



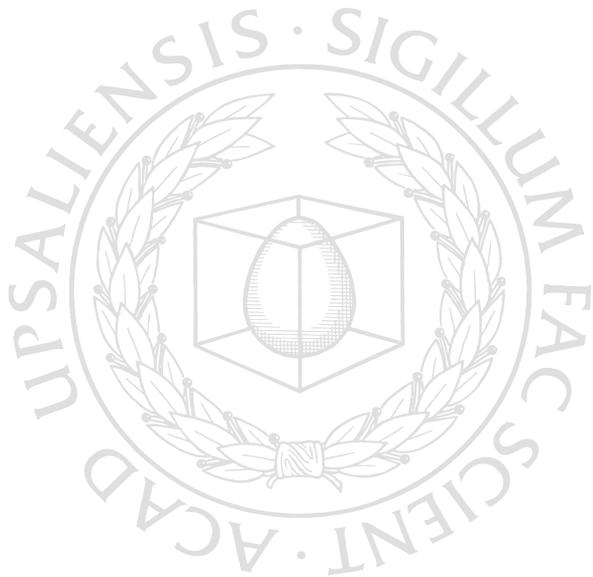
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Sex in Murky Waters

*Anthropogenic Disturbance of Sexual Selection
in Pipefish*

JOSEFIN SUNDIN



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Abstract

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Animals experience variation in their environment because of natural changes. However, due to anthropogenic disturbance, the speed and severity of these changes have recently increased. This thesis investigates how reproductive behaviours may be affected by human induced environmental change. In specific, I investigate how visual and chemical changes in the aquatic environment, caused by eutrophication, affect mating systems and sexual selection in fish. Broad-nosed- and straight-nosed pipefish, which both have been studied in detail for a long period, were used as model organisms. These two species are particularly suitable model organisms since they perform complex courtship behaviours, including the advertisement of ornaments and a nuptial dance. Further, two distinct populations were studied, one on the Swedish west coast and one in the Baltic Sea, as these two locations vary in the degree and extent of environmental disturbance, in particular turbidity. I found that changes in the visual environment had no impact on the development of female sexual ornaments in these sex-role reversed pipefishes, but it hampered adaptive mate choice. Turbidity also had a negative effect on reproductive success in the Baltic Sea population. Changes in the chemical environment in the form of increased pH reduced the probability to mate, while hypoxia did not alter mating propensity. However, hypoxic water delayed the onset of both courting and mating. Hence, human induced change in aquatic environments may alter the processes of sexual selection and population dynamics.

Keywords: Mating system, Mate choice, Courtship, Eutrophication, Turbidity, Hypoxia, Ocean acidification, Syngnathidae

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Till pappa (1944 – 2009)

The following papers were written during the course of my doctoral studies but are not part of the present dissertation.

Sundin, J., Jacobsson, Ö., Berglund, A. & Rosenqvist, G. 2011. Straight-nosed pipefish *Nerophis ophidion* and broad-nosed pipefish *Syngnathus typhle* avoid eelgrass overgrown with filamentous algae. *Journal of Fish Biology* 78:1855-1860.

Lindqvist, C., **Sundin, J.**, Berglund, A. & Rosenqvist, G. 2011. Male broad-nosed pipefish *Syngnathus typhle* do not locate females by smell. *Journal of Fish Biology* 78: 1861-1867.

Landis, S*, **Sundin, J***, Rosenqvist, G. & Roth, O. 2012. Behavioural adjustment of a pipefish to bacterial vibrio infection. *Behavioural Ecology and Sociobiology* 66: 1399-1405. [*equal contribution to the manuscript.]

Aronsen, T., Mobley, K., Berglund, A., **Sundin, J.**, Billing, A. & Rosenqvist, G. *The operational sex ratio and density influence spatial relationships between breeding pipefish*. [Accepted, Behavioral Ecology].

Sundin, J., Sagebakken, G. & Kvarnemo, C. *Female mate choice is not affected by mate condition in a fish with male care*. [Provisionally accepted, Acta Ethologica].

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. Sundin, J., Berglund, A. & Rosenqvist, G. (2010) Turbidity hampers mate choice in a pipefish. *Ethology*, 116: 713-721.
- II. Sundin, J., Aronsen, T., Rosenqvist, G. & Berglund, A. Human induced turbidity alters reproductive success and the strength of sexual selection in a pipefish. *Manuscript*.
- III. Sundin, J., Rosenqvist, G., Myhren, S. & Berglund, A. Male mate choice, but not female ornamentation, is impaired by turbidity in the straight-nosed pipefish. *Manuscript*.
- IV. Sundin, J., Rosenqvist, G. & Berglund, A. (2013) Altered oceanic pH impairs mating propensity in a pipefish. *Ethology*, 119: 86-93.
- V. Sundin, J., Rosenqvist, G. & Berglund, A. Hypoxia delay mating in the broad-nosed pipefish. *Manuscript*.

