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ORIGINAL PAPER

Eutrophication alters social preferences in three-spined sticklebacks (*Gasterosteus aculeatus*)

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Abstract Algae blooms, which can be caused by eutrophication, drastically influence the ecology and behaviour of aquatic organisms. Such impact is often demonstrated in the context of mate choice and predator–prey interactions. In contrast, the influence of increased turbidity on social behaviour is less well understood, although it may have strong influence, at both the level of the individual and the population. We aimed to address this gap in our knowledge by using the well-described preference of three-spined sticklebacks (*Gasterosteus aculeatus*) to shoal with the larger of two shoals as model behaviour. In our experiments focal fish had the choice between two shoals of different sizes, either in clear or in turbid water containing green algae. Fish in clear water spent significantly more time near the larger shoal, while fish in algae water showed no significant preferences. Furthermore, fish tested in clear water changed more often between the shoals than fish tested in algae water. These results indicate that eutrophication-induced algae blooms have the potential to alter social decisions of sticklebacks. Such changes of social decisions do not only influence the behaviour of individuals, furthermore it might influence entire populations. This might eventually lead to changes of the structure of the social system.

Keywords Shoaling · Schooling · Algae blooms · Group living · Fish · Aquatic ecosystems

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Introduction

Human interference not only alters the appearance of natural landscapes, but they also have secondary effects on the behaviour and development of the animals exposed to these changes (Darimont et al. 2009; Tuomainen and Candolin 2011). In aquatic systems, human impacts often result in increased eutrophication through increased nutrient input (Smith 2003; van der Sluijs et al. 2011). Such inflow of nutrients, especially phosphorus and nitrogen, increases algae growth and can change the algae species composition as well as the turbidity of the water (Candolin 2009; van der Sluijs et al. 2011). Animals facing such increased turbidity may respond to these new environments through new behavioural patterns. Cues to identify mating partners could be hindered, influencing the expression of mate preferences based on these cues (Seehausen et al. 1997; Candolin 2009; Sundin et al. 2010). As well as affecting communication between mates, eutrophication can also have broad implications on the ecosystem networks (Utne-Palm 2002). For example, turbidity might lead to an increased growth rate in some species (e.g. Stuart and Drawbridge 2011 and citations therein), alter habitat preferences (Meager and Utne-Palm 2008) or influence prey recognition and therefore the behaviour of the predators as well as their prey (Granqvist and Mattila 2004; Meager and Batty 2007; Salonen et al. 2009).

While there are a growing number of studies focussing on the influence of eutrophication-induced turbidity on mate choice and predator–prey interaction, studies focussing on the consequences of increased turbidity on social behaviours are rather scarce (but see Franck et al. 2001). Yet, by altering social preferences, changes in turbidity might influence disease transmission, anti-predator behaviour or social learning. For example, it is known that three-spined sticklebacks rely on different food patch information cues if tested alone or with conspecifics (Webster and Hart 2006).

Furthermore, in a field study, Krause et al. (2000a) found that fish shoals are assorted by active choice of individuals, indicating that individual behaviour is altered by their social environment under natural conditions. Thus, environmentally induced changes in social behaviours could have strong consequences both on the individual as well as at the population level.

In the current study, we investigated how changes in turbidity caused by algae blooms influence social preferences of three-spined sticklebacks (*Gasterosteus aculeatus*). Three-spined sticklebacks occur in shallow freshwater and marine habitats, which are strongly affected by eutrophication and algae blooms (Candolin 2009). Increased nutrient input has been shown to lead to a reduction of stickleback biomass and even to the extinction of whole populations (Moran et al. 2010). Furthermore, several studies demonstrated an influence of increased turbidity on the sexual behaviour of sticklebacks (see Candolin 2009 and citations therein). On the other hand, the foraging efficiency of three-spined sticklebacks was not affected by turbidity created with suspended clay (Webster et al. 2007), indicating that fish might use olfactory cues where visual prey detection is difficult (Johannesen et al. 2012). Outside the breeding season, sticklebacks form mixed-sex shoals (Wootton 1976); the composition of which is influenced by a range of factors. For example, sticklebacks prefer to shoal with similar sized fish (Ranta et al. 1992; Barber 2003) and those with low parasite loads (Barber et al. 1995; Barber 2003). Furthermore, several studies showed that satiated fish preferred to spend more time next to larger shoals (Krause 1993), with conspecifics (Barber et al. 1995) or familiar fish (Frommen et al. 2007b). Shoal characteristics are often perceived visually (e.g. Ranta et al. 1992; Modarressie et al. 2006; Frommen et al. 2009; Harcourt et al. 2009), leaving this mode of perception vulnerable to disruptions through increased turbidity. Still, little is known about the effects of increased turbidity on stickleback's shoaling behaviours. We aimed to fill this gap by using the well-described preference of sticklebacks for the larger of two shoals (e.g. Keenleyside 1955; Krause 1993; Tegeder and Krause 1995; Barber and Wright 2001; Frommen et al. 2009) as a research model.

