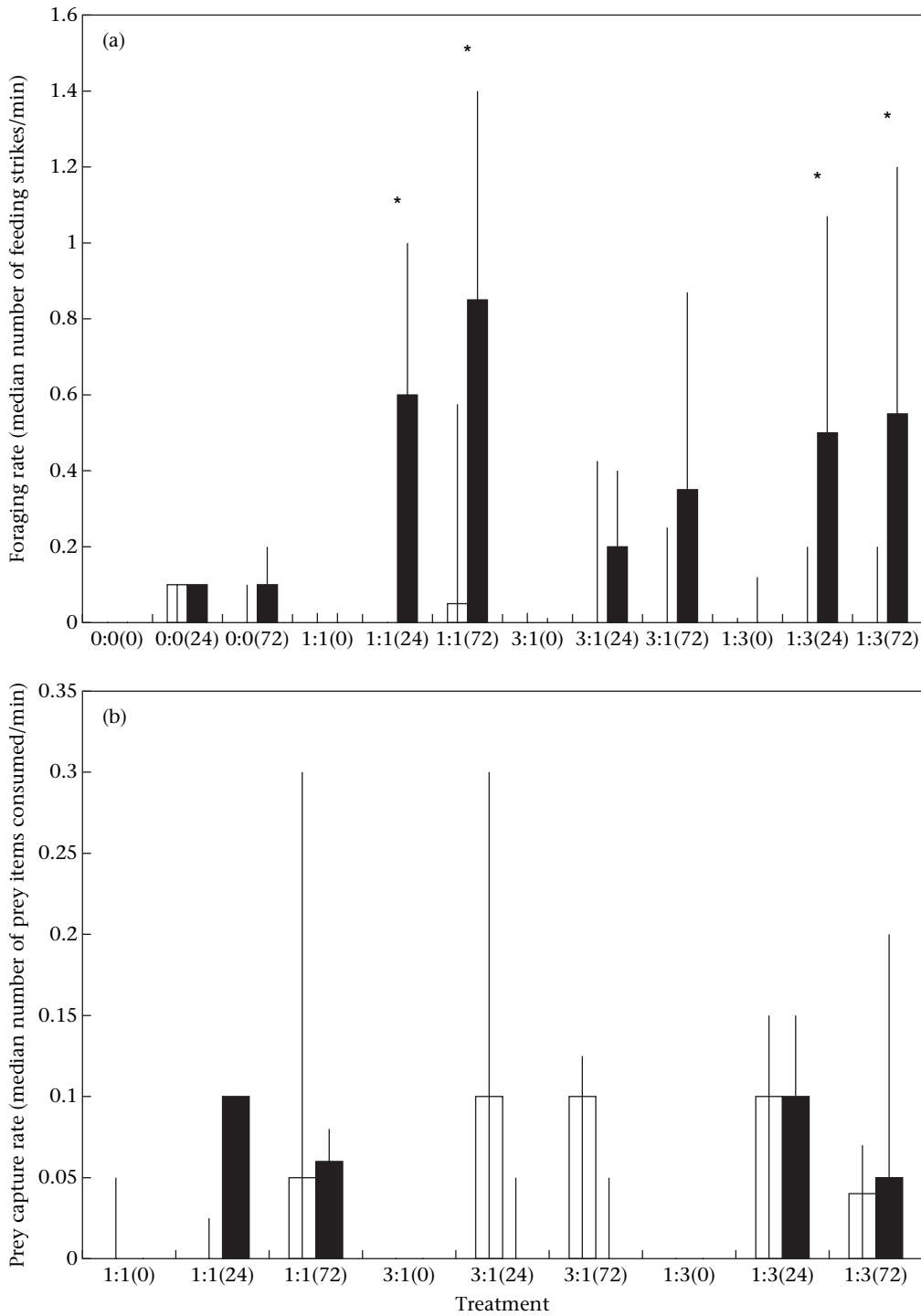We suggest that three-spined sticklebacks favour the complex substrate because it is associated with potentially