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Illustrations by Robert Sundin

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Introduction

Ecosystems all around the world are changing due to anthropogenic disturbance. An organism's resilience to such fast and drastic environmental change largely depends on its ability to disperse, how mobile it is, its behavioural plasticity, and the fitness consequences related to the environmental change (Dall et al. 2005, Donaldson-Matasci et al. 2008). The initial response, most often a behavioural adjustment, is important since the first reaction to rapid human-induced environmental change will determine if individuals or populations survive the early stages of changing environments (Tuomainen and Candolin 2010). If the possibility to move to a more favourable environment exists, this could be thought of as a means of escaping the disturbed habitat. However, the dispersion in turn has the potential to alter species compositions and interactions, which could have consequences for biodiversity (Davis et al. 1998). When dispersal is no alternative, only those individuals best able to cope with the new conditions will survive and reproduce, hence adapting to the new environment through natural selection. Sexual selection, as a part of natural selection, drives the evolution of traits that increase success in the competition for mates and fertilization (Andersson 1994). The costs and benefits of the main components of sexual selection, intersexual selection (i.e. mate choice), and intrasexual selection (i.e. competition within a sex), are to a large extent influenced by the abiotic and biotic environment. Hence, the modules of sexual selection must be adapted to the environment to maximize reproductive success (Andersson 1994, Maynard Smith and Harper 2003, Bradbury and Vehrencamp 2011). If the environment undergoes a drastic change, as often is the case with anthropogenic disturbance, sexually selected signals may become dysfunctional under the new environmental conditions (Tuomainen and Candolin 2010). As mate choice requires that a receiver accurately perceives a signal, transmission failure can impair mate choice, lowering fitness of the sender and/or the receiver, thereby potentially reducing e.g. population viability (Andersson 1994, Maynard Smith and Harper 2003). However, phenotypic plasticity can allow animals to adjust behaviours and sexual signals as a response to environmental change (Endler 1992, Tuomainen and Candolin 2010, Bradbury and Vehrencamp 2011). However, since anthropogenic disturbance often alters the environment dramatically and/or rapidly, as well as in a way that the organisms have not encountered during their evolutionary history, maladaptive behavioural responses are quite likely (Ghalambor et al. 2007, Tuomainen and Candolin

2010). Environmental change may not only affect reproduction through signals, but can also alter mating systems (Olsson et al. 2011). Since the mating system can vary with the state of the environment, they are known to be flexible rather than fixed (Shuster and Wade 2003). Several environmental factors, such as temperature, food availability, habitat structure and the spatial and temporal distribution of mates, all shift the mating system to fit the environment at each given time and place (Gwynne 1990, Rowe et al. 1994, Olsson et al. 2011). Hence, the evolution of mating systems not only depends on gamete size and the degree of mating competition, but also on various ecological factors that may constrain sexual selection (Emlen and Oring 1977).

Anthropogenic disturbance in aquatic environments

Environmental change in coastal aquatic ecosystems, such as eutrophication and chemical pollution, may affect sexual selection in the communities inhabiting those ecosystems (Seehausen et al. 1997, van Doorn et al. 1998, Järvenpää and Lindström 2004, Genner and Turner 2005, Fisher et al. 2006, Candolin et al. 2007, Candolin et al. 2008, Candolin and Heuschele 2008, van der Sluijs et al. 2011). Marine ecosystems are particularly sensitive to environmental change, with overfishing, eutrophication, and the destruction of physical and biogenic habitats as some of the most pervasive threats (Orth et al. 2006). Extensive changes in habitat structure, species composition and abundance due to an altered environment have been noted around the world (Duffy 2006). Consequently, increased amounts of phytoplankton and filamentous algae alter the environment of marine organisms that have to adapt to changes in pH, oxygen, and visibility (Heuschele and Candolin 2007, Candolin and Heuschele 2008, Switzer et al. 2009).

Eutrophication and overfishing can lead to extreme plant growth and phytoplankton blooms (Smith 2003), which make 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 and van Alphen 1998). A reduction in water transparency may affect a range of reproductive behaviours and sexually selected signals. As the visibility of sexual signals may be substantially reduced, this could relax sexual selection on colourful signals, leading to dull colouration, as shown in lake Victoria cichlids (Seehausen et al. 1997, Maan and Seehausen 2010, Maan et al. 2010). Conversely, a turbid environment may select for a compensatory increase of a visual signal, as shown in the red shiner (Dugas and Franssen 2011), in brown trout (Eaton and Sloman 2011), and in sticklebacks (Engström-Öst and Candolin 2007). Finally, visual signals may stay unaffected, as observed in a goodeid fish (Moyaho et al. 2005). Hence, whether turbidity decreases, increases or leaves colouration unaffected may

vary depending on exposure time, condition, population and species. Regardless of whether the signal is altered or not, turbidity may disrupt the link between the signal and individual quality, which diminishes honest signaling of mate quality (Wong et al. 2007). A decrease in visibility may also increase the probability of reproduction for parasitized males (Heuschele and Candolin 2010). Further, turbidity may relax sexual selection on mate size (Järvenpää and Lindström 2004), and on courtship activity (Candolin et al. 2007), and lead to a decrease in parental care (Järvenpää and Lindström 2011). On the other hand, turbidity may enhance reproductive success through increased reproductive lifespan, hatching success (Candolin et al. 2008), and increased egg survival (Järvenpää and Lindström 2011), implying complex interactions between turbidity and reproductive behaviours.

Turbidity not only influences the visual environment; increased amounts of algae may also alter the chemical environment by decreasing levels of dissolved oxygen and altering the pH of the water (Lapointe and Matzie 1996, Perus and Bonsdorff 2004, Diaz and Rosenberg 2008, Rabalais et al. 2010). Hypoxia may affect nest care, hatching success and brood survival in many species of fish (reviewed in: Pollock et al. 2007). An increase in pH has the potential to alter reproductive behaviours, for example by an increase in the signal value of olfactory cues, but studies on this are very few (Heuschele and Candolin 2007). Thus, both changes in the visual and chemical environment have the potential to alter sexual selection and reproductive behaviours of aquatic organisms, but several questions remain unanswered (reviewed in: Tuomainen and Candolin 2010, van der Sluijs et al. 2011).