In our experiments, we gave three-spined sticklebacks the choice to shoal either with a group of six or of three individuals. Preferences of each fish were measured twice, once in clear water and once in turbid water, caused by green algae. As increased turbidity disturbs visual perception of the focal fish, we predicted that test fish will no longer discriminate between the two shoals. Furthermore, as assessment of predation risk and the perception of predators should be more difficult in algae water, we predicted a general increase in anti-predator behaviour, i.e. an increased overall time spent shoaling and a reduced willingness to

switch between shoals. On the other hand, prey capture rates by predators are often lower in turbid water (Utne-Palm 2002) and turbid habitats may serve as refuge (Engström-Öst et al. 2009). Thus, anti-predator benefits of being a member of a large group might be lower under turbid conditions which might result in losing the preference for a particular shoal.

Methods

Study species

We used F1 offspring generation of wild caught three-spined sticklebacks. Parental fish were caught during their spring migration in 2010 on the Island of Texel, The Netherlands, and brought to the Konrad Lorenz Institute for Ethology, Vienna, Austria. F1 fish were obtained by mating 50 pairs of adults. Each adult was used only once. Offspring were kept in large (approx. 1,000 l) outdoor tanks. All fish were fed daily in excess with frozen mosquito larvae. In the experiments, sub-adult fish (aged approx. 6 months) were used. Prior to the first trial, 30 individuals were haphazardly chosen as test fish and transferred to an indoor aquarium (100×40×50 cm, $l \times w \times h$) to acclimatize them to the laboratory surroundings. As three-spined sticklebacks form mixed-sex shoals outside the breeding season and sexes of sub-adults are difficult to assess without dissecting them, we did not control for the influence of sex on shoaling decisions (c.f. Tegeder and Krause 1995; Barber and Wright 2001; Frommen et al. 2007a). However, such influences are and to the best of our knowledge not described for non-reproductive three-spined sticklebacks.

Experimental design

Experiments were carried out in September and October 2010. To measure shoaling preferences, we used a standard two-choice design (Wright and Krause 2006). The experimental aquarium (80×40×40 cm) was divided into three sections, two stimulus compartments at the left and right end (20×40×40 cm) and one choice compartment in the middle (40×40×40 cm). Perforated clear Plexiglas was used as partitions, allowing both visual and olfactory contact. Preference zones of 10 cm (approx. three body length of the test fish; Pitcher and Parrish 1993) were later marked on the computer screen next to each stimulus compartment. The aquarium was illuminated by a fluorescent tube (30 W). Interactions with the environment were prevented by a black curtain tightened around the aquarium.

In total, 30 paired trials were performed. For each trial, nine fish were haphazardly caught from the outside tanks and assigned to either a large shoal containing six

