Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues

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Summary

In aquatic habitats turbidity can affect the foraging efficiency of visual predators, directly influencing their capacity to detect prey. In a laboratory study we tested the effect of different loads of suspended sediment upon the foraging rates of threespine sticklebacks (*Gasterosteus aculeatus*). We compared the foraging rates of fish under a series of different turbidity treatments, testing fish originating from four habitats within a single drainage basin that differed in a number of environmental parameters including turbidity. Although we found habitat specific differences in foraging rates, these did not correspond to local turbidity levels. The findings of a follow up experiment revealed habitat-specific variation in boldness, which may be indirecly linked to the observed differences in foraging rate. The main finding of our study was that turbidity alone had no impact upon their prey capture rates, but that high turbidity in combination with saturation with prey odour extract caused prey capture rates to fall significantly. This suggests that olfactory cues can be more important than visual cues in determining foraging performance in this species, potentially influencing how they cope with naturally occurring periods of turbidity, and how they adapt to human-induced eutrophication.

Keywords: eutrophication, *gasterosteus aculeatus*, habitat complexity, predator-prey interactions.

Introduction

Habitat structure can directly influence the rate at which predators detect and capture prey, affecting their foraging efficiency and ultimately their fitness.

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In aquatic habitats turbidity can be a major contributor to effective structural complexity, influencing the attenuation of light and, therefore, the effectiveness of vision in navigation and foraging tasks. As a consequence of changing turbidity, predator-prey interactions can be dramatically altered (Utne-Palm, 2002) and visual predators adapted to foraging in low turbidity habitats can suffer reduced foraging efficiency as turbidity increases (Sweka & Hartman, 2001, 2003)

Human activity can have substantial effects upon turbidity in aquatic systems, by promoting eutrophication processes or by increasing the amount of suspended sediment entering rivers, often with negative ecological consequences (Davies-Colley & Smith, 2001; Smith, 2003). Accordingly, there is much research interest in quantifying and predicting the behavioural and ecological responses of organisms to increasing turbidity (Utne-Palm, 2002).

In the first of two laboratory experiments we sought to determine the effects of increasing turbidity upon the foraging rates of threespine sticklebacks (*Gasterosteus aculeatus*). Sticklebacks, in common with many freshwater fishes, have been suggested to be primarily visual foragers (Wootton, 1976, 1984) and should, therefore, be expected to forage with less efficiency under increasingly turbid conditions. Despite this longstanding assumption, a recent study revealed that although the distance at which sticklebacks reacted to prey did indeed decrease with increasing turbidity, their overall rates of attack and prey consumption remained unchanged (Quesenberry et al., 2007). These authors suggested that sticklebacks might maintain their prey capture by relying upon other sensory modes, such as olfaction. A similar suggestion was put forward by Mussen & Peeke (2001) who described increased foraging behaviour in sticklebacks presented with prey cues in total darkness. In our first experiment we set out to explicitly test this possibility, by comparing the foraging rates of sticklebacks not only under conditions of increasing turbidity, but also in the absence and in the presence of excess prey chemical cues. In addition to this we sought to determine whether intrapopulation variation with respect to foraging efficiency occurred, by comparing fish from four habitat types lying within a single drainage network. Qualitative measurements revealed that these habitats differed from one another in their turbidity, while previous studies have shown that fish from this drainage network exhibit significant habitat-specific variation in their morphology and anti-predatory behaviour (Webster et al., data not shown). Given this, it is not unreasonable to expect that members of this population might

also exhibit habitat-specific variation in their foraging responses to increasing turbidity. We tested three predictions: (1) that prey capture rates would not decline as turbidity increased (this is supported by the recent Quesenberry et al. (2007) finding), (2) that saturation with excess prey chemical cues combined with high turbidity levels would decrease prey capture rates by preventing fish from using either visual or chemical cues to locate prey and (3) that we would observe intra-population variation in foraging rates. We elaborated upon the final prediction with two alternative, but not mutually incompatible further predictions: firstly that sticklebacks from more turbid habitats would forage more efficiently under increasingly turbid conditions, and secondly that habitat-specific differences in foraging rate would be underpinned by habitat-specific differences in boldness. Boldness, the threshold of risk incurred by individuals when undertaking certain behaviours such as foraging, exploring or competing (Wilson et al., 1994; Wilson, 1998; Sih et al., 2004), has been shown to vary both between and within populations as a function of factors such as predation risk (Brown et al., 2005a,b). For this reason we conducted a second experiment in which we sought to determine whether sticklebacks from the four habitat types differed in their latency to begin foraging in the novel surroundings of a test tank, and to resume foraging following a simulated predator attack.

