RESEARCH PAPER

Turbidity Hampers Mate Choice in a Pipefish

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Abstract

European coastal waters have in recent years become more turbid as algal growth has increased, probably due to eutrophication, global warming and changes in fish communities. Turbidity reduces visibility, and such changes may in turn affect animal behaviour as well as evolutionary processes that are dependent on visual stimuli. In this study we experimentally manipulated water visibility and olfactory cues to investigate mate choice using the sex role-reversed broad-nosed pipefish *Syngnathus typhle* as our study organism. We show that males spent significantly longer time assessing females when they had access to full visual cues, compared to when visibility was reduced. Presence or absence of olfactory cues from females did not affect mate choice, suggesting that the possible use of smell could not make up for a reduction in visibility. This implies that mate choice is environmentally dependent and that an increased turbidity may affect processes of sexual selection through an impaired possibility for visually based mate choice.

Introduction

Adaptive mate choice requires honest signalling, but also that the receiver accurately perceives the signal (Maynard Smith & Harper 2003). A transmission failure can impair mate choice, lowering the fitness of the sender and/or the receiver, thereby potentially reducing population viability (Andersson 1994). Environmental change may alter signal transmission, one example being a reduction in the transmission of visual signals because of increased water turbidity. Animals may also adjust the signal to the habitat, which makes signals vulnerable to environmental change (Marten & Marler 1977; Endler 1992; Bradbury & Verhencamp 1998). If mate choice is visually based a reduction in visibility can decrease the possibility for individuals to perform an adaptive mate choice, or to successfully compete for mates. However, if sexual selection on visual signals is impaired, other signals, such as chemical or auditory signals might be targeted or become more important (Heuschele et al. 2009). In mate choice, relying on

multiple signals is particularly beneficial because of the complexity involved in conveying individual quality, and multiple sensory modalities are therefore often used in sexual communication (Partan & Marler 1999).

Sexually selected signals as well as mating systems can be affected by human-induced environmental changes (Møller 2004; Gaston et al. 2005; Torti & Dunn 2005). Costal aquatic ecosystems may be particularly sensitive to human-induced environmental changes, and sexual selection in these communities can be affected by eutrophication and chemical pollution (Seehausen et al. 1997; van Doorn et al. 1998; Järvenpää & Lindström 2004; Genner & Turner 2005; Fisher et al. 2006; Candolin et al. 2007, 2008; Candolin & Heuschele 2008). Eutrophication leads to extreme plant growth and phytoplankton blooms (Smith 2003), which makes the water turbid. Algal-induced turbidity decreases water transparency and obscures objects in the water. It also reduces the light intensity and narrows the light spectrum (Jerlov 1976; Seehausen & van Alphen 1998). The

reduced visibility may cause changes in the mate choice and reproductive behaviour of fishes (Luyten & Liley 1985, 1991; Seehausen et al. 1997; Seehausen & van Alphen 1998; Järvenpää & Lindström 2004; Heubel & Schlupp 2006; Candolin et al. 2007, 2008; Engström-Öst & Candolin 2007; Wong et al. 2007; Candolin & Heuschele 2008).

The eutrophied North Sea suffers an increased abundance of planktonic algae (Reid et al. 2003; Beaugrand et al. 2003; Beaugrand & Reid 2003; Lindahl 2003; Erlandsson et al. 2006; Rosenberg et al. 2009), leading to decreased visibility (Secchi-depth; Enebjörk & Fränne 2006). Pipefishes (Syngnathidae) belong to a family of highly visually oriented fishes (Berglund et al. 1986b; Rosenqvist 1990; Collin & Collin 1999; Mosk et al. 2007; Silva et al. 2007). In the broad-nosed pipefish *Syngnathus typhle* the importance of visual cues in mate choice is well known (Berglund et al. 1986a,b; Rosenqvist 1990; Berglund & Rosenqvist 1993, 2001a,b; Rosenqvist & Johansson 1995; Sandvik et al. 2000; Silva et al. 2006, 2007; Widemo 2006), but the use of other signals, such as chemical or auditory cues, is poorly understood (but see Ripley & Foran 2007; Ratterman et al. 2009). In this species both males and females choose between mates if given the opportunity (Berglund et al. 1986b; Sandvik et al. 2000). Females and males prefer large partners over small ones, and fecundity increases with size (Berglund et al. 1986a,b; Sandvik et al. 2000). Mating preference for large body size is very common (Andersson 1994), and can potentially be assessed independently using several different sensory modalities, such as visual (Long & Houde 1989), chemical (Marco et al. 1998), electrical (Curtis & Stoddard 2003), sound (Arak 1988), or the lateral line system (Hassan 1989). Fish are known to be able to use only non-visual cues to assess mate body size (Plath et al. 2007), and to use olfactory cues to assess other indicators of mate quality (Reusch et al. 2001; Shohet & Watt 2004; Fisher & Rosenthal 2006).