individuals or a small shoal containing three individuals. Test fish and stimulus fish were obtained from different tanks to avoid confounding effects of familiarity or kinship (Frommen et al. 2007c). As hunger level is known to influence shoal size preferences in sticklebacks (Krause 1993), all fish were fed to satiation 1 h before testing. Each test fish was tested twice, once in turbid conditions and once in clear water. The order of clear water and algae water altered between the trial pairs to avoid sequence effects. In half the trials, the fish therefore experienced clear water first followed by algae water second, whereas in the other half of the trials, the fish underwent the algae water treatment before the clear water treatment. The interval between the two treatments was approximately 30 min. For the clear water treatment, we filled the tank to a level of 20 cm with 1-day-old tap water. For the algae treatment, we filled the tank to a level of 20 cm with a mix of tap water and green algae grown in 20 outdoor tanks to resemble natural conditions. To obtain the same amount of turbidity in all trials, three Secchi discs (5 cm in diameter) were attached to the back wall of each compartment. We filled the experimental aquarium with a mixture of tap water and algae water until the Secchi discs were not visible anymore, thus achieving a Secchi depth of 40 cm. According to Carlson (1977), this equals a concentration of 56 mg/m³ chlorophyll in the water body, resembling the conditions of a hypertrophic lake. Stimulus shoals were placed into the left and right stimulus compartments; the side of the larger shoal was changed between trials. Shoals were allowed to acclimatize for 5 min. Afterwards, the test fish was put in the middle of the choice compartment. The trials started after the test fish started to swim and crossed a middle line dividing the test compartment in two equal-sized halves for the first time, maximising the chances that the fish entered both preference zones. The movements of the test fish were recorded for 20 min using a web cam connected to a computer outside the curtain. Afterwards, all fish were caught and placed in separate aquaria. The water in the test aquarium was replaced with water of the opposite type and trials were repeated. After testing, the standard length of all fish was measured to the nearest 0.5 mm. Fish of large and small shoal pairs did not differ significantly in mean standard length (mean±SD small, 2.39±0.23 cm; large, 2.37±0.22 cm; paired *t* test, *N*=30, *t*=0.716, *p*=0.479). Finally, all fish were placed back to the housing tank. To reduce the overall number of stimulus fish, some of them were used more than once; however, never on the same day or in the same combination of individuals.

Analyses

We measured the time the test fish spent in the respective choice zones for 20 min using Observer XT[®]. From the

absolute time values, we calculated a preference index by subtracting the time spent near the small shoal from the time spent near the large shoal (hereafter referred to as PI). Thus, positive values indicate a preference for the larger shoal. Furthermore, we counted how often the test fish switched between choice zones (that is leaving one choice zone and entering the other) and we calculated the overall time spent shoaling by adding the time spent in both choice zones. Finally, we divided the PI by the total time spent shoaling to correct for possible differences in the overall willingness to shoal (referred as NPI). The observing person was naïve concerning the position of the respective shoals. As most data were not normally distributed according to Kolmogorov–Smirnov tests with Lilliefors correction, non-parametric statistics were conducted using SPSS 17. Test probabilities are two-tailed throughout.

Results

Test fish of both experimental conditions spent most of their time in the preference zones (Fig. 1a). Both preference indices (PI and NPI) of fish tested in clear water differed significantly from the ones of fish tested in algae water (PI: Wilcoxon test, *N*=30, *Z*=−3.240, *p*=0.001, Fig. 1b; NPI: Wilcoxon test, *N*=30, *Z*=−3.135, *p*=0.002). In clear water, fish stayed near the larger shoal significantly longer (absolute values: Wilcoxon test, *N*=30, *Z*=−4.515, *p*=0.001; relative values: Wilcoxon test, *N*=30, *Z*=−4.746, *p*=0.001), while in algae water, they showed no preference for either of the sides (absolute values: Wilcoxon test, *N*=30, *Z*=−0.237, *p*=0.813; relative values: Wilcoxon test, *N*=30, *Z*=−0.739, *p*=0.460). Fish tested in clear water changed between choice zones significantly more often (Wilcoxon test; *N*=30, *Z*=−2.741, *p*=0.006, Fig. 1c). However, the test fish did not significantly differ in their total amount of time spent shoaling in the two different treatments (Wilcoxon test, *N*=30, *Z*=−1.563, *p*=0.118, Fig. 1a).

Discussion

Our experiments reveal that the preference of three-spined sticklebacks for larger shoals diminishes when visibility decreases. Furthermore, sticklebacks in clear water switched between shoals more often.

In many fish species, living in larger groups is beneficial in terms of protection from predation (Krause and Godin 1995; Sogard and Olla 1997), foraging efficiency (Magurran and Pitcher 1983), speed and accuracy of decision making (Ward et al. 2011) or finding a mating partner (Wedekind 1996; Hutter et al. 2010). These benefits also apply in three-spined sticklebacks (e.g. Ranta and Kaitala 1991; Krause