Materials and methods

Fish collection and housing

We collected sub-adult (age 0+) threespine sticklebacks (33-35 mm standard length) during September and October 2005 from each of four distinct but interconnected habitats within the drainage of the Great Eau in eastern England: the river channel, connecting man-made drainage ditches, the coastal saltmarsh and the estuary. These habitats differ markedly in a number of environmental parameters, including their turbidity (Ward et al., 2007; Table 1). In the laboratory the fish were assigned to several 25-litre housing tanks at a density of 20 fish per tank. Fish from different habitats were housed separately. The light: dark regime was held at 12:12 and the temperature at 10°C for the duration of the study. The fish were fed daily with chopped frozen bloodworms. They were held under these conditions for five weeks before the experiments began.

Table 1. Variation in environmental parameters between the four habitat types. Salinity and turbidity were measured monthly between May and November 2005 when the local population densities of sticklebacks were greatest. The values given below represent the minimum and maximum values recorded during this period. Turbidity was measured using a black and white marker strip similar to a Secchi disc (Cole, 1994) to gauge the visibility range to the nearest 5 cm. Salinity was measured using a specific gravity meter.

	Ditch	River	Saltmarsh	Estuary
Maximum channel width (m)	2	10	300×30[a]	20
Maximum depth (m)	0.6	3	1.2	6
Maximum flow rate (m/s)	0.1	0.3	None	0.3
Turbidity: visual range (cm)	10-50	150-300	100	5-30
Range in Salinity (specific gravity)	1.006-1.014[b]	1.00	1.022-1.035[b]	1.000-1.024[c]
Predatory fishes	Absent	Present	Absent	Present at low tide only
Predatory birds	Present	Present	Present	Present

[a] Maximum surface area.

[b] Seasonal variation, determined by rates of precipitation and evaporation.

[c] Determined by tidal cycle.

Part 1. The effects of turbidity and prey odour cue saturation upon foraging rate

We performed four turbidity treatments, by suspending known quantities of inert clay particles (diameter > 2 μm, manufactured by Boal, Birmingham, UK) in the water of the test tank. Pilot tests revealed that clay particles remained in suspension for up to 5 h, much longer than our 10-min trial duration. We used a black and white marker strip similar to a Secchi disc (Cole, 1994) to gauge the visibility range of a human observer within the tanks (we make no inferences about the visibility range of the test fish). Our high turbidity treatment aimed to approximately replicate the highest level of turbidity seen in the drainage network that the fish were collected from (see Table 1). The four treatments were (1) a clear water treatment with no suspended clay particles present, with visibility extending to 41 cm, the maximum length of the test tank; (2) a low turbidity treatment, achieved by adding 0.06 g/l of clay particles. In these trials visibility extended to 12 ± 0.4 cm; (3) a high turbidity treatment, achieved by adding 0.12 g/l of clay particles. Here, visibility extended to 4 ± 1.1 cm. Finally (4), a high

turbidity treatment as previously, in which prey odour cues were also present. We crushed 3 g (wet mass) of frozen bloodworms in 100 ml of tank water, filtered out the remaining solid material and mixed 30 ml of the resulting extract into the water of the experiment tank prior to the introduction of the test fish. Our aim was to saturate the chemical cues that the fish may have been using to detect prey, and in doing so to separate any combined effects of vision and chemosensory ability.