Here, we experimentally investigated the consequences of a decrease in visibility, simulating the effects of turbidity, for adaptive mate choice in the broad-nosed pipefish *Syngnathus typhle*. Specifically we considered the role of visual and chemical cues using a mate choice trial design where males were allowed to choose mates with access to varying levels of visual and olfactory cues. By this, we are testing whether an increase in water turbidity influences mate choice patterns and if olfactory signals can counter effects from reduced visibility.

Methods

Experimental Design

All experiments were carried out at Sven Lovén centre for marine sciences, Kristineberg, at the west coast of Sweden during April to June in 2009. *Syngnathus typhle* were caught in shallow (<10 m depth) meadows of eelgrass, *Zostera marina*, in bays of the Gullmar Fjord, nearby the centre (58°15′N, 11°28′E), using a small beam trawl (mesh size 4 mm) pulled by a boat. Trawling was conducted before the onset of the breeding season. In the laboratory the pipefish were kept in 200-l barrels, with the sexes separated. The barrels were equipped with continuously renewed seawater and artificial eelgrass for shelter. Temperature and salinity followed the natural conditions in the area (temperature 12–20°C, salinity 18–20‰), and the light cycle was L16 h:D8 h, also close to natural conditions. The fish were fed three times a day with living *Artemia* sp., frozen mysid shrimp and *Artemia* sp. The barrels were cleaned daily.

We first ran a mate choice experiment using mate choice trial aquaria (40 × 60 × 70 cm) divided into three compartments by plastic sheets. At the back of each aquarium there were two compartments and each contained one stimulus female. At the front, one large compartment contained the focal (choosing) male. To prevent any interaction, visual or olfactory, between the females their compartments were separated by an opaque white Perspex sheet, allowing no water exchange between the females.

We manipulated the visual and olfactory cues from the females to the male at two visibility levels (full vision or impaired vision, as if the water was turbid) and at two olfactory levels (no smell or smell), producing four treatments. A divider between the male and the females was designed according to the different treatments. The treatment allowing full vision and smell to reach the male employed a clear Perspex divider, attached with silicone into the aquaria. Six holes (5 mm in diameter) in the divider, 10 cm from the bottom of the aquaria, allowed water to pass from the females (Fig. 1). The treatment allowing full vision but no smell employed the same design without holes.

The impaired vision treatments, simulating turbid water, was achieved using a semitransparent divider between the females and the male. Semi-transparency was obtained by attaching an adhesive plastic film (Alkor-Vénilia alcor DecoDesign; Vitrodecor, Gräfelfing, Germany) to the clear divider. The semitransparent divider obscured objects on the other side of it,
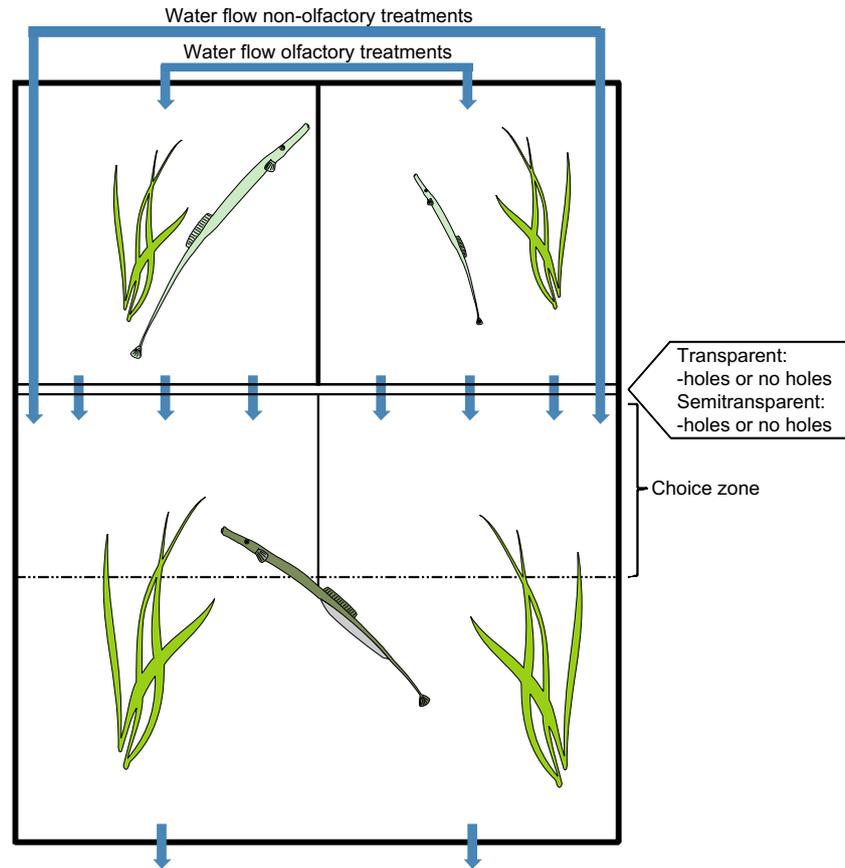
Fig. 1: The design of the mate choice aquaria with a manipulation of visual and olfactory cues at two levels.