Aims

The aim of this thesis is to improve our knowledge of how anthropogenic induced environmental change affects sexual selection, mating behaviours and mating systems. For this, two species of sex-role reversed pipefish are used as model organisms. More specifically, I investigate how changes in the environment can alter development of sexual ornaments (**paper III**), courtship behaviours (**paper V**), mate choice (**paper I, II, III**), mating propensity (**paper II, IV, V**), reproductive success (**paper II, IV, V**) and mating systems (**paper II**). The focus of this thesis is on the most preeminent change in aquatic environments caused by humans, namely eutrophication, which alters both visual and chemical characteristics of the aquatic environment.

Methods

Study species

Pipefish, together with seahorses and seadragons (Syngnathidae), is a family of highly specialized fish that practice male pregnancy. The female transfers her eggs to the male who then broods the eggs for several weeks. For many species, females can produce eggs at a higher rate than males can brood them, leading to a surplus of eggs. Consequently, males are the limiting resource during reproduction, which in turn often generates choosy males and competition between females (Berglund et al. 1986a, b, 1988). Most species of pipefish are associated with the seagrass habitats, which they mimic in colour, shape and behaviour (Howard and Koehn 1985, Kendrick and Hynes 2003). Seagrass beds that are not affected by eutrophication are preferred to seagrass beds overgrown with algae (Wennhage and Pihl 2007, Sundin et al. 2011). During courtship, conspicuous behaviours and ornaments typically replace the cryptic lifestyle so characteristic of these pipefish. Males and females perform a lengthy, ritualized, mutual dance before the female transfers her eggs into the male's brood pouch or, in some species, directly onto his body (Berglund 1993). In this thesis I used two species of pipefish, the broad-nosed pipefish, *Syngnathus typhle*, (**paper I, II, IV, V**), and the straight-nosed pipefish, *Nerophis ophidion*, (**paper III**). Both species are highly visually oriented (Berglund et al. 1986b, a, Rosenqvist 1990, Collin and Collin 1999, Mosk et al. 2007, Silva et al. 2007), and the use of other signals, such as chemical or auditory cues, is poorly understood (but see: Ripley and Foran 2007, Ratterman et al. 2009, Lindqvist et al. 2011). Females typically display an ornament, and males prefer to mate with ornamented females (Berglund et al. 1986b, a, Rosenqvist 1990a, Vincent 1992, Berglund and Rosenqvist 2001, 2003). Males also show a preference for larger females, which also is a male trait selected for by females when choosing mates, if females have the opportunity to choose (Berglund et al. 1986a, b, Rosenqvist 1990, Sandvik et al. 2000). Both size and ornaments are signals that could potentially be affected by a decrease in visibility, especially for these pipefish species so dependent on visual cues in mate choice. Their well-known complex courtship and mating ritual further makes these species particularly suitable for testing possible effects of an altered visual and chemical environment.

Study sites

These studies were conducted at Sven Lovén Centre for Marine Sciences, Kristineberg, at the west coast of Sweden (**paper I, II**), and at Ar research station on Gotland situated in the Baltic Sea at the east coast of Sweden (**paper II, III, IV, V**). Fish used in the experiments were captured at the respective locations. While the pipefish on the west coast of Sweden have been the subject to some 30 years of extensive studies (Rosenqvist and Berglund 2011), much less is known about pipefish inhabiting the Baltic Sea. Pipefish from the Baltic Sea and the west coast of Sweden were previously believed to belong to the same population, based on samples of pipefish collected from Europe and the west- and east coast of Sweden (Rispoli and Wilson 2008). However, when pipefish from the coasts around the island of Gotland was included in the analysis a different pattern arose (Landis, Roth, unpublished data). This study showed that the pipefish from Gotland stands out as a separate population from the other Baltic Sea pipefish. During the past years our knowledge about the differences between the populations has increased. For example, the well-known preference in the broad-nosed pipefish for large mate size is not found in the Baltic Sea (**paper IV**). Except for the obvious differences in salinity between the west coast and the Baltic Sea there are also large differences in the level of eutrophication and turbidity. While the west coast has relatively low levels of turbidity (Lundälv and Jonsson 2005), the Baltic Sea is many times more turbid, and has been so for a longer period of time (Bonsdorff et al. 2002, Salonen et al. 2009, Veneranta et al. 2011).

Catching and handling

All pipefish were caught before or during the onset of the breeding season (April, May), in shallow (<10 m depth) meadows of eelgrass, *Zostera marina*, using a small beam trawl (mesh size 4 mm) pulled by a boat. During the holding period, i.e., in-between catching the pipefish and performing the experiments, I kept the fish separated by sex in large holding tanks/barrels in the laboratory. The holding tanks and barrels had continuously renewed seawater and artificial eelgrass for shelter. The fish were fed three times a day with live and frozen mysid shrimps and *Artemia* sp. The tanks/barrels were cleaned daily. The light cycle was set to mimic the natural day length. As a flow through system was used, with water pumped directly from the sea into the holding tanks/barrels, temperature and salinity followed natural conditions at each study site (specified in each paper).