Figure 2. The rates of (a) foraging and (b) prey capture $\pm$ quartiles in foraging three-spined sticklebacks over structurally simple ($\square$) and complex ($\blacksquare$) substrates. The category ratios on the X axis refer to the experimental prey density ratio in each trial (simple:complex). 0, 24 and 72 refer to the period of food deprivation, either 0 h (satiated), 24 h or 72 h. Asterisks indicate a significant bias in feeding strike direction between substrate types ($P < 0.05$). Differences in feeding strike and prey capture rates on different substrates were compared using the Mann–Whitney U test (two-tailed). (a) Feeding strike rate ($N_1 = N_2 = 12$ per treatment): 0:0(0): $U = 72$, $P = 1.000$; 0:0(24): $U = 65.5$, $P = 0.682$; 0:0(72): $U = 39$, $P = 0.060$; 1:1(0): $U = 72$, $P = 1.000$; 1:1(24): $U = 18.5$, $P = 0.001$; 1:1(72): $U = 25$, $P = 0.006$; 3:1(0): $U = 66$, $P = 0.755$; 3:1(24): $U = 45$, $P = 0.107$; 3:1(72): $U = 41$, $P = 0.078$; 1:3(0): $U = 72$, $P = 1.000$; 1:3(24): $U = 16.5$, $P = 0.001$; 1:3(72): $U = 14.5$, $P < 0.001$. (b) Prey detection rate ($N_1 = N_2 = 12$ per treatment): 1:1(0): $U = 60$, $P = 0.148$; 1:1(24): $U = 45$, $P = 0.051$; 1:1(72): $U = 46.5$, $P = 0.089$; 3:1(0): $U = 72$, $P = 1.000$; 3:1(24): $U = 58$, $P = 0.287$; 3:1(72): $U = 67.5$, $P = 0.732$; 1:3(0): $U = 72$, $P = 1.000$; 1:3(24): $U = 65$, $P = 0.652$; 1:3(72): $U = 68.5$, $P = 0.821$.

higher relative prey density. Major prey items such as chironomid larvae occur in greater densities in more poorly sorted, heterogeneous sediments in natural systems, where they seek refuge among interparticle voids (De Bisthoven & Gerhardt 2003; Gayraud & Philippe 2003). Alternatively, three-spined sticklebacks may preferentially forage on complex substrates not because they harbour more prey, but because fish can forage more effectively upon them. The nature of this substrate may make prey easier to detect or capture, perhaps because they are forced to use interparticle voids which are easier for certain benthic predators to enter or excavate than consolidated silts or sands. This is speculative, however, and we found no difference in prey capture rate between substrates. Three-spined sticklebacks disproportionately favour patchily distributed food resources, preferentially feeding upon spatially and temporally variable aggregations of prey over those that are widely dispersed (Jakobsen & Johnsen 1987; Hart & Gill 1994). The preferences seen in this study are consistent with feeding strategies that are good for exploiting patches, since spatial variability in substrate architecture facilitates such uneven distributions of refugia-seeking macroinvertebrates.

The preferences seen here may be the result of a search strategy, based on experience, and an inherent anticipation of higher prey density on complex substrates. Searching strategies based upon experiences of food distribution exist in some other fish species. In a study by Ryer & Olla (1995), walleye pollock, *Theragra chalcogramma*, that had fed upon patchily distributed food were introduced to a dispersed-food regime. Instead of adopting the feeding strategies associated with conditioned dispersed-food foragers of the same species, they persisted in the use of patch foraging tactics, that is, group foraging with local enhancement. This suggests that the usually plastic foraging repertoires of many fish species are capable of incorporating a degree of more rigid, experience-based searching behaviour.

Useful further work could examine the relative importance of experience on microhabitat selection in foraging fish. Coolen et al. (2003) found that three-spined sticklebacks were unable to assess patch quality by monitoring conspecific public information, but that they were able to determine patch location using visual cues generated by those already feeding. If experience-based searching is important for foraging decision making, as our results suggest, then substrate complexity may be used as a proxy indicator for potential prey density. The ability to recall experiences of habitat type in a predator–prey context should be evolutionarily advantageous to a foraging fish.

Acknowledgments

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