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Population responses to anthropogenic disturbance: lessons from three-spined sticklebacks *Gasterosteus aculeatus* in eutrophic habitats

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Human-induced environmental changes differ from most natural changes in which they happen at a faster rate and require quicker responses from populations. The first response of populations is usually phenotypically plastic alterations of morphology, physiology and behaviour. This plasticity can be favourable and move the population closer to an adaptive peak in the altered environment and, hence, maintain a viable population, or be maladaptive and move the population further from the peak and increase the risk of extinction. The radiation of the three-spined stickleback *Gasterosteus aculeatus* from the ocean to different freshwater habitats has provided much information on adaptation to new environmental conditions. Currently, human-induced eutrophication is changing the breeding areas of these fish, which creates a model system for investigation of responses to rapid environmental disturbance. Results show that a primary reaction is plastic alterations of behaviour, with some adjustments being adaptive while others are not. At the same time, the strength of sexual selection on several traits is relaxed, which could increase the relative importance of survival selection. Whether this will restore population viability depends on the amount of standing genetic variation in the right direction. Human disturbances can be dramatic and resolution of the limit of flexibility and the possibility of genetic adaptation should be important targets of future research.

Key words: contemporary adaptation; environmental deterioration; evolution; mate choice; natural selection; phenotypic plasticity.

INTRODUCTION

The habitats of the earth change constantly due to fluctuating climate conditions, species extinctions and natural selection, which gradually create and transform species. Currently humans are causing sudden and drastic environmental perturbations through their activities. In attempting to unravel the consequences that this may have for the living world, model species are needed. It is possible with these, more easily than for endangered species, to determine the effects of anthropogenic disturbance on population dynamics, evolutionary responses and species interaction and, hence, the ultimate effects on biodiversity and the processes of speciation and extinction. With knowledge gathered from different model systems, a more holistic

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picture of the consequences of human activities for the biosphere can be gained, which hopefully will improve the ability to predict and prevent negative long-term effects.

The three-spined stickleback *Gasterosteus aculeatus* L. is an important model species in ecological and evolutionary research. The radiation of *G. aculeatus* from the marine environment into different freshwater habitats over the past 20 000 years has provided compelling support for the theory of natural selection (McKinnon & Rundle, 2002). Together with the ease with which the species can be held in the laboratory and observed in the field, the many conspicuous and quantifiable traits, along with recent advances in molecular work, have made it one of the most important species in the investigation of phenotypic and genetic adaptation to environmental conditions (McKinnon & Rundle, 2002; Kingsley & Peichel, 2007). For the same reasons, the fish represents an ideal species for investigating individual and population level responses to anthropogenic disturbances. Research on changes in phenotypic and genetic variables of traits that determine population viability and evolutionary processes, such as behavioural and life-history traits, can yield valuable information on the future of populations subject to human disturbance. Moreover, *G. aculeatus* are sensitive to stress in the environment and are good bioindicators in ecotoxicological research. The species is, therefore, successfully used in the evaluation of the occurrence of oestrogens and androgens in waters and in assessing the effects of endocrine disrupters on reproduction (Scholz & Mayer, 2008).

Here, the response of individuals and populations to anthropogenic disturbance is considered, and the way in which research on *G. aculeatus* has provided enlightenment on a series of questions is discussed. The main mechanisms of adjustment to new conditions, phenotypic plasticity and genetic changes are reviewed, considering various factors that influence these processes, such as standing genetic variation, mutation rate, gene flow and covariation between traits. The theory is then discussed in the light of results that have been obtained for *G. aculeatus*, with an emphasis on the effect of eutrophication of waters on reproduction and sexual selection. To unravel how different factors and processes influence adaptation to rapid human-induced environmental changes is a challenging task where *G. aculeatus* have provided much valuable information.

MECHANISMS

PHENOTYPIC PLASTICITY

Human-induced environmental changes differ from most natural changes in that they happen at a faster rate and hence require quicker responses from populations. The risk that a population will not be able to adapt to the changed conditions and will perish is therefore larger. Populations that survive the initial change are often those whose individuals can quickly adjust their phenotype to the new conditions (Price *et al*., 2003; West-Eberhard, 2005; Kinnison & Hairston, 2007). Alternatively, populations may be canalized and produce the same phenotype despite changes in the environment (Rutherford & Lindquist, 1998). This outcome is only beneficial if the canalized phenotypes maintain their fitness under the new conditions.

In support of the importance of phenotypic plasticity in adaptation to abrupt changes, a recent meta-analysis on >3000 rates of phenotypic change in a total of 68 species showed rates of phenotypic change to be higher under rapid human-induced changes than under slower natural changes (Hendry *et al*., 2008). Moreover, this is evident in wild animals but not in common garden or quantitative genetic studies, which suggests that the contribution of genetic changes to sudden human-induced phenotypic changes is generally small. Hence, plasticity appears to be the main mechanism behind rapid adjustments to human-induced environmental changes.

The benefit of rapid plastic responses to altered conditions depends on the influence of the response on the fitness of the individuals in the new environment, *i.e.* how close to the new phenotypic optimum, or adaptive peak, the population is moved (Fig. 1) (Pigliucci, 2001; Ghalambor *et al*., 2007; Crispo, 2008). Plasticity is favourable if it places the population closer to the new optimum (Price *et al*., 2003; West-Eberhard, 2003; Ghalambor *et al*., 2007). If plasticity produces phenotypes that are almost perfectly adapted to the new conditions, then stabilizing selection can follow and no genetic differentiation is expected. If plasticity results in changes in the right direction but the phenotypes are still displaced from the optimum, *i.e.* incomplete adaptive plasticity, however, then directional selection towards the optimum may follow. Plasticity can then facilitate adaptation by preventing individuals from suffering high fitness losses and give the population additional time to adapt to the new conditions (Pigliucci, 2001).

Plasticity can also be non-adaptive under altered conditions, particularly if the population encounters conditions that differ substantially from what it encountered during its history (Pigliucci, 2001). The mean phenotype is then moved further from its optimum expression in the new environment, and the fitness of the individuals are reduced. This situation will result in strong directional selection that will favour individuals that are closest to the new optimum (Ghalambor *et al*., 2007). Populations, however, usually cannot respond rapidly enough to strong selection through genetic changes, since these changes require time. Most individuals might, therefore, not