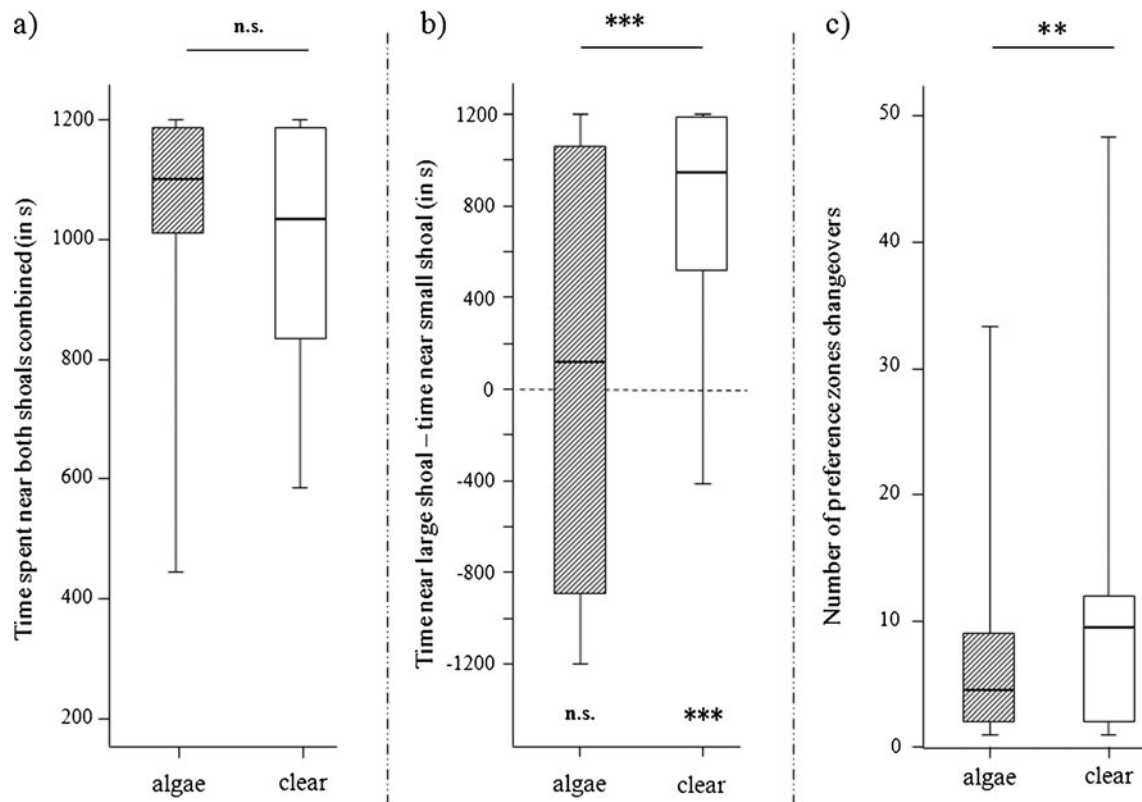


Fig. 1 Behavioural differences between fish tested in clear water and algae water. **a** The total amount spent shoaling did not differ significantly between the two treatments. **b** In clear water fish spent significantly more time near the larger shoal, while they showed no significant preference in

algae water (lower statistics). The difference between both groups was highly significant (upper statistics). **c** Fish tested in clear water switched significantly more often between the shoals than fish tested in algae water. *** $p < 0.001$, ** $p < 0.01$, n.s. $p > 0.1$

1993; Tegeder and Krause 1995; Barber and Wright 2001; Frommen et al. 2009; Ward et al. 2011). Therefore, choosing a small shoal might bear costs that will eventually reduce individual fitness. Furthermore, as for many other fish species (e.g. Krause et al. 2000b), stickleback shoals are subject to fission–fusion processes, with individuals frequently changing between groups. Changing among groups can facilitate transfer of social information (e.g. Krause et al. 2000b; Webster and Laland 2012; Zala et al. 2012), but also increase transfer of parasites (Johnson et al. 2011). Both will be reduced by a reduction in shoal changes. Social information is very important for learning new foraging routes (Krause et al. 2000b), implying that a reduction in social learning opportunities, with a lower encounter rate of individuals, may impact foraging efficiency.

The change in the preference for the larger shoal might be explained either as the result of constraints due to increased algae concentration or as adaptive responses to different costs/benefits in the two conditions. The visual ability of the test fish to perceive the two shoals simultaneously in turbid water may be reduced. Therefore, it is plausible that test fish were not aware of the second group or of its quality and thus remained next to their shoal, regardless of its size.