Fish were selected at random from their housing tanks and moved to 14-litre tanks where they were housed in pairs for 24 h. Within each treatment no two fish were drawn from the same housing tank. During this period they were not fed in order to standardise hunger levels and generate motivation to forage. Fish were tested individually in an experimental tank with a base area measuring 41 $\times$ 27 cm and with a water depth of 15 cm. The test tank contained a fine sand substrate (particle diameter 1-2 mm) with a uniform depth of 1 cm. The sand particles were too heavy to become suspended and did not affect turbidity. The sides of the tank were covered in black plastic screening, preventing light from entering via the sides of the tank. The tank was illuminated from above by a single 750-mm-long, 60 W white light striplight positioned centrally, 60 cm above the water surface. The striplight generated approximately 900 lux of illumination, which falls within the natural range of light intensities occurring during daylight. A perforated clear Perspex holding unit (11.5 cm diameter, 22 cm tall) was placed in the centre of the tank. This held the fish prior to the beginning of the experiment, allowing it to acclimatise and assimilate visual and chemical cues within the tank. Ten 3-mm-long sections of bloodworm were distributed haphazardly across the substrate of the test tank 5 min before the fish was added to the holding unit. The fish was then introduced into the holding unit and allowed to acclimatise for a further 5 min before the holding unit was raised and removed, releasing the fish and beginning the trial. The trial ran for 10 min and immediately following the end of the trial the fish was removed and the remaining prey were sieved and counted. Following each trial the prey, water and substrate materials were replaced. We performed 18 replicates for each of the four habitat groups per treatment and no fish was tested more than once.

The data set satisfied the requirements of parametric analysis. The effects of habitat of origin and the experimental turbidity treatment upon foraging rate were assessed using a two-way ANOVA with Tukey's HSD post-hoc analyses.

Part 2. Boldness: foraging under simulated predation risk

Foraging animals are usually compelled to cease feeding and seek refuge or take evasive action when predators attack. They face a trade-off regarding when to resume feeding following a failed attack; too soon and the predator may still be close by, too late and they miss out on potential foraging opportunities. In this test we measured the latency of sticklebacks from each of the four habitats to resume foraging following a disturbance intended to simulate a failed predator attack. Predatory fish (northern pike, *Esox lucius* and Eurasian perch, *Perca fluviatilis*) are not present in all of the four habitat types (Table 1); however, piscivorous birds (blackheaded gulls, *Larus ridibundus*, grey herons, *Ardea cinerea*, kingfishers, *Alcedo atthis* and little egrets, *Egretta garzetta*) occur throughout the drainage and it is likely that they prey upon sticklebacks in all of the habitat types.

We used a test tank and procedure adapted from that described by Ward et al. (2004a) and Webster et al. (2007). Two 12 × 12 × 30 cm tall glass containers were placed next to each other at the end of a 60 × 30 × 30 cm tank. The container on the left held the focal fish, which was able to see both into the adjacent container and also into the main tank. The main tank contained abundant artificial vegetation, intended to create the illusion of refuge in order to minimise stress in the test fish. Both the main tank and the containers contained a 2 cm layer of 5 mm gravel and were filled with clear water to a depth of 27 cm. Ten 3 mm long sections of bloodworm were placed across the bottom of the container on the left 5 min before the fish was added. A 100 g weight was suspended 20 cm above the container on the right. The fish was added to the container on the left and allowed to begin to feed. After the fish had consumed one prey item the weight was released and allowed to drop into the container on the right. This caused a disturbance that was sufficient to induce a freezing response in all of the tested fish. In each trial we recorded the latency of the fish to begin foraging, and to resume foraging following the simulated attack. Following each trial the water and prey were replaced in the container on the left before the next trial was carried out. We performed 20 replicates for each of the four habitat groups and no fish was tested more than once.

The data set satisfied the requirements of parametric analysis. For each habitat group we determined the mean latency to begin foraging, and to resume foraging. We compared each of these two measurements in turn

between the four habitat groups using one-way ANOVAs and Tukey post-hoc analyses.