Experimental design

To investigate how changes in the visual and chemical environment affect reproductive behaviours, mating systems and sexual selection, I performed a set of controlled laboratory experiments. I investigated if and how turbidity would alter the development of female sexual ornaments, mate choice, mating system, and reproductive success by lowering water transparency using either artificial techniques (**paper I**), or phytoplankton (**paper II and III**). I further investigated if and how altered pH-levels would influence mating propensity (**paper IV**), as well as effects of hypoxia on courtship behaviours and mating behaviour and mating outcome (**paper V**). As courtship behaviours, the use of sexual signals, male mate choice, and mating propensity are behaviours that can be monitored within a fairly short time frame, individuals were either observed in real time (**paper I, IV**), or video recorded (**paper V**). On the contrary, the development of female sexual ornaments and potential changes in mating system required a longer-term setup (**paper II, III**). The long-term setup did not allow for continuous observations of behaviours, partly due to time limitations, but also since these experiments involved an algae treatment, which alters visibility and thus prevented an observer from observing the fish. Instead, fish were monitored at the beginning and end of the experiment, and/or with the use of molecular techniques (**paper II, paper III**).

As body size is a sexually selected trait in these species (Berglund et al. 1986a), body length was measured, or estimated visually, prior to all experiments. Thus, the fish did not vary in length within or between replicates, unless the experimental design required so. Further, fish with more than 20 visible skin parasites, *Cryptocotyle* sp., were not used in any experiments as parasites may reduce mate attractiveness (Rosenqvist and Johansson 1995). To study the development of female sexual ornaments over time (**paper III**), I also photographed females and assessed skin fold size prior to and after the experiment. After placing the fish in the aquaria or tanks, time was given for the fish to acclimate before the observations started. In the cases where length was only visually estimated prior to the experiment, fish were measured to the nearest mm at the end of experiments (**paper V**). After the experiments, fish from experiments that only employed behavioural observations (**paper I, IV, V**) were released back into the wild at the location of capture. In order to analyse the genetic mating system (**paper II**) a small fraction of the tail fin from females was sampled before females were released. To enable parentage analysis of embryos, brooding males were kept in aquaria after the experiment until the embryos had developed eyespots (Jones et al. 1999). Males and embryos were then sacrificed for parentage analysis. In order to measure ovary weight at the end of an experiment (**paper III**), females were sacrificed as well.

To allow continuous observations of courtship behaviours, the use of sexual signals, male mate choice, and mating propensity (**paper I, IV, V**), see-through aquaria of approximately 70 litres were used (which is enough space for the fish as I included a maximum of three fish per replicate). During the longer-term experiments, where I investigated the development of female sexual ornaments and mating system, pipefish were not continuously observed (**paper II, III**), and opaque tanks or barrels of approximately 200-600 litres were used (which is again enough space for the fish as here I included a maximum of eight fish per replicate). Water was provided to the aquaria and tanks either by a flow through system (**paper I, II**), or, if the experimental design required it, the water was standing still (**paper IV, V**), or exchanged at a fixed interval (**paper II, III**). In all experiments, water from each respective site was always used so that water temperature and salinity followed natural conditions. For most experiments, oxygenation of the water was either not needed, as I used a flow-through system, or I exchanged and aerated the water to ensure oxygenation (**paper II, III, IV**), or the oxygen level was manipulated as a part of the experimental treatment (**paper V**). Water was always exchanged in-between each set of replicates. Experiments that lasted over several days (**paper II, III**) had controlled light regimes to follow natural conditions and fish were fed three times a day with live and frozen mysid shrimp and *Artemia* sp. Fish were not fed during the short-term experiments as they only lasted for a couple of hours. I used plastic eelgrass for shelter at all times. As all long-term experiments involved an algae treatment, which prevented me to see the fish, the tanks/barrels could not be cleaned on a daily basis. Instead, they were cleaned in between each set of replicates (**paper II**), or at a fixed interval when the fish were removed from the tanks/barrels (**paper III**).

Results and discussion

Development of sexual ornaments

Several aquatic species have been observed to develop less prominent ornaments and sexual signals in turbid environments, where turbidity was caused by anthropogenic disturbance (Seehausen et al. 1997, Secondi et al. 2007, Wong et al. 2007, Maan and Seehausen 2010, Maan et al. 2010), and it was therefore predicted that pipefish would respond in a similar way. However, the development of sexual ornaments in female straight-nosed pipefish from the Baltic Sea was not affected by turbidity (**paper III**). If anything, there was a trend in the opposite direction, in that more females developed a larger ornament in turbid environment. This suggests that the turbid environment may potentially have caused a compensatory increase of the visual signal, something that has been demonstrated for other species (Engström-Öst and Candolin 2007, Dugas and Franssen 2011, Eaton and Sloman 2011). Although I recognize that more studies are needed to verify such a scenario, it at least shows that predicting signal expression in turbid environments is complex, a notion that is strengthened by previous studies showing both a decrease and an increase in signal expression in response to altered turbidity. Moreover, turbidity has been shown to have no effect on nuptial colouration, as also found here. In an experiment using stickleback males it was shown that males in good condition did not alter signal expression in a turbid environment, whereas males in poor condition displayed less nuptial colouration (Wong et al. 2007). Thus, my finding that female ornamentation in pipefish (**paper III**) was unaffected by turbidity may be due to females overall being in very good condition. This idea is supported by the fact that females increased in body length, skinfold size, and colour contrast during the experiment, which is not to be expected for animals in poor condition (Höglund et al. 1992). As visual sexual signals may increase, decrease, or stay unchanged in response to a turbid environment, more studies are needed to confirm if there are any predictable patterns of anthropogenic influence on sexual ornaments in aquatic environments.

