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The influence of eutrophication on sexual selection in sticklebacks

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ACADEMIC DISSERTATION

To be presented, with permission of the Faculty of Biosciences of the University of Helsinki, for public criticism in the Lecture Room of Tvärminne Zoological Station (Tvärminne) on 27th of February 2009 at 12 o'clock noon.

Helsinki 2009

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Contents

List of original publications

This thesis is based on the following publications:

I   Candolin U. and Heuschele J. (2008) Is sexual selection beneficial during adaptation to environmental change? Trends in Ecology and Evolution. 23. 446-452

II   Heuschele J., Fisken Ø. and Aksnes D. A spectral model of detection distance in fish. Manuscript.

III   Heuschele J. and Fisken Ø. The influence of eutrophication on encounter rates in sticklebacks. Manuscript.

IV   Heuschele J., Mannerla M., Gienapp P. and Candolin U. Environment-dependent use of mate choice cues in sticklebacks. Manuscript

V   Heuschele J. and Candolin U. (2007) An increase in pH boosts olfactory communication in sticklebacks. Biology letters. 3. 411-413.

VI   Heuschele J. and Candolin U. Improved mating success of parasitized stickleback males in dense vegetation. Manuscript.

The publications are referred to in the text by their roman numerals.

Contributions concerning co-authored papers

Paper	I	II	III	IV	V	VI
Initial idea	UC, JH	JH, ØF	JH, ØF	JH	JH	JH
Study design	UC	JH, ØF, DA	JH, ØF	JH, UC	JH, UC	JH, UC
Data collection	UC, JH	JH	JH	MM, UT, JH	JH, JA, EK	JH
Analysis	UC	JH, ØF, DA	JH, ØF	JH, PG, UC	JH, UC	JH, UC
Manuscript preparation	UC, JH	JH, ØF, DA	JH, ØF,	JH, UC	JH, UC	JH, UC

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Abstract

The increasing ecological footprint of the human population alters ecosystems worldwide. A growing number of studies reveal that human-induced changes interfere with natural and sexual selection. The aim of this thesis was to determine how environmental change alters sexual selection by using eutrophication of the breeding habitats of the threespine stickleback *Gasterosteus aculeatus* as a model system. Sexual selection is an important evolutionary process, with consequences at individual, population and species level (Chapter I). The different parts of the thesis focus on the influence of eutrophication on mate detection, the use of visual and olfactory mate choice cues, and the distribution of mating success among nesting males.

In Chapter II and III, we simulate how phytoplankton turbidity decreases mate encounter rate by constraining the visual range. We show that the reduction in mate encounter rate is moderate at the breeding grounds in the Baltic Sea at normal spring bloom turbidity values. This suggests that phytoplankton turbidity is unlikely to decrease assortative mating due to increased search costs. Chapter IV shows that sticklebacks alter the use of cues used in mate choice when visibility decreases, reducing the use of visual cues and increasing the use of olfactory cues. Moreover changes in the water chemistry in eutrophied areas, caused by intensified photosynthetic production, seem to facilitate the use of olfactory cues (Chapter V). However, a field experiment revealed that breeding in eutrophied waters could be costly at both the individual and the population level, since more parasitized males received more eggs in eutrophied waters, although these males most likely are of low genetic quality (Chapter VI).

Eutrophication clearly affects mate choice and mate competition by influencing mate detection, mate assessment and the distribution of mates on the breeding grounds, but the consequences this may have on sexual selection on traits and ultimately on population dynamics and persistence remain unclear. The thesis shows the difficulty in predicting the consequences of human-induced environmental change on sexual selection at the individual and the population level.

The influence of eutrophication on sexual selection in sticklebacks

1. Human environmental change

The increasing ecological footprint of the human population alters ecosystems worldwide. Every aquatic and terrestrial is influenced directly or indirectly by human impact (Vitousek et al. 1997). This influence reaches even remote ecosystems (e.g., the Antarctic Ocean, Halpern et al. 2008) through overfishing, pollution or global warming. The earth has never been a stable place, but with the exceptions of catastrophic events, such as volcanic eruptions or earthquakes, 'natural' changes tend to reoccur in time and/or happen at a relatively slow pace. In contrast, human environmental change can generate sudden novel conditions (e.g. deforestation).

Studies of anthropogenic impact on ecosystems and species tend to focus mainly on ecological consequences, such as changes in the distribution of species and their abundance. Indeed, alterations of the abiotic and biotic environment can have both direct and indirect impacts on population dynamics. For example, human hunting pressure on sea lions led orcas to shift their diet to sea otters. This

shift initiated a trophic cascade, which allowed sea urchins populations to thrive and over-graze kelp forests in North America. As a result, the abundance of species depending on the kelp forest ecosystem declined dramatically (Estes et al. 1998). In addition to such ecological effects, changes stemming from anthropogenic sources often lead to novel selective pressures and ultimately, evolutionary change. In the last decade, several studies have documented evolutionary change originating from human impacts (Palumbi 2001). The development of resistance in agricultural pest species against aggressive pesticides is a convincing example of human induced evolution (reviewed in Roush and McKenzie 1987). Moreover, multi-resistant pathogens have developed resistance to common antibiotics. This has become a global epidemic problem in hospitals (Dennesen et al. 1998). Evolutionary adaptations are not limited to resistance traits, but can also more generally affect life history traits. For example, increased fishing pressure on larger and older individuals can cause fisheries induced evolution. In North Atlantic cod (*Gadus morhua*) the size and age at maturation was significantly