with decreasing visibility at greater distance, giving a Secchi disc depth of 3 m (measured in clear water using a Whipple sector disc). This lies within the natural range in the area where the pipefish were caught (2.8–9.4 m, Enebjörk & Fränne 2006). Previous studies manipulating turbidity have typically used some algae suspension to experimentally increase turbidity. However, to avoid confounding a reduction in visibility with other effects from phytoplankton, such as those from algae-derived chemical exudates, turbidity was mimicked artificially by placing the semi-transparent screen between potential partners. Phytoplankton produces odours which may affect the smell of fishes (Engström-Öst & Candolin 2007), and some algae may produce toxin that interferes with fish behaviour (Burkholder 1998; Landsberg 2002; Anderson et al. 2008). By using the transparent screen design we hoped to single out the effects from a reduction in visibility. The impaired vision treatment allowing smell employed the same design as the full vision/smell treatment by using holes and water flow, the only difference being the semitransparent divider. The impaired vision treatment without smell employed the same design without any holes (Fig. 1).

To measure the difference between the clear and the semi-transparent dividers a densitometer scanner was used (GS-800 Calibrated Densitometer; Bio-Rad Laboratories, Hemel Hempstead, United Kingdom). The optical density was measured in white light (400–750 nm) transmission mode (background subtraction method: global). The optical density for the clear divider was 3.0 OD/mm^2 and the optical density for the semi-transparent divider was 8.5 OD/mm^2 (Quantity One software version 4.5.2.; Bio-Rad Laboratories). We also measured the light transmittance of the clear and the semi-transparent dividers using a computer-controlled spectrophotometer (AvaSpec-2048FT-SPU; Avantes, Eerbeek, The Netherlands) with illumination from a TOP Sensor Systems DH-2000 combined deuterium–halogen light source. Relative to light transmittance in air, the transmittance of the clear divider was close to 100% whereas the transmittance of the semitransparent divider was 90%.

The four aquaria, one for each treatment, were placed in a row in the laboratory. Each aquarium was moved one step to the right every third day, except the aquarium in the fourth position which was moved to position one, to control for position

effects. In the two treatments allowing smell, sea water entered each aquarium from the surface in both rear female compartments. It was then forced down through the holes in the divider between the females and the male, and then flowed out from the top of the male compartment. This arrangement forced the water to flow through the entire volume of each compartment. Water flow was controlled using MicroDrip valves and pipes (Gardena, Ulm, Germany), set to approximately 10 ml/s. The full and impaired vision treatments without smell allowed no water exchange between the females and the male compartments. Here, water entered the aquarium at the bottom of the male compartment and overflowed from the top of it, while the females had no water exchange during trials. Water was changed after all trials in all aquaria. The temperature followed the natural conditions in the area, varying between 10 and 13°C. One plant of artificial eelgrass was placed in the middle of each of the female compartments and two plants were paced in the male compartments, in front of each of the female compartments.

To test whether olfactory cues were used under conditions of completely blocked vision, a second experiment was carried out. The set up of this experiment was identical to the treatments allowing smell, except for a white, opaque plastic divider between the females and the male.