Courtship

Courtship is an important part of the reproductive process with functions such as ensuring reproductive compatibility, reducing hostility between the potential partners, and conveying individual quality (Bateson 1983, Andersson 1994). The impact of anthropogenic disturbance on courtship behaviours was investigated in both the straight-nosed pipefish and in the broad-nosed pipefish, for the stressors turbidity and hypoxia. In the broad-nosed pipefish, hypoxia prolonged latency to court, but it did not influence total time spent courting, dancing or latency until dancing (**paper V**). In the straight-nosed pipefish there was no difference in courtship frequency between females that had experienced a turbid environment and females had experienced a clear environment (**paper III**). Further, as only the possible effects of *previously* having experienced a turbid environment were investigated. I do not know whether courtship behaviours would be affected if the water was turbid while the courtship behaviour was performed. The result found here are, however, in accordance to what was found for stickleback males, where courtship activity was not adjusted to water turbidity (Engström-Öst and Candolin 2007).

The result that hypoxia prolonged latency until courting (**paper V**), are also in agreement with previous studies who found that reproductive behaviours, such as nest care, hatching success and brood survival, typically are affected by hypoxia (reviewed in Pollock et al. 2007). Thus, this study adds to the knowledge on how reproductive behaviours are affected by hypoxia. Courting may have been delayed in the hypoxic environment because hypoxic conditions can increase energy demands, and courtship displays are often time consuming and energetically costly (Hunt et al. 2004). Previous studies have found that ventilation rates in the broad-nosed pipefish increased in response to low oxygen (Braga Goncalves 2010), and higher ventilation rates impose a higher energetic cost (Hughes 1973, Kramer 1987). It was also shown that broad-nosed pipefish males grew less under hypoxic conditions, which further implies that hypoxia is energetically demanding for this species (Braga Goncalves 2010). Even though not significant, I did find a trend for lower activity in the hypoxic environment, which could be an effect of an increased energy demand in this environment. As human activities, such as eutrophication, currently causes hypoxia and algal induced turbidity, studies of how aquatic organisms respond to these changes are an important research topic. This is not only to understand how anthropogenic disturbance affects population viability and for nature conservation, but also to understand how environmental variation and change affects animal behaviour as well as evolutionary processes.

Mate choice

Another important component of sexual selection is mate choice, i.e. intersexual selection. Given that environmental interactions play an important part in sexual selection (Andersson 1994), it is not surprising that several studies have shown that anthropogenic disturbance, such as increasing turbidity, most often relax the strength of sexual selection (Järvenpää and Lindström 2004, Candolin et al. 2007, Wong et al. 2007). In this thesis, the impact of anthropogenic disturbance on mate choice was studied for both straight-nosed and broad-nosed pipefish, focusing on effects from turbidity. I found differences in the response between as well as within the populations from the Baltic Sea and the Swedish west coast (**paper I, II, III**). Impairing visibility hampered the adaptive male mate choice for a larger mate in the broad-nosed pipefish from the west coast (**paper I**). This result was also found in the straight-nosed pipefish from the Baltic Sea population, where algal turbidity resulted in random male mate choice (**paper III**). However, when investigating the genetic mating system in the broad-nosed pipefish another pattern arose (**paper II**). For the west coast population there was no difference in mating success for large or small males between the clear and turbid environment (**paper II**). Instead, mated males were always larger than unmated males, showing that females could perform their adaptive mate choice for a larger mate regardless of treatment. Since male mate choice for female size was hampered by impaired visibility (**paper I**), this was expected to be true also for female mate choice. However, as large males had a higher mating success regardless of treatment, turbidity seems not to hamper a females' ability to practice an adaptive mate choice, or, alternatively, a male's ability to locate and mate with a female. For the Baltic Sea population, a positive interaction between treatment and male length in mating success showed that larger males had a higher probability of acquiring more mates also in this population, with the difference that the relationship was stronger in turbid environments. However, in contrast to the west coast population, a preference for mate size has not been demonstrated in the Baltic Sea population, neither for males nor for females (**paper IV**, Lindqvist et al. unpublished data). Hence, these studies suggest that male body size is not a factor determining mating success in clear water. It is thus surprising that the positive relationship between male body size and number of mates was stronger in turbid environments (**paper II**), especially since several studies have shown that turbidity typically relaxes sexual selection (Järvenpää and Lindström 2004, Candolin et al. 2007, Wong et al. 2007). Direct comparisons between these studies should however be done with caution. In the investigation of male mate choice (**paper I**) females could not compete, and male-male competition for access to females was also excluded. When investigating effects of turbidity on the mating system, where female mate choice was investigated (**paper II**), both competition between females and

between males could have occurred. My studies show that turbidity has the potential to alter mate choice and/or the ability to find mates, and further emphasizes that different outcomes could apply to either sex within the same species and even within the same population.

Mating propensity

Mating propensity affects core processes of sexual selection (e.g. Andersson 1994 and references therein) as well as population dynamics. Changes in mating propensity are especially important if the observed difference is permanent over time, both within and across breeding seasons (Andersson 1994). Thus, changes in the environment that has the potential to alter mating propensity are an important research topic within both evolutionary and conservation biology. I investigated the impact of anthropogenic disturbance on mating propensity, focusing on changes in pH, hypoxia and turbidity. I found that while an increase in water pH reduced the probability to mate (**paper IV**), a decrease in pH, as well as hypoxia had no impact on mating propensity (**paper IV, V**). Turbidity did influence mating propensity, although in different ways for different populations (**paper II**). Lowered mating propensity would lead to a lowered reproductive output, which would have a strong impact on the viability of populations (e.g. Turchin 2003). The direct effect of increased pH on mating propensity is a discovery that represents particularly valuable information regarding the effects of anthropogenic disturbance on reproduction. Studies on how increased pH may influence reproductive behaviours are, to my knowledge, very few. However, an increase in pH has been shown to facilitate the signal value of olfactory cues in the threespine stickleback (Heuschele and Candolin 2007). Together with the results found here, it shows that an increase in pH has the potential to alter reproductive behaviours and mating propensity, implying far-reaching consequences from eutrophication.