reduced even years after a total fishing moratorium, compared to earlier measurements (Olsen et al. 2004). In addition to effects associated with naturally selected traits, a growing number of studies have shown that human induced changes of the environment can also influence sexual selection. The influence on sexual selection is caused by numerous factors, including climate change (Weatherhead 2005), eutrophication (Seehausen et al. 1997), alien species (Taylor et al. 2006) or construction works (Waples et al. 2008). However, the impact of human-induced change on patterns of sexual selection has received relatively little attention (e.g. in comparison to work on resistance, life-history evolution). Thus, in the following, I focus primarily on the effect of anthropogenic effects on sexual selection. I first provide an overview of the general importance of sexual selection, and then discuss proximate pathways of the influence of human environmental change on sexual selection and consequences at individual and population levels.

2. Sexual selection

Sexual selection drives the evolution of traits that improve fertilization success in situations with limited access to gametes of the other sex (Andersson 1994, Kokko and Jennions 2008). Sexual selection in general stems from mate choice, intra-sexual competition for mates, and mate coercion, and leads to the evolution of elaborate traits such as the extreme antler size of elk and deer (e.g. Darwin 1859, 1871; Gould 1974) or the song repertoire of birds (Catchpole and Slater 1995). Sexual selection is also important for macro-evolutionary patterns and biodiversity. Divergent mate preferences can lead to a prezygotic isolation and sexual selection is a major force in reinforcing reproductive isolation at the secondary contact of allopatric populations. Moreover the initial divergent trait evolution can also be induced by sexual selection itself (reviewed in Schluter 2001). For example, the rapid radiation (12500 years) of haplochromine Cichlids can be partially explained by sexual selection acting on colour polymorphisms (Seehausen and van Alphen 1999).

2.1 Costs and benefits

Animals can gain direct and indirect benefits from assortative mating (reviewed in Andersson 1994). However, behaviours such as mate coercion and mate competition can be costly for both the competitor and the mate.

In the following discussion I will assume females to be the choosy sex and males to compete for mates. This is the predominant case in natural systems, although sex roles are reversed in a number of species, e.g. certain pipefishes (e.g. Vincent et al. 1994).

Direct benefits

Female choice can be associated with direct benefits including increased fertility, paternal care and nuptial gifts for the choosy individual. These are more or less direct investments or features that increase the immediate success of the females. Many territorial fish species, for example, provide paternal care, which consists of aerating eggs and defending the brood against predators and conspecifics (e.g. Forsgren 1997). Direct benefits can, but do not have to be, correlated with indirect benefits associated with mate choice (Møller & Thornhill 1998).

Indirect benefits

Indirect benefits increase the lifetime reproductive success of the female by providing favourable sets of alleles to her offspring. Females can choose for "good genes" by selecting mates with traits that indicate heritable viability of the father (Houle and Kondrashov 2002). In three-spined sticklebacks, for example, the intensity of red nuptial colouration of the males correlates with heritable parasite resistance (Barber et al. 2001, Milinski and Bakker 1990). The costs of such traits ensure their honesty indicating "good" males (Hamilton and Zuk 1982). Honesty can therefore be enforced through male-male competition (Candolin 2000a), predation pressure (Forsman and Hagman 2006) or limited resource availability. For example, carotenoid-based coloration is constrained by the availability of food items, as these molecules cannot be produced *de novo* by vertebrates.

Indirect benefits for the offspring can also evolve independently of traits reflecting viability. Fisher (1930) envisaged a self-sustained process, whereby genes for a female preference and "good" genes for the preferred trait become genetically correlated. This is called a Fisherian runaway selection or Fisher-Zahavi process (reviewed in

Kokko et al. 2006). According to this hypothesis, females are expected to choose males with ornamental traits that are likely to increase the attractiveness of offspring (i.e. sexy sons hypothesis), which in turn is expected to increase female fitness.

Selection for compatible sets of alleles also produces offspring of favourable genetic combinations and higher fitness (Neff and Pitcher 2005). Preference for genetic compatibility has been found to be especially important in the evolution of the major histocompatibility complex (MHC). Indeed, MHC-dependent mating preferences have been demonstrated in humans, mice and sticklebacks (reviewed in Penn and Potts 1999).

From a population-level perspective, sexual selection can reduce the mutational load due to the positive covariance between male condition and sexual signals (Agrawal 2001, Siller 2001). It also eases the fixation of beneficial alleles (Whitlock 2000). A theoretical study showed that the covariance between signal and condition could also arise from sexual selection alone (Lorch et al. 2003).

Costs

Despite potential benefits, sexual selection is also associated with a variety of costs that can have both individual and population-level consequences. For example, sexual selection can lower the overall viability of a population, and some have hypothesized that sexual selection can lead to population extinction in some cases (e.g. Tanaka 1996). The exaggeration of signals during Fisherian runaway selection can decrease fitness of the organisms displaying the ornaments, and choice may negatively affect choosing females (Friberg and Arnqvist 2003).