Mate Choice

As males are the more choosy sex in this species, and because body size has been shown to be important when choosing mates (Berglund et al. 1986a,b; Vincent et al. 1994; Sandvik et al. 2000; Berglund & Rosenqvist 2001b), the mate choice experiment was designed so that each replicate had one male choosing between two females that differed in size (Table 1). Males prefer to mate with larger females, here labelled an adaptive mate choice, as larger females have more and larger eggs than smaller females (Berglund et al. 1986a,b). Standard length was mea-

sured to the nearest millimetre. The large females were significantly larger than the males, which in turn were significantly larger than the small females (ANOVA: $F_{2, 237} = 150.87$, p < 0.001). The maximum width of the females trunk was also measured, using a slide calliper, to the nearest 0.1 mm (Table 1). Males and females did not differ between treatments in any of the measured variables (Table 1).

New individuals were used in each replicate, in total 192 females and 96 males for the 24 replicates we ran. All trials started with a 30-min acclimation period for males and females. After that, the position of the focal male was recorded every fifth minute for 150 min (making up 30 readings). When the male actively approached the female compartments to within 15 cm we recorded this as a choice. Males that did not change side at least once were excluded from the analysis (leaving 160 females and 80 males, 20 replicates in the full vision/no smell and full vision/smell treatments, 21 in the smell/impaired vision treatment and 19 in the impaired vision/no smell treatment). As turbidity may affect courtship activity (Candolin et al. 2007) male and female activity (i.e. swimming or resting) were noted.

In the second experiment (smell/no vision), the same procedures were applied. Here, 24 males and 48 females were used. Males that did not change side at least once were excluded from the analysis, leaving 34 females and 17 males.

To avoid any potential side biases, the large females were placed alternately to the right or left. Further, the number of skin parasites (*Cryptocotyle* sp.) was counted for all individuals, as large numbers of the parasite can impair fecundity as well as increase mortality and males prefer parasite-free over parasitised females (Rosenqvist & Johansson 1995; Mazzi 2004). Only fishes with fewer than 20 visible parasites were used, and males and females did not differ between treatments in parasite numbers (Table 1). During the 180-min trials fish were not fed, and no fish were harmed (ethical permission Dnr 118-2008). After the trials all fish were released back into the wild approximately where they were captured.

Table 1: Mean standard length, number of parasites and width for males and females and statistics from ANOVA comparing treatments. N = 80 males, 80 large females, 80 small females (replicates where males did not change side during the whole trial were excluded)

	Length (mm)			Parasites (numbers)			Width (mm)		
	x̄ ± SD	F	p	x̄ ± SD	F	p	x̄ ± SD	F	p
Male	179.9 ± 24.7	0.105	0.957	2.4 ± 3.1	1.427	0.242			
Large female	216.8 ± 23.4	0.142	0.934	3.0 ± 3.5	2.142	0.102	9.5 ± 1.4	0.915	0.438
Small female	156.4 ± 17.8	0.053	0.984	1.8 ± 2.7	0.425	0.736	6.3 ± 1.5	0.188	0.904

Statistical Analysis

Male proportion of time spent assessing females, i.e. time spent in front of females divided by total time, was analysed using a two fixed factor ANOVA. The initial model included vision and smell as fixed factors as well as the interaction between them. The model was then reduced to a minimum adequate model using stepwise backward deletion. Proportion of time spent choosing the large female, i.e. time spent in front of the large female divided by total time spent assessing females, was compared using a one sample t-test against a value of 0.5. The proportions were normally distributed. To determine whether the males placed themselves randomly in the aquaria within treatments we used a one sample t-test against an expected value of 0.4, as the choice zone represented 40% of the aquaria volume. Statistical probabilities reported are two-tailed and a significance level of 0.05 was used. We used JMP 8 software (SAS Institute Inc., SAS Campus Drive, Building S, Cary, NC, 27513, USA) for all analyses.

Results

Male Choice

When males had access to full vision they spent significantly more time assessing the females than when vision was reduced (vision: $F_{1, 78} = 62.24$, p < 0.001, Fig. 2). There was neither no effect of smell ($F_{1, 77} = 0.01$, p = 0.911) nor was there any interaction between vision and smell ($F_{1, 76} = 0.44$, p = 0.507), and both were therefore excluded from the final model. Further, males preferred larger females only under full vision (one-sample t-test against expected mean 0.5: $t_{39} = 2.59$, p = 0.013, Fig. 3), but not when visibility was reduced (one-sample t-test against expected mean 0.5: $t_{39} = 0.26$, p = 0.800, Fig. 3). Given that impaired visibility changed male behaviour, as shown above, we also tested how males distributed their time when visibility was and was not impaired. Males in the full vision treatments spent significantly more time within the choice zone than expected by chance (one-sample t-test against expected mean 0.4: $t_{39} = 4.56$, p < 0.001). However, males with impaired vision instead spent significantly less time in front of females than expected by chance (one-sample t-test against expected mean 0.4: $t_{39} = -7.66$, p < 0.001).