Results

Part 1. The effects of turbidity and prey odour cue saturation upon foraging rate

A two-way ANOVA revealed significant effects of both habitat of origin ($F_{(3,15)} = 12.77$, $p < 0.001$), and the experimental turbidity treatment ($F_{(3,15)} = 21.09$, $p < 0.001$) upon fish foraging rates, whilst the interaction between these variables had no effect ($F_{(3,15)} = 0.79$, $p = 0.62$, Figure 1). Specifically, Tukey's HSD post-hoc analyses revealed that fish from the river

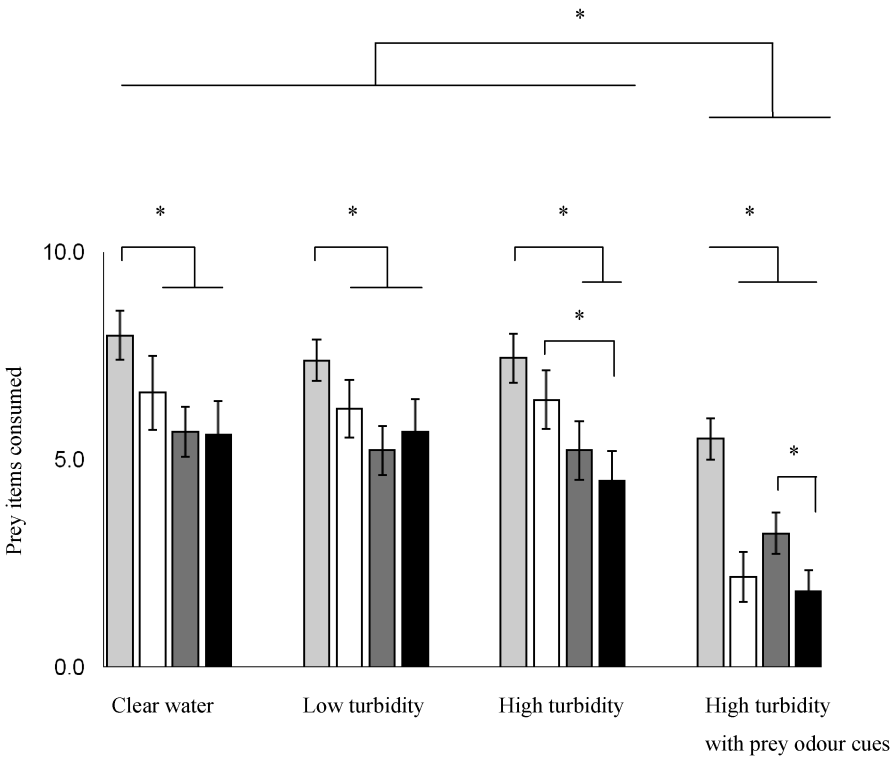

Figure 1. The foraging rates (mean number of prey consumed in 10 min ± standard error) of fish from the four habitat types. White bars represent fish from the ditch, light grey bars from the river, dark grey bars from the saltmarsh and black bars from the estuary. $^{*}p < 0.05$.

habitat captured more prey than did fish from any other habitat ($p < 0.001$ in all comparisons within each turbidity treatment). Fish from all of the habitats consumed fewer prey in the trials where turbidity was high and excess prey odour cues were present compared to trials in which prey odour cues were at natural levels ($p < 0.001$ in all comparisons within habitat of origin). Increasing turbidity alone, in the absence of excess prey odour cues, appeared to have no effect upon fish foraging rates.

Part 2. Boldness: foraging under simulated predation risk

A one-way ANOVA revealed a non-significant trend for fish from the ditch to take longer than fish from the other habitats to begin feeding initially ($F_{(3,76)} = 0.98$, $p = 0.08$, Figure 2). More strikingly, fish from this habitat took significantly longer to resume feeding following the simulated predator attack ($F_{(3,76)} = 3.81$, $p = 0.011$) than fish from either the river, the saltmarsh or the estuary (Tukey's HSD post-hoc analyses: $p = 0.012$, $p = 0.048$ and $p = 0.050$, respectively; Figure 2).