In contrast to the effect of increased pH, no impact on mating propensity by a decrease in pH was found (**paper IV**). This contradicts other studies on how acidified seawater effect fish behaviour (Munday et al. 2009, Dixson et al. 2010, Munday et al. 2010, Cripps et al. 2011, Ferrari et al. 2011, Simpson et al. 2011, Ferrari et al. 2012a, b). Although none of these studies investigated reproductive behaviours, they do show that a reduction in pH has the potential to affect a variety of fish behaviours. One explanation to the lack of response to decreased pH that I found is that it may take several days of exposure to lowered pH before a behavioural response can be detected (Munday et al. 2010). Therefore, the short-term exposure to decreased pH used in my experiment may not have elicited a reproductive behavioural response. However, the drastic impact of elevated pH on reproduction found in this

experiment suggests that a short-term exposure indeed would alter pipefish behaviour, but more studies are required.

Moreover, neither hypoxia nor turbidity altered mating probability (**paper II, V**). However, even though hypoxia did not alter mating probability, it did increase the latency until mating. For animals in general it may come with several benefits to mate quickly, and a delay between the first encounter between a male and a female until courting and mating could lead to reduced fitness (Prakash 1967, Meek and Lee 1993). Further, the risk of another individual taking over the opportunity to mate, or sneak copulations, may increase if time until mating is long (Pruitt and Riechert 2011). Since courtship and mating behaviours often are conspicuous by nature, the risk of being detected by a predator often increases when these behaviours are performed (Sakaluk and Belwood 1984, Lima and Dill 1990, Zuk and Kolluru 1998, Hoefler et al. 2008), and latency to mate can increase in the presence of a predator (Fuller and Berglund 1996, Wong et al. 2009). For the broad-nosed pipefish, mating fast may be of particular importance to females in a low oxygen environment as oxygen levels are higher in the bottom section of the pouch (Braga Goncalves 2010). As the eggs in the brood pouch of the male will be organized according to mating order (Jones et al. 1999), the first female to mate will have her eggs placed at the pouch bottom with a higher oxygen concentration for the embryos throughout the male pregnancy. Since the oxygen level within the pouch is lower than the levels in the surrounding water, whether the ambient oxygen concentration is high or low (Braga Goncalves 2010), it may be particularly important for the female that her eggs are located in the area of the pouch that is best oxygenated. Even though embryo survival during the brooding period seems not to be affected by hypoxia, embryo growth is (Braga Goncalves 2010), and the size of the embryo at birth affects survival with smaller offspring being more vulnerable to predation (Ahnesjö 1992).

The pattern of mating propensity in turbid water (**paper II**) differed between populations. In the west coast population male body length determined whether males mated or not, with larger males having a higher probability to mate. For the Baltic Sea population, however, the relationship with mating probability and male body size was stronger in a turbid environment. In clear water mated and unmated males were of equal size, while small males remained unmated in turbid water (see discussion above about mate choice).

Reproductive success

Human induced environmental change may alter reproductive success, and the cause for the current decline in many fish species is most likely due to anthropogenic disturbance (Vallin et al. 1999, Rowe and Hutchings 2003).

Here, I tested whether turbidity, hypoxia and altered pH would influence reproductive success of the broad-nosed pipefish (**paper II, IV, V**), and further whether the response would differ between different populations (**paper II**). I found that neither altered pH nor hypoxia influenced reproductive success, as none of the stressors decreased the proportion of the male pouch that was filled with eggs (**paper IV, V**). On the other hand, the impact of turbidity on reproductive success differed between the two studied populations (**paper II**). For the Baltic Sea population the turbid environment caused a reduction in reproductive success. For the west coast population there was a positive interaction between treatment and body length, indicating that larger males had a higher reproductive success, and that this relationship was stronger in turbid environments. A decrease in reproductive success in a turbid environment contrasts with findings on nest building fish, where reproductive success increased under turbid conditions (Candolin et al. 2008, Järvenpää and Lindström 2011). In these studies eggs may benefit from a turbid environment in terms of an improved oxygen supply in the nest through algal photosynthesis (Candolin et al. 2008, Järvenpää and Lindström 2011). In the broad-nosed pipefish this is not relevant, as males brood the eggs in a brood pouch. The higher reproductive success in clear water found here might be due to more eggs being transferred per mating event. When the male and/or the female has the possibility to assess the mate properly, as in clear water, more eggs may be transferred than in turbid water, where pre-copulatory mate assessment is more difficult. In addition to the effect of turbidity we found that larger males had a higher reproductive success, which is expected as larger males accommodate more eggs (Berglund et al. 1986a). Thus, these studies show that anthropogenic disturbance may alter reproductive success, and that the outcome may vary between different stressors.