In the second experiment, completely removing vision but allowing smell, males did not spend more time in front of females (one-sample t-test against
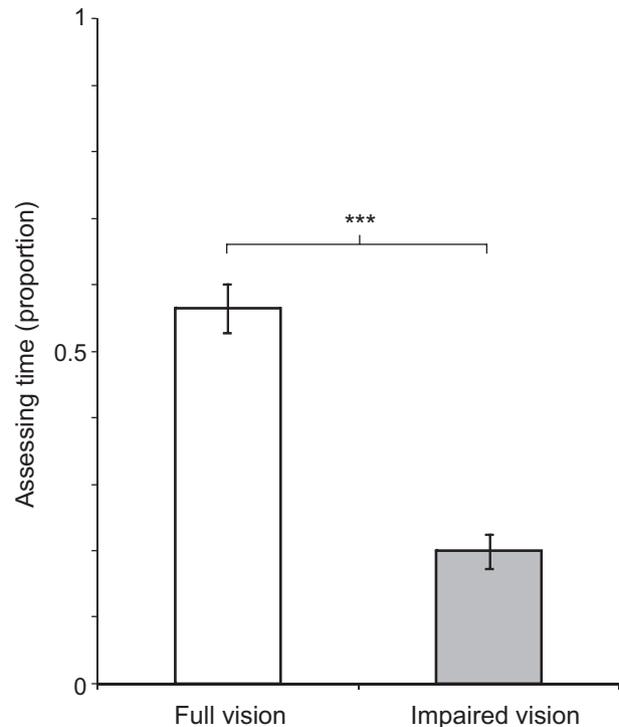

Fig. 2: Males that had access to full visual cues spent significantly more time assessing the females compared with males in impaired vision treatments. Assessing time shown in proportion, i.e. time spent assessing females divided by total time. Error bars indicate standard error.

expected mean 0.4: $t_{16} = -0.30$, p = 0.772) and did not prefer one female to the other (one-sample t-test against expected mean 0.5: $t_{16} = -1.59$, p = 0.131).

Activity

Female activity across the different treatments did not differ significantly (amount of time spent swimming; large females: ANOVA: $F_{1, 78} = 1.08$, p = 0.363; small females: ANOVA: $F_{1, 78} = 0.69$, p = 0.569). However, the large females were significantly less active than the small females (t-test: $t_{159} = -4.93$, p < 0.001). Males did not differ in activity across treatments (ANOVA: $F_{1, 78} = 1.77$, p = 0.160). An inclusion of the second experiment, where visibility was completely blocked, gave the same result regarding male activity (ANOVA: $F_{1, 95} = 1.57$, p = 0.189). The females in this experiment were not visible to the observer so their activity could not be recorded.

Discussion

We have experimentally shown that male mate choice in S. typhle is affected by visibility. In clear
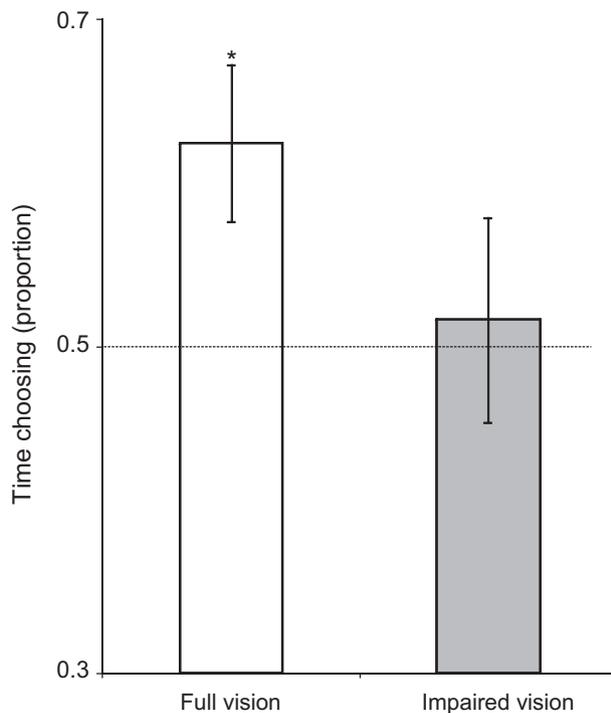
Fig. 3: Males that had access to full visual cues spent significantly more time choosing the large female than males in the in impaired vision treatments. Time spent choosing the large female compared to a random distribution of 0.5. Time spent choosing shown in proportion, i.e. time spent in front of the large female divided by total time spent assessing females. Error bars indicate standard error.