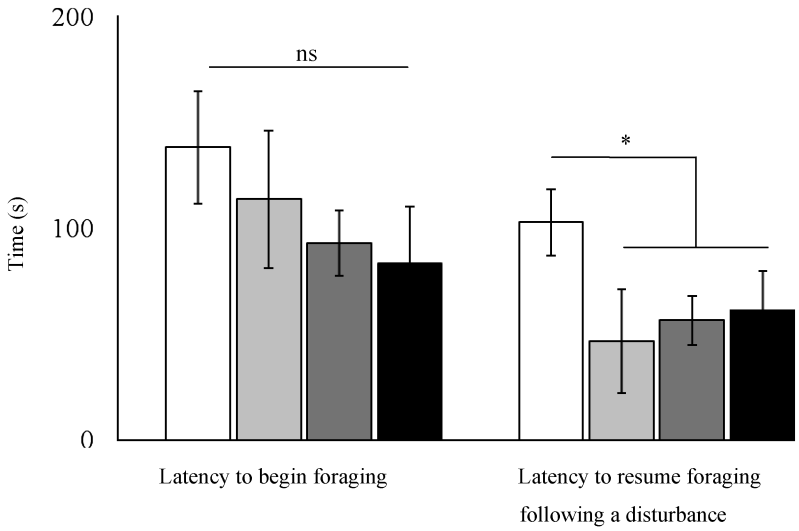

Figure 2. The latency (mean in s ± standard error) of fish to begin feeding in a novel habitat, and to resume foraging following a simulated predator attack. White bars represent fish from the ditch, light grey bars from the river, dark grey bars from the saltmarsh and black bars from the estuary. $^{*}p < 0.05$.

Discussion

As initially predicted, and in accordance with the findings of Quesenberry et al. (2007) we saw no effect of increasing turbidity upon the prey capture rates of threespine sticklebacks. Instead, prey capture rates decreased significantly only when the tank water was saturated with excess prey odour cues in the second high turbidity treatment. This suggests that the sticklebacks were relying upon chemical cues to a greater extent than visual cues to detect prey. Neurological studies have revealed that members of the Gasterosteidae (which includes the threespine stickleback) are microsmatic, possessing relatively poorly developed olfactory sense organs compared to other fish families (Hara, 1975). As a consequence, sticklebacks have generally been supposed to be primarily visual foragers, making little use of olfactory cues when foraging (Wootton, 1976, 1984). Visual cues, when they are available, are clearly important in the foraging behaviour in this species; sticklebacks use them not only to detect prey (Ohguchi, 1978), but also in collecting social information about the foraging behaviour of others (Webster & Hart, 2006). The findings of this study however reveal that the chemosensory detection of prey is a more important component of the foraging strategy of this species than may have been previously thought. This is significant since the threespine stickleback is a well-established and widely used model species in the study of many aspects of behavioural ecology. Our findings, therefore, highlight the need for caution when designing experiments in which sticklebacks are used as a model species to investigate phenomena such as spatial learning and social information use, in order to ensure that this potentially confounding factor is adequately controlled for. Indeed, when viewed along with the findings of other studies, it is clear that the detection of chemical cues underpins many day-to-day aspects of stickleback behaviour including kin recognition (Frommen & Bakker, 2006), social organisation (Ward et al., 2004b, 2005, 2007; Webster et al., in press) and mate choice (Milinski et al., 2005; Rafferty & Boughman, 2006).

Searching for prey using primarily olfactory cues allows fish to exploit periodically turbid habitats, such as those subject to seasonal algal blooms or floods. It may also allow species vulnerable to predation to forage during periods of low light intensity such as at dawn or dusk when risk of attack from other visual predators is potentially lower. Furthermore, there is evidence to suggest that elevated turbidity might to an extent actually benefit fish that

are vulnerable to predation, by concealing them from their own predators. Lehtiniemi et al. (2005) reported that juvenile Northern pike foraging in the presence of predator cues displayed less anti-predator behaviour when in turbid water than they did in clear water. Meager et al. (2006) found that intermediate levels of turbidity increased the likelihood of juvenile Atlantic cod (*Gadus morhua*) escaping from a simulated slow swimming predator relative to clear water conditions, but found that cod were less likely to escape when turbidity was higher. These authors also found that the likelihood of escaping from a fast swimming predator decreased dramatically as turbidity increased. It seems that the effects of increasing turbidity upon predator-prey interactions are complex, and dependent upon a number of factors including the properties of the suspended particles, predator attack capabilities, prey behavioural strategies, and the sensory modes used by both parties (Utne-Palm, 2002).