If traits indicate viability, they are supposed to be costly, so that only high quality partners can express them (Hamilton and Zuk 1982). This may lead to a reduction of the potential investment in the offspring in species with paternal care (Price et al. 1993). Mate coercion costs for females often emerge from direct harm induced by males. For example, in Drosophila, males try to increase their fertilization success by transferring a seminal fluid together with sperm. This fluid, however, increases the mortality of females (Chapman et al. 1995). A comparison between monogamous and promiscuous populations revealed a higher net

reproductive rate of the monogamous populations (Holland and Rice 1999). Hence, in this example, sexual selection for "harmful" males reduced the populations' potential reproductive rate.

2.2 Sexual signalling and mate choice cues

Mate choice cues are traits, which are used in mate choice decisions. These can be phenotypic traits but also resources such as territorial quality, which are assumed to reflect mate quality. If cues have undergone selection to function in communicative purposes, they are called signals (Candolin 2003).

Mate choice and mate competition involve the assessment of traits of potential mates, and such traits are assumed to reflect aspects of male quality of prospective partners. Mate choice decisions are often based on more than one cue (Candolin 2003), including acoustic, tactile, visual, and olfactory signals. The multiple message hypothesis for the use of multiple cues suggests that different cues are used to assess different aspects of male quality (Møller and Pomiankowski 1993). For example, human male odour contains information about their major histocompatibility alleles, which can be perceived by females (Wedekind and Furi 1997). Likewise, visual cues (e.g. facial features) can be used to assess the physical strength of prospective mates, and hence potential direct benefits in species in which females benefit directly by associating with relatively strong males (Sell et al. 2008).

However, different types of cues can also indicate similar qualities, in which case using multiple cues can be a back-up strategy that increases the likelihood of an optimal decision by females, even if the assessment of some of the cues is constrained (Møller and Pomiankowski 1993, Candolin 2003).

3. The influence of environmental change on sexual selection

The biotic and abiotic environment determines the costs and benefits of sexual selection. The display of ornaments and mate choice signals are normally adapted to particular environmental conditions (Cockburn et al. 2008), in which a balance between viability and sexual selection is established. If human impact alters environmental conditions, the current selective regime is expected to change.

11

The role of sexual selection in adaptation

An environmentally induced shift in the balance between the costs and benefits of sexual selection might impose substantial fitness costs at the individual level, which in turn might decrease the possibility of successfully adapting to a novel environment. However, the benefits of sexual selection might ease the adaptation of individuals and populations to novel conditions. In chapter I U. Candolin and I review past and current literature to evaluate the overall role of sexual selection in the ability of organisms to adapt to novel environments. Despite the growing number of studies in this field, the role of sexual selection in adaptation to novel environments is still uncertain.

Numerous studies show that constrained mate choice and mate encounter rates in novel environments can relax sexual selection. Strong sexual selection reduces the amount of genetic variance in a population (Kirkpatrick and Ryan 1991). Genetic diversity is a necessity for populations to respond to novel selection pressures. Hence, relaxed sexual selection in a changing environment might be beneficial to maintain this variance and therefore preserve a population's ability to cope with future

environmental change. The mechanistic pathways through which environmental change decrease sexual selection will be discussed in detail in the following paragraphs.

If sexual selection is strong and does not oppose natural selection, then sexual selection can have positive effects on the ability of a population to adapt to novel environment conditions (Spottiswoode et al. 2006). However, most empirical studies have found either no effects or negative effects of sexual selection on the rate of adaptation (Holland 2002, Rundle et al. 2006). If these effects are sufficiently strong, they can potentially drive a population to extinction (Doherty et al. 2003), or in case of hampered mate choice, to reversed speciation (Seehausen et al. 1997).

Due to the important role of sexual selection in enforcing reproductive isolation between separated populations, environmental change and novel sexual selection pressures can also lead to speciation (Schluter 2001).

Environmentally altered sexual selection can constrain or boost the ability of a population to cope with human induced changes. In summary, possible evolutionary consequences that arise from interference with sexual selection

are (1) adaptation, (2) speciation, (3) reversed speciation and (4) extinction, with adaptation and reversed speciation being the most likely ones (Chapter I).