water males assessed females and preferred the larger of the two. Impairing visibility altered the male's willingness to assess females as well as his preference: males spent less time assessing females and no longer preferred large over small females. Allowing males to use olfactory cues did not influence these patterns.

In *S. typhle*, like in many fish species, body size is associated with fitness and thus an important trait in mate choice (Berglund et al. 1986a,b). Here, impaired vision hampered an adaptive male mate choice. Moreover, the addition of olfactory cues could not compensate for the reduction in visibility; in fact, males did not seem to use olfactory cues at all to assess female quality/size. These results agree with a study of a goodeid fish, *Xenotoca variatus*, where females preferred more ornamented males only in clear water (Moyaho et al. 2004). Like in this study, turbidity also affected the number of mate choice visits in the goodeid fish: the number of female visits to males was significantly higher in clear then in turbid water (Moyaho et al. 2004). Such interactions between mate choice activity and turbidity have also been show in other fish species

(Heubel & Schlupp 2006; Engström-Öst & Candolin 2007).

Although males spent more time with some females in the treatments involving full vision than in treatments without, this did not affect female activity. Similar results were obtained in three-spine sticklebacks, *Gasterosteus aculeatus*, where the choosing sex did not adjust courtship activity according to water turbidity (Engström-Öst & Candolin 2007). The lack of response in the chosen sex (i.e. in sticklebacks females and in pipefish males) appears nonadaptive in sticklebacks as well as in pipefish (this study), as this sex may have needed to court more in turbid than in clear water in order to receive the same amount of interest from the choosing sex (i.e. in sticklebacks males and in pipefish females). However, an increased courtship activity does not necessarily affect the choice of the choosing sex, as shown in sticklebacks (Candolin et al. 2007).

Increased turbidity leads to a reduction in the strength of mate choice in several species of fish, all using visual cues in sexual signalling (Seehausen et al. 1997; Järvenpää & Lindström 2004; Candolin et al. 2007). However, environmental factors, such as turbidity, did not seem to affect the genetic mating system of the dusky pipefish, *Syngnathus floridae* (Mobley & Jones 2009). Hence, as pipefish clearly use visual cues in mate choice in clear water (Berglund et al. 1997; Berglund & Rosenqvist 2001a,b) one may expect that auditory or chemical cues are to be used in turbid conditions. However, sound is unlikely to affect the mate choice since pipefish do not seem to vocalise during courtship, spawning or competition (Ripley & Foran 2007). In sticklebacks, chemical cues are more reliable in turbid than in clear water for mate choice (Heuschele et al. 2009). Chemical cues have been shown to allow male *Syngnathus scovelli* pipefish to discriminate between sexes, although smell alone did not appear to influence male mate choice (Ratterman et al. 2009). However, we found that *S. typhle* did not rely on olfactory cues for mate choice in this study, neither when visibility was impaired nor when it was blocked completely. These results may be an effect of using semitransparent Perspex dividers rather than algae to manipulate visibility. Had we used algae to reduce visibility, the pH may have increased (Reddy 1981; Perus & Bonsdorff 2004). This in turn may enhance the signal value of odour in mate assessment (Heuschele & Candolin 2007). On the other hand, the algae themselves may produce odours that can mask the olfactory cues from the fish (Engström-Öst & Candolin 2007).

In conclusion, we here present experimental evidence showing that impaired water visibility hampers adaptive mate choice in male broad-nosed pipefish, and that males do not compensate for a reduction in visibility by using olfactory cues, or that females compensate by increasing their activity. Thus, if adaptive mate choice is vital to population viability (Taylor et al. 2006; Candolin 2009), the present-day increase in turbidity because of human activities may pose a threat to these pipefish populations.

Acknowledgements

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