However, all test fish crossed the middle of the tank at least once; thus, they were aware of both shoals at least at the beginning of the experiment. Further, fish may be unable to compare the sizes of two different shoals without direct visual contact, perhaps due to cognitive constraints of recalling the number of individuals in each shoal. This would only be possible if they see both shoals at the same time, thus test fish in the algae treatment would simply not have been able to detect differences between groups. Finally, eutrophication can lower the dissolved oxygen concentration in water leading to a hypoxic environment (Pollock et al. 2007). There are several studies showing that hypoxia impacts the behaviour of fish. For example, Atlantic cod (*Gadus morhua*) decreases their swimming speed if the concentration of dissolved oxygen is low (Schurmann and Steffensen 1994). Reduced activity may also explain our results, as sticklebacks switched less often between shoals in the algae water treatment. Still, both tap and algae water was aerated using air stones until the beginning of the respective experiments, thus oxygen saturation should have been comparable in both conditions.

Alternatively, our results could be explained by adaptive responses to different costs and benefits of living in different

environments. When visibility is low, visual detection of potential predators will be impaired, and sticklebacks may limit movements to reduce the risk of predation in turbid water. This argument is supported by the finding that fish in algae water switched less between choice zones. By doing so, they increased their time in the safety of the group, regardless of its size, and decreased the time spent swimming alone in uncertain waters. If the algae water treatment is perceived as more risky in terms of predator detection, test fish should have spent more time near other conspecifics. However, total time spent shoaling did not differ significantly between the different experimental conditions, implying that reduced switching is more likely due to the fact that test fish found it difficult to locate the other shoal and therefore avoided the risk of becoming isolated from their social companions.

An alternative explanation for the loss of preference for larger groups might be that living in a large shoal is not as beneficial in turbid conditions as in clear water. Generally, living in a larger group also comes with costs. For example, individuals face increased competition and social stress in larger groups (Herczeg et al. 2009) as well as increased risk of parasitism (Poulin 1999). As the distance of prey detection by large fish shortens under turbid conditions (Utne-Palm 2002), the dilution and confusion effects of large groups might be reduced. Thus, when the risk of being attacked by a visual predator is low under turbid conditions (Meager and Batty 2007), the anti-predator benefits of a large group may no longer counterbalance the costs, leading to a loss of preference for larger groups. Further, several studies have shown that larger groups are more conspicuous and are consequently attacked more often (Uetz and Hieber 1994; Hebblewhite and Pletscher 2002; Botham et al. 2005). Predators show a higher activity under turbid conditions increasing the probability of encountering prey (Meager and Batty 2007). Therefore, larger groups may be detected faster and attacked more often compared to small groups under turbid conditions. Consequently, the benefit of joining a large shoal might be eliminated. Thus, fish in smaller shoals might face comparable benefits as fish in larger shoals, making a choice for one of the shoal sizes unnecessary.

In our study, we were only able to investigate short-term changes in behaviour. In a mate choice context, African cichlid fish are highly responsive to changes in turbidity, switching between courtship behaviour and foraging within minutes (Gray et al. 2011). Comparably, flexible responses should also be expected in sticklebacks (Candolin 2009). However, with increasing eutrophication, many shallow water bodies become consistently more turbid, which might eventually lead to morphological or behavioural changes. Indeed, sticklebacks show a high range of morphological and behavioural phenotypes depending on habitat structure (Hendry et al. 2009), feeding regime (Wund et al. 2008),

predation risk (Dingemans et al. 2009; Frommen et al. 2011) or light regime (Boughman 2001; Candolin 2009). For example, Webster et al. (2011) showed that three-spined sticklebacks in human-managed habitats and natural habitats developed different habitat-specific morphological adaptations, suggesting that human influences on natural habitats may create morphological variations. In a mate choice context, different light environments have been shown to lead to divergence among populations in male signal colour as well as in female preference, eventually leading to reproductive isolation of these populations (Boughman 2001). Thus, the question of how constant increased turbidity might change social preferences of three-spined sticklebacks will be worth investigating in future studies.

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Conflict of interest The authors declare that they have no conflict of interest.

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Ethical standards

The experiments followed the “ABS/ASAB guidelines for the treatment of animals in behavioural research and teaching” and comply with the current laws of Austria.