Mating systems

Since mating systems are flexible and can vary with the state of the environment (Shuster and Wade 2003), several environmental factors, such as temperature, food availability, habitat structure and the spatial and temporal distribution of mates all have the potential to shift the mating system to fit the environment at each given time and place (Gwynne 1990, Rowe et al. 1994, Olsson et al. 2011). Thus, in theory, anthropogenic change of environments could alter animal mating systems (Andersson 1994), and a few studies do indeed point in this direction (Rowe and Hutchings 2003, Olsson et al. 2011). Therefore, I investigated the possible impact of anthropogenic disturbance on mating systems (**paper II**). Here, I used turbidity as an environmental stressor, and the results differed to some extent between the two studied populations. As described above, there was a positive correlation

between number of partners and male body length in the Baltic Sea population, which was stronger in the turbid environments. This indicates that turbidity affected the strength of sexual selection, with small males not mating at all in turbid environments. For the west coast population turbid environments did not influence mating systems, as there were no difference in number of partners between treatments. For this population, male body size was equally important in both environments to acquire mates, with large males having greater mating success. These results are not in accordance with my prediction that turbidity would shift the mating system towards polyandry. The prediction stems from an occurrence of almost exclusive polyandry (most males mating with one female only) in a Venice lagoon population (Rispoli and Wilson 2008). There, turbidity levels far exceed those observed in the North Sea (North Sea: Lindahl 2003, Enebjörk and Fränne 2006, Venice lagoon: personal communication M. B. Rasotto). Thus, one explanation for a shift from polygynandry, which is the mating system observed in the Baltic Sea and at the Swedish west coast (Berghlund et al. 1989, Rispoli and Wilson 2008), towards polyandry, as observed in the Venice lagoon (Rispoli and Wilson 2008) could be an increase in turbidity. Further, I predicted that the shift towards mating with fewer mates would be particularly evident in the Baltic Sea population, as the Baltic Sea, in comparison to the west coast, is more turbid (Baltic Sea: Bonsdorff et al. 2002, Salonen et al. 2009, Veneranta et al. 2011; Swedish west coast: Lindahl 2003, Lundälv and Jonsson 2005, Enebjörk and Fränne 2006). No such relationship was, however, found, and most likely other factors than turbidity shaped the mating system in the Venice lagoon. As there are, to my knowledge, very few studies on the influence of anthropogenic change on animal mating systems (Rowe and Hutchings 2003, Olsson et al. 2011), these results nevertheless add valuable knowledge to this field.

Conclusions and future challenges

In conclusion, I have shown that anthropogenic disturbance has the potential to alter several aspects of reproduction and sexual selection, including the development of sexual ornaments, courtship behaviour, mate choice, mating propensity and reproductive success. Furthermore, I have shown that the way in which the environmental stressors affect reproduction may vary both between and within species and populations. Indeed the effect of different environmental stressors elicited different responses on reproductive behaviour, sometimes in opposite directions. This emphasises the complex way in which environmental change may alter reproductive behaviours. Further, as a range of different environmental stressors may operate simultaneously, investigating the combined effects of these stressors is an important task for future work.

A challenge for future studies is also to incorporate the variation between and within sexes, populations and species when investigating the impact of human induced environmental change. Given the increase in human disturbance on ecosystems, answering these questions is not only important to better understand how environmental fluctuations affect evolutionary processes, but also for conservation biology and studies of the resilience of organisms to anthropogenic induced environmental change.

Sammanfattning på svenska

Miljön varierar ständigt på grund av naturliga förändringar. Tyvärr har människans framfart medfört förändringar som inte är naturliga, utan som orsakats av oss (Tuomainen och Candolin 2010). Påverkan på naturen i form av global uppvärmning, övergödning och ett alltför hårt och riktat fiske har fått allvarliga konsekvenser för vår havsmiljö (Duffy 2006). Ökad algblomning, förekomst av fintrådiga alger samt förändringar av vattenkemin, så som förändrat pH, temperatur, och syrenivåer, är några av de problem som följt (Switzer m.fl. 2009). Fokus för denna avhandling kretsar kring vilka konsekvenser mänsklig inverkan på havsmiljön kan ha för fiskars reproduktiva beteenden.

Som studieorganism har jag använt arterna tångsnälla *Syngnathus typhle*, och mindre havsnål, *Nerophis ophidion*, som båda tillhör familjen kantnålar. Detta är en mycket specialiserad familj där det är hanen som är gravid. Efter en ritualiserad uppvaktningsdans överför honan sina ägg till hanen (Berglund 1994). Hos mindre havsnål bär hanen äggen klistrade på överkroppen, medan tångsnälla har en så kallad yngelpåse på stjärten som äggen ligger i. Hanen bär äggen i några veckor och förser dem då med näring och syre. Det är just denna överföring av näring och syre från hanen till äggen som är nyckeln till att man talar om hanlig graviditet i detta system, till skillnad från till exempel mun-ruvare, där hanen ruvar äggen i munnen, men för den sakens skull inte kallas gravid. Kantnålarna finner man om sommaren på grunda sandbottnar där det finns ålgräs, *Zostera marina*, en slags undervattensört även kallad bandtång. Kantnålarna är anpassade för att lika ålgräset till färg, form och rörelse. Ålgräsängarna är mycket viktiga för kantnålarna, men även för andra fiskar och andra marina organismer. Ålgräsängarna är också känsliga för störningar så som övergödning, vilket leder till blomning av fytoplankton samt ökad tillväxt av fintrådiga alger. Dessa snabbväxande alger växer på ålgräset och kväver det. Fintrådiga alger samt fytoplankton förändrar alltså kantnålarnas habitat till något som de inte längre föredrar att vistas i (Wennhage och Pihl 2007, Sundin m.fl. 2011), men det förändrar även vattnets genomsiktighet och ett flertal vattenkemiska faktorer.