Pathways of influence on sexual selection

In the following, the influence of human environmental change on mate detection (Chapter II-III), the use of mate choice cues (Chapter IV-V) and induced changes in the density and operational sex ratio (i.e. ratio of males and females prepared to mate, operational sex ratio (OSR); Emlen and Oring 1977) of the population (Chapter VI), and its consequences for the strength of sexual selection are discussed. Figure 1 illustrates the general pathways of human influence on sexual selection that are discussed in this thesis. I use the eutrophication of breeding habitats of three-spined stickleback *Gasterosteus aculeatus* as a model system.
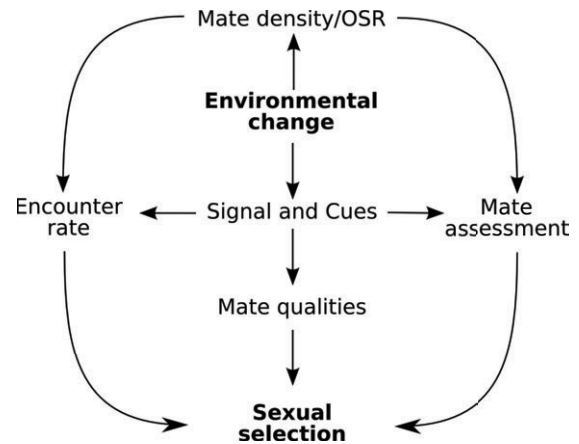

Figure 1: General overview over the different pathways and interactions between human environmental change and sexual selection discussed in this thesis

Eutrophication

Eutrophication is the enrichment of ecosystems with nutrients like phosphorus and nitrogen. The increased nutrient input from human origin has made it one of the main pressures on aquatic ecosystems worldwide (Smith 2003). Eutrophication has severe ecological impacts on both organisms and habitats, including the formation of hypoxic bottom layers (Bonsdorff et al. 1997, Karlson et al. 2002). Additionally, eutrophication might also affect the behaviour of aquatic organisms by limiting searching efficiency (Utne-Palm 1999) and mate choice (Seehausen et al. 1997, 2008, Wong et al. 2007). In the Baltic Sea, a shallow brackish sea in northern Europe, eutrophication has led to increased phytoplankton turbidity (Wasmund and Uhlig 2003) and increased growth of filamentous algae mats. These cover large parts of the shallow benthic zone (Lehvo and Bäck 2001). Phytoplankton turbidity is known to relax sexual selection in several fish species (eg. Järvenpää and Lindström 2004) and can cause reversed

speciation (Seehausen et al. 1997). One of the species affected by Baltic eutrophication is the three-spined stickeback, *Gasterosteus aculeatus* L (Candolin et al. 2007, Wong et al. 2007).

A short primer to stickleback biology

Distribution

The species *Gasterosteus aculeatus* belongs to the order Gasterosteiformes within the family Gasterosteidae. It is an extensively studied model organism in evolutionary and behavioural biology, where detailed knowledge about mating preferences and behaviour is available (e.g. Wootton 1984, Bell and Foster 1994). The ecological distribution of three-spined sticklebacks spans the whole northern hemisphere. They inhabit fluvial and lentic freswater habitats, as well as are part of coastal saltwater and brackish ecosystems. (Bell and Foster 1994).

Life history

In the Baltic Sea, three-spined sticklebacks take 1 to 2 years to reach maturity. Under favourable laboratory conditions sticklebacks can live up to 5 years and complete up to 5 breeding cycles. (Bell and Foster 1994). However, fish of the Baltic Sea population typically experience only one breeding season after which they die. The breeding season in southern Finland (Tvärminne research station) begins in the beginning of May and lasts until mid July.

Breeding behaviour

Breeding grounds occur in shallow waters and have been documented to depths of 6 meters (Kynard 1978). In the Baltic Sea the exact depth distribution is unknown, and presumably depends on the local properties of the habitat (e.g. substrate, latitude). Males are territorial and provide paternal care for the offspring (van Iersel 1953; Wootton 1976). They build a nest on the sea bottom from various materials, including algae, plant material, and sand (Wootton 1976). These materials are adhered together with spiggin, which is produced in the kidneys of the fish (Jakobsson et al. 1999). When a female decides to spawn with a male, she enters a tunnel through the nest and deposits her clutch inside the nest. Immediately afterwards, the male fertilizes the eggs. During a given reproductive period, males accumulate eggs from several females (Wooton 1976). During the egg stage, the parental male maintains the nest and fans the eggs to deliver oxygen rich water. After approximately 8 - 14 days the fry hatch, and the males guard them for additional 2 weeks (Whoriskey and Fitzgerald 1994). Both males and females typically have several egg cycles within their breeding season (Wootton 1976).

Evolutionary aspects

North American marine sticklebacks repeatedly recolonised freshwater habitats after the ice age (McKinnon and Rundle 2002). This demonstrates the species general ability to adapt to novel environments. Moreover, several sympatric species pairs have been documented (reviewed in McKinnon and Rundle 2002). In one of those pairs, limnetic and benthic forms showed differences in the use of olfactory cues. This difference in cue use potentially enhances reproductive isolation between the two species (Rafferty and Boughman 2006). The introduction of an alien species, the crayfish *Pascifasticus lenisculus*, may have reversed the isolation and led to the hybridization of the species pair (Taylor et al. 2006). This scenario could be

comparable to the hybridization events of Cichlid species following eutrophication of Lake Victoria (Seehausen et al. 1997, 2008).

3.1 Interference with mate encountering

Sexual selection is a frequency-dependent process, and is therefore influence by population density and the number of possible mates (reviewed in Kokko and Rankin 2006). However, individuals do not have universal information about the real mate availability and have to gather information regarding prospective mates based on the encountered males (Janetos 1980, Real 1990). Therefore, not only density, but rather the actual encounter rate influences the strength of sexual selection.