Another finding of our study was that of habitat-specific differences in prey capture rates. Interestingly, it was sticklebacks from the river, rather than the more turbid estuary that captured more prey. The reasons for this finding are unclear, since we might intuitively expect that fish from highly turbid habitats should be better adapted at foraging under such conditions. It is possible that variation in turbidity within and between the habitats is substantial, and that fish in some or all habitat types are adapted to enduring a range of conditions. We performed only a limited evaluation of the variation in turbidity within each habitat, collecting data for only part of one year. Our sample may, therefore, have been insufficient to capture the full range of this variation.

An alternative explanation is that these differences are related to variation in the boldness of the fish from the four habitat types. Our second experiment directly tested this possibility, though its findings only indirectly support the notion that boldness differences might underlie the observed variation in foraging rates between the fish from the four habitats. The second experiment did indeed reveal habitat-specific variation in boldness, however we saw no tendency for the river fish to behave significantly more boldly than those from the other habitats. Rather, we found that fish from the ditch took significantly longer to resume foraging following a disturbance than those from the other three habitats. Fish from the ditch also exhibited a marginally non-significant tendency to take longer to begin feeding initially. Intrapopulation

variation in boldness might reflect habitat specific variation in predation pressure, which might in turn be underpinned by genetic differentiation between fish from different habitats, or by environmentally induced phenotypic plasticity. Patterns of intrapopulation variation in boldness have been described within several wild populations of the Poecilid fish *Brachyraphis episcopi*, where fish occupy both low and high predation sites within the same river channel (Brown et al., 2005a,b). We did not quantify predation pressure with each of our studied habitats, however we do know that predatory fish are absent from the ditch and saltmarsh habitats, but are present in the river and in the estuary. Predation by piscivorous birds, which are found throughout the drainage of the Great Eau, might also be more severe in some habitats than in others. Clearly, further research is required in order to determine the source of the observed behavioural variation.

While the observed variation in boldness and foraging rate seen in our study may have arisen in response to any one or a combination of different factors, the important aspect, from the point of view of this study, is that different subsets of a population can differ from one another in their behavioural responses to common environmental conditions. Our findings suggest that the short term foraging success of species such as sticklebacks, that forage using prey odour cues in addition to visual cues, is unlikely to be impaired by heightened turbidity. Similar findings have been reported in other species that forage using prey odour cues such as Atlantic cod (Meager et al., 2005). In other species however, compensatory foraging strategies are required in order to maintain a constant rate of prey intake. This can be achieved by increasing the proportion of time spent foraging, at the cost of reducing investment in other activities such as reproduction, or by increasing swimming speed in order to enhance prey encounter rates (Sweka & Hartman, 2001; Granqvist & Mattila, 2004). In undertaking such compensatory foraging behaviour individuals are likely to expend more energy per prey item captured, reducing foraging efficiency (Sweka & Hartman, 2001). Furthermore, by becoming more active and by spending longer foraging, they may increase their own risk of being preyed upon, because their potential encounter rate with predators is greater. Such compensatory foraging behaviour may, therefore, carry negative consequences for long term fitness. In species which pursue compensatory strategies such as these, and which also show habitat specific variation in behaviour, such as boldness or foraging rate as seen in our study, then it is possible that the different constituent groups of

the population will respond differently to the pressures exerted by increasing turbidity. It is unclear for example, whether the relative boldness of one habitat group will impact upon the degree to which they incur risk when engaging compensatory foraging behaviour and, therefore, whether long term episodes turbidity acting across a population will lead to habitat specific asymmetry in fitness costs. Further work in this area would be useful.

Increasing turbidity, arising from eutrophication processes and channel-bound suspended sediment resulting from erosion represents a major threat to biodiversity in many aquatic ecosystems (Davies-Colley & Smith, 2001; Smith, 2003). In this study we have only focussed upon one aspect of behavioural ecology, individual foraging behaviour. There is substantial evidence that turbidity can influence other aspects of behaviour that depend upon visual cues too, as recent work demonstrating the disruptive impacts of turbidity upon male displays and sexual selection in sticklebacks has demonstrated (Candolin et al., 2007; Engstrom-Öst & Candolin, 2007). Useful further research could focus on the potential fitness costs to animals of living in altered environments by drawing together the various effects of such change upon different aspects of their behavioural ecology and life histories. Doing so could further our understanding of the consequences of both natural and human induced turbidity at the local, population and community levels.

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