Genom en rad studier har jag undersökt hur kantnålar påverkas av dessa miljöförändringar. I **kapitel I** visar jag att minskad genomsiktighet i vattnet hämmar val av partner hos tångsnälla. Jag såg också att möjligheten att använda lukt, tillsammans med, eller i stället för syn, inte kunde kompensera för den reducerade synligheten. I **kapitel II** visar jag genom genetiska ana-

lyser att reproduktionsframgången hos tångsnälla är lägre i grumligt vatten (grumligheten orsakad av algbloomning) samt att sexuell selektion på storlek av partner förändras. I **kapitel III** undersökte jag om utveckling av sexuella ornament påverkas av algbloomning. Till stor del verkar inte utvecklingen av honornas ornament påverkas av den grumliga miljön. Dock såg vi att hanarna inte längre kan välja den mest ornamenterade honan, som också är den mest fekunda honan, i grumligt vatten. Alltså kan sexuell selektion för ornament förändras, även om honorna själva inte verkar påverkas. I de två sista kapitlen undersökte jag hur andra vattenkemiska faktorer än genomsiktlighet påverkade kantnålarnas beteende. I **kapitel IV** såg jag att förhöjt pH, vilket är en av följderna av övergödning, drastiskt minskade antalet tångsnällor som parade sig. Jag undersökte även effekter av reducerat pH, vilket är en av följderna av ökade koldioxidutsläpp, och där såg jag att ett reducerat pH, i motsats till det förhöjda, inte hade någon märkbar effekt på hur många fiskar som parade sig. Slutligen, i **kapitel V** undersökte jag hur låga nivåer av syre, vilket också är en följd av övergödning, påverkade uppvaktning, dans och parningsframgång hos tångsnälla. Jag fann att medan det inte blev någon skillnad i den totala tid som fiskarna spenderade med att uppvakta varandra mellan lågt syre och kontrollen, så tog det längre tid innan uppvaktningen först skedde i lågt syre. Jag såg också att det tog längre tid för fiskarna att para sig i lågt syre än i kontrollen.

Genom dessa studier har jag visat att miljöförändringar kan påverka en mängd aspekter av djurs reproduktiva beteenden. Hur miljöförändringar påverkar reproduktiva beteenden kan variera från art till art, men även inom en och samma art, samt inom och mellan populationer. Jag visade också att hanar och honor kan påverkas olika. Detta innebär att det är svårt att generalisera hur miljöförändringar påverkar reproduktiva beteenden eftersom det beror vilken art, från vilken population, och vilket kön man undersöker. För framtida studier är det således viktigt att inkludera variationen inom och mellan arter, populationer och kön. Eftersom miljön påverkas av många olika faktorer samtidigt är det också en viktig uppgift för framtida forskning att se på den sammantagna effekten av olika faktorer. Eftersom mänsklig påverkan på ekosystem fortsätter att öka är det inte enbart viktigt att söka svar på dessa frågor för att bättre förstå hur förändringar i miljön påverkar evolutionära processer, utan även för bevarandebiologi, och för studier om organismers tolerans mot miljöförändringar.

Acknowledgements

Hang on folks, its time to get sentimental...

Once upon a time there was a little girl, playing in the garden in the early summer sun. Suddenly she comes up with the fantastic idea to see if there might be a viper under the old wooden board up in the forest where they are usually to be found. She walks up there and lifts the board, and yes, underneath lays a viper! Quickly, she grabs the snake by its tail, and puts it in a small plastic bucket. Proudly she walks back to the house to show her family what she, on her own, with absolutely no help from her older siblings, managed to not only find, but also to catch! Her father opens the door and she shows him the bucket, impatiently waiting to be praised. Instead, to her surprise, her father starts to tell her off: *Why did you catch this venomous snake on your own? Have I not told you not to play with venomous animals!* The father then looks down the bucket, with great curiosity, and he says: *Well, let's bring it inside then, and have a look at it...*

With this story I would like to thank my father, for he taught me the joy of nature. He had the greatest interest in all animals, from birds to fish to snakes... This interest he passed to me, for which I am grateful.

Det var en gång en liten flicka som lekte i trädgården en solig försommar-dag. Plötsligt kommer hon på en idé, varför inte gå och se om det ligger en huggorm under den gamla brädan uppe vid skogen? Sagt och gjort, hon går upp till skogsbrynet och lyfter på plankan, och tänk, därunder ligger det en huggorm! Blixtnabbt tar hon tag i ormens stjärt och lägger den i sin plasthink. Bubblande av stolthet går hon tillbaka till huset för att visa vad hon, helt utan hjälp från sina äldre syskon, inte bara hittat, utan också fångat! Hennes pappa öppnar dörren och hon sträcker fram hinken, otåligt väntandes på beröm. Döm om hennes förvåning när hon istället blir utskäld: *Varför har du fångat huggormen helt själv? Har jag inte sagt till dig att du inte ska leka med giftiga djur!* Pappan tittar sedan ner i hinken, med stor nyfikenhet, och säger: *Hrm, ja, vi tar väl in den då, så vi får se lite på den...*

Med denna historia vill jag tacka min pappa. Han var intresserad av alla djur, från fåglar till fiskar till ormar... Detta intresse förde han vidare till mig, vilket har lett mig till där jag är idag. För det är jag evigt tacksam.

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"tillfälligt normala inga garantier; fisk med stjärt; don't mess with my flap; mätbrädan blir mer och mer hydrofob; lappar flyter utom synhåll; jag heter hara kan hoppa 2 steg i taget; Nissling skär gurkor till ögon; hälften av hälften som är slut; grav grov afasi; hjärnan förtvinar hämtar sig aldrig; jag kommer liksom inte ihåg; ice metallic firre; bara snyta sig osnuten; pas de flap; Anders morrar tappar kontrollen; svin och svibsish; oj oj oj oj skitbra bara rassla iväg; mama mia"

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