Environmental change can affect encounter rate by either changing the absolute number of available partners or the detection of prospective partners.

Decreased visibility limits encounter rates in turbid habitats (Utne-Palm 2002). Phytoplankton blooms in eutrophied areas, for example, decrease underwater visibility and change the spectral composition of downwelling light (Mobley 1994).

A model of detection distance is a prerequisite to determine the influence of environmental change on encounter rates. In chapter II, together with collaborators, I develop a spectral model of visual detection distance in fish. The presented model accounts for the spectral properties of the environment (water and target) and for the visual sensitivity of the fish species. We extended an established model of visual range (Aksnes and Giske 1993, Aksnes and Utne 1997) using sensitivity data from optomotoric experiments. These data are available for numerous fish species, thus making it easier to apply our approach to other species. The model was calibrated using data from two-spotted gobies *Gobiusculus flavescens* (Utne -Palm and Bowmaker 2006). The comparison with the original model revealed that a spectral approach might prevent errors in predicting the visual range of fish, particularly for clear waters deeper than 10 m and for phytoplankton rich water below 5 m depths. Our model provides a tool to explore effects of spectral changes in aquatic environments and to approximate the detection range in fish. In chapter III we apply this bio-optical model of visual range (Chapter II) to determine how phytoplankton turbidity hampers visibility and encounter rates in three-spined sticklebacks.

We parameterized the model so that it simulates the changing spectral properties of the Baltic Sea using a bio-optical model for Baltic Case II (visually complex) waters. We further accounted for increased growth of filamentous algae, the visual sensitivity of stickleback females, and the breeding colouration of the territorial males. Although the detection distance was strongly constrained by increasing phytoplankton turbidity, the model predicts only modest changes in mate encounter rate over shallow regions during the day. However, nests located deeper than a few meters will experience reduced frequency of female visits under eutrophic conditions, which may reduce the strength for sexual selection through female mate choice in those habitats. Moreover, encounter rates will be reduced at overcast days and during nighttimes. Whether a small decrease in encounter rate can cause time and energy costs big enough to reduce the strength of sexual selection cannot be answered with our model. Experimental tests with sticklebacks showed that time costs are not as important as energy costs for the strength of sexual selection (Milinksi and Bakker 1992). Our model also points towards the importance of behavioural traits such as swimming speed and

boldness. If sticklebacks increase their velocity while searching they could easily compensate for the loss in vision. Interestingly, the peak sensitivity of sticklebacks corresponds to the lowest attenuation caused by the phytoplankton in Type II waters. The evolutionary history of sticklebacks in habitats with natural occurring eutrophication might explain this seemingly adaptive trait.

3.2 Interference with mate assessment

Traits and individuals are selected under the prevailing conditions of a habitat; hence over evolutionary time individuals should become adapted to an environment. This process can take many generations, but some traits even change within a dozen generations (Hendry et al. 2007). The intensity of the display of ornaments and the mate choice cues themselves (Endler 1993, Cockburn et al. 2008) are adjusted to the environment by predation pressure, as well as physiological or physical constraints. In *Photinus* fireflies the main cost of signalling is imposed by predation pressure rather than physiological costs of producing bioluminescent flashes (Woods et al. 2007). Besides the display, the sensitivity of organisms to these cues is also tuned to the environment

(Boughman 2001) Human activities change chemical and physical habitat properties directly or indirectly, and thus the signalling environment. The spectral properties are particularly changed in aquatic environments, for example by phytoplankton and clay turbidity or humic acids (see Seehausen et al. 1997, 2008, Utne-Palm 2002). In lake Victoria in Africa, human induced changes in water turbidity led to the hybridization of two closely related sympatric sister species. Reproductive isolation was based on the visual cues of the body coloration. In this case, the changed spectral condition of the water inhibited the assessment of the colouration of prospective partners, which led to the hybridization of these two species (Seehausen et al. 1997).

Visual cues

In many stickleback populations, males express intensive red nuptial throat coloration, as well as intensely blue coloured eyes (Frischknecht 1993), which give them a reproductive advantage through female mate choice. Coloration has been shown to reflect immunocompetence of the males (e.g. Milinski and Bakker 1990), parenting ability (Candolin 2000b), and increased parasite resistance of their offspring (Barber et al. 2001). Male colouration

not only serves as an attractant and cue for females, but also plays a major role in male-male competition (Candolin 2000a). Strongly coloured males are able to suppress attacks by other males better than moderately coloured ones. In contrast, duller males induce fewer attacks. A comparison of the bio-optical model of diffuse attenuation (Kaczmarek and Wozniak 1995) and the spectral sensitivities of sticklebacks shows that the diffuse attenuation coefficient caused by phytoplankton turbidity is strongest in a region of the wavelength spectrum which is important for sticklebacks to decode the red nuptial coloration (Rowe et al. 2004, Chapter III). Therefore, females might not be able to assess males based on the red nuptial coloration even in shallow eutrophied waters.

Visual cues also lose their honesty in turbid waters, due to a lack of male-male competition (Wong et al. 2007). It is known that in addition to phytoplankton turbidity, increased growth of filamentous algae reduces male-male competition in this species (Candolin et al. 2008).

Individuals may try to compensate for constraints on visual mate assessment by using different cues. Sensory compensation has been found in fathead

minnows (Hartman and Abrahams 2000) and diving beetles (Åbjörnsson et al. 1997), where the response to alarm substances was increased in visually constraint environments.

Olfactory cues

Besides vision, olfaction plays a major role in mate choice in sticklebacks. Females are able to assess the major histocompatibility complex (MHC) alleles of a male, by evaluating the MHC peptide ligands that are released into the water from the males (Milinski et al. 2005). The relationship between mate choice, major histocompatibility complex and olfaction has been found in many vertebrate species, including humans (Penn and Potts 1999). MHC-genes code for two different classes of MHC-peptides, which are essential for vertebrate immunological self-recognition and immune response. Hence mate choice for these alleles ensures a favourable set of alleles to the offspring (Penn and Potts 1999). Whereas many other vertebrate species choose partners with a dissimilar set of MHC alleles (e.g. Wedekind et al. 1995, Richardson et al. 2005), sticklebacks have been found to choose a partner with a compatible and optimal number of MHC class II alleles (Aeschlimann et al. 2003).

Hence, in sticklebacks the use of these olfactory and visual cues appears to be more consistent with the multiple messages hypothesis than the back-up hypothesis.

Environment-dependent use of cues

In Chapter IV we studied the influence of phytoplankton turbidity on the relative use of visual and olfactory cues in sticklebacks. Gravid females were allowed to choose between two nesting males in the presence of visual cues, olfactory cues, and both visual and olfactory cues in either clear or turbid water. Under turbid conditions, females primarily used olfactory cues in mate choice in comparison to visual cues. In clear water, the opposite behaviour was observed. Interestingly, the mate preference of females seems to vary across the olfactory and visual cues conditions. This suggests that human induced environmental changes can lead to shifts in the underlying targets of sexual selection.

Because the use of olfactory cues becomes more important in eutrophied environments, it is of interest to determine how this signal is influenced by eutrophication. Increased algae growth (phytoplankton and filamentous algae) alters not only the visibility of the

water, but also changes the chemical characteristics of the water. Augmented photosynthetic production can lead to diel pH fluctuations in the water (Reddy 1981), by reducing the amount of dissolved carbon dioxide in the water. In the experimental study described in chapter V, gravid female sticklebacks were exposed to water containing male odour. This water was either kept at an ambient pH (similar to the natural conditions) or the pH was increased by adding NaOH. Females clearly favoured male smell that entered the test aquaria with a raised pH value. A general preference for more alkaline water was ruled out. This indicates that the changed chemistry in eutrophied waters might favour olfactory cues, which could compensate for constrained visual communication in those habitats.

Generality of results

Although most empirical examples of human interference with signalling and signal patterns are from aquatic habitats, similar interference patterns with mate choice cues occur in terrestrial ecosystems. Gomez and Théry (2004) showed that plumage colouration of rainforest birds is adapted for crypsis to the light conditions in their habitats. Deforestation in such areas can directly influence the light and acoustic properties in the surrounding areas (Endler 1993). There is also growing empirical evidence that organisms show an adaptive response to acoustic masking stemming from city and traffic noise. Urban great tits showed a shift of their minimum song frequency in city areas. This is thought to prevent the signal from being masked by noise of lower frequency generated by modern traffic (Slabbekoorn and Peet 2003). In a similar way European nightingales from noisy areas sing louder compared to calmer areas (Brumm 2004). Besides the modulation of signals, organisms sometimes also show an amplification of the signals, to ensure the transmittance of their signals.

3.3 Interference with mate density, OSR and quality distribution

The previous paragraphs have described how human environmental change constrains and alters the use of signals and cues in mate detection and mate assessment. The strength of sexual selection also depends on the spatial distribution and abundance of potential mating partners (Emlen and Ohring 1977, reviewed in Kokko and Rankin 2006). The ratio of available males to females, i.e. the operational sex ratio (OSR), is advocated as a good proxy of

the strength of sexual selection (Emlen and Ohring 1977, Kvarnemo and Ahnesjö 1996), if monopolization is maintained with increasing sex biases (Klug et al. unpublished data).

The benefits of mate choice also depend on the extent of variation in mate quality of the other sex (Parker 1983, Reynolds and Gross 1990, Real 1990, Johnstone et al. 1996). Hence, any external influence of the mate quality distribution is likely to influence the strength of mate choice in a mating system, especially since variation in mate choice can be of bigger importance for sexual selection than other factors such as the potential reproductive rate (Kvarnemo and Forsgren 2000). The environment can determine the OSR, by limiting the number of possible territories in sticklebacks and in other breeding systems with territorial males. This can happen directly by limiting the number of nest sites (Borg et al. 2002) or indirectly by influencing the intensity of male-male competition. In sticklebacks, increased growth of filamentous algae seems to lead to reduced male-male competition and also to changes in the distribution of eggs amongst males (Candolin 2004, 2007). Candolin (2004) found that eggs were distributed more evenly amongst male nests in densely vegetated areas. The consequences of such a relaxation in sexual selection depend on the density and quality of nesting males in affected areas.

I tested the mate distribution of three-spined sticklebacks in sparse and densely vegetated patches in a field experiment (Chapter VI). Using submersed vegetation patches I simulated densely and sparsely vegetated patches. Stickleback males accepted these structures almost immediately and built their nests within these areas. Many more males were nesting in dense vegetation. Since the percentage of males, which received eggs, did not differ between the treatments, it resulted in a much higher egg number at the end of the season. Interestingly, highly parasitised males had more eggs in their nests than males with few or no parasites. This contradicts earlier findings that find less parasitised males to be more successful (Milinski and Bakker 1990, Blais et al. 2004).

Whether the observed pattern arises through changes in female choice or male-male competition has yet to be determined. However both factors are potentially affected by reduced visibility (Candolin et al. 2007, Wong et al. 2007, Engström-Öst and Candolin 2007).

Dense vegetation limits the ability of females to compare males based on visual cues and prolongs female inspection times (Candolin et al. 2007, Engström-Öst and Candolin 2007). As previously mentioned, reduced visibility due to algae growth also reduces interactions among males and hence the social control of honest signalling. This allows for increased dishonest signalling of males (Candolin 2000, Wong et al. 2007). Therefore, females were potentially less able to judge male condition in dense vegetation.

Whether the success of parasitised males has long-term consequences for population viability depends on whether mating with parasitised males is beneficial for females. This in turn depends on the direct and indirect benefits these males can provide (genetic quality, parental effort). As parasitized males may have a low probability of future reproductive success they might invest more into current reproduction than males with more future reproductive opportunities (Candolin 2000b). The increased number of eggs might result in a higher number of offspring, possibly compensating for lower individual survival due to presumably poor genetic

background of the fathers. In addition, areas with filamentous algae increase the parenting ability of males and the survival rates of the offspring, probably due to higher oxygen levels and reduced guarding efforts (Candolin 2008).

4. Conclusion

The world is changing at an accelerating pace due to human impact. This has consequences for ecological and evolutionary processes. Sexual selection is an important part of natural selection, with consequences for individuals, populations, and species.

The aim of this thesis was to determine how environmental change alters sexual selection by using the eutrophication of the breeding habitats of the three-spined stickleback *Gasterosteus aculeatus* as a model system. The different parts of the thesis focus on the influence of eutrophication on mate detection, the use of visual and olfactory mate choice cues, and the distribution of mating success.

In an initial step, we simulated to which extent phytoplankton turbidity decreases male encounter rates by constraining the visual range of the fish (Chapter II/III). We showed that this reduction was very moderate at the typical depth of the breeding grounds and turbidity values of

spring blooms in the Baltic Sea. This suggests that a reduction in encounter rates due to phytoplankton turbidity is unlikely to cause time costs large enough to decrease assortative mating in females. Chapter IV shows that sticklebacks compensate for the lack of visibility in turbid environments by increasing the use of olfactory cues. Because various mate choice cues can code for different benefits, shifts in the importance of cues (Chapter IV) can ultimately alter the genetic composition and evolutionary trajectory of the population. Moreover, changes in the water chemistry in eutrophied areas, caused by intensified photosynthetic production, actually seem to support the use of olfactory cues (Chapter V). A field experiment further revealed an unusual pattern in reproductive success (Chapter VI). Despite the higher abundance of males, parasitised males were more likely to receive eggs in dense vegetation. An overview over the different pathways tested and discussed in this thesis is described in figure 2.

The work presented herein illustrates the difficulty in predicting the consequences of human-induced environmental change on sexual selection. Eutrophication clearly affects mate choice and mate competition by influencing mate detection, mate assessment and the distribution of mates on the breeding grounds, but the consequences this may have on sexual selection on traits and ultimately on population dynamics and persistence remain unclear.

Human impact on sexual selection is not restricted to fish or aquatic habitats, but can be anticipated in almost all ecosystems affected by humans, which nowadays is almost every single system on this planet (Vitousek et al. 1997, Halpern et al. 2008).

Because of worldwide species decline and unprecedented environmental changes, studies of sexual selection and their mechanistic and causal pathways are certainly necessary to anticipate and potentially counter evolutionary effects of anthropogenic impact.
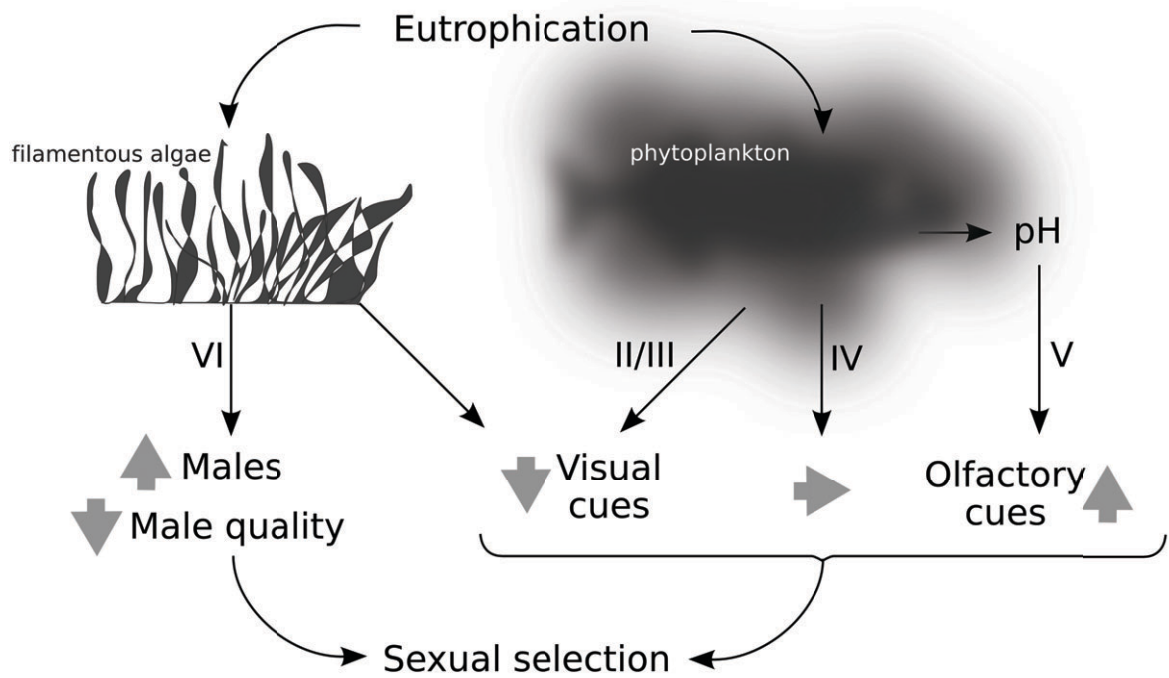
Figure 2. The influence of increased growth of filamentous algae and phytoplankton on sexual selection in sticklebacks for the pathways discussed in the different chapters (referred to by Roman numerals). Grey arrows indicate the direction of the observed effects of eutrophication.

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Acknowledgements

This thesis and my life would consist of nothing but blank pages, if it wouldn't be for friends, colleagues and my family who accompanied me all this time.

I guess there wouldn't even be a 'book', wouldn't Ulrika have given me the opportunity to come to Finland and by this to fulfill a kids dream of mine - getting actually paid for watching fish. Thanks a lot for answering patiently to all my questions and for surviving my denglish manuscripts. I hope your happiness-curve will continue to have a steep positive slope.

I am also grateful for the people of my group and the students who helped and worked with me in the field. Wouldn't it be for Miia, Ulla, Leon, Johanna, and Essi sample sizes in this thesis would be much smaller. Thanks a lot for taking away some of the workload, I hope I wasn't the only one who profited.

Important parts of this thesis were developed in close collaboration with Øyvind and Dag in Norway. Especially I want to thank Øyvind for always welcoming me in Bergen, and for introducing me to the world of modelling. I also want to thank all the other great people there, Sigrunn, Anne-Christine, Agur, Olav, Nico, Nicolas, Loïc, Stephanie, Christian, Katja, Øystein and Per, who gave important impulses for all of my papers and made my visits always a pleasure.

A "dankeschön" also to Hanna and her Kokkos. Although I often was lost in our journal club, it certainly triggered some kind of "logical scientific thinking" in my brain. Thanks to Jostein, Christoph, Wouter, Mike, Ayco and Chris for always being a challenge at the Tischfussball.

I am also grateful to Sofia, Jonathan, Katja, Pekka and Phillip who were a big help and good friends during my time in Finland, and especially the last one had to suffer severely from my constant statistic questions. Thanks also to the goby girls Marja (turbid) and Maria.

Thanks Hope, for being the perfect wine-drinking companion during the Tvärminne summer, and for your willingness to proofread large parts of this thesis.

Most of the work for this PhD was done in Tvärminne. In all my field seasons I had a great 'relaxing' time. A big part of that was due to the friendly and nice stuff and scientists there, Marko, Magnus, Raija, Björn, Thomas, Dieter, Annette, Tina to name just a few.

Thanks to Veijo for agreeing to be the Custos in this defense and to Lotta for coming to Finland to be an opponent. I am also grateful for the comments and reviews from Bob Wong and Jenny Boughman.

And of course a big thanks goes to all the friendly people in the Viikki institute and particularly in the office (Raine, Tiina).

I also want to thank my friends and family in Germany and elsewhere for not forgetting me during my stay here in the north, and for always being such nice hosts during my visits. I am grateful for Thomas' comments on the introduction, and Stu's comments on an early version of the modeling paper.

I especially cannot thank my friends here in Helsinki enough, as the time with them was great even in the darkest winter days. Seba and Felice, sorry for being such a risky captain during your stay in Tvärminne, and thanks a lot Feli for the cover illustration. Thanks Fanny for being the most welcoming Finn on earth and a big merci goes also to Nadia (the star), Silvia, Francesco, Lucia, Elissa and Brenda.

The biggest hug goes out to Bea; thanks for being there these years and for what you are. Life would be boring without you. Merci vielmals.

And without my parents, I wouldn't actually be here after all, which makes this thesis theirs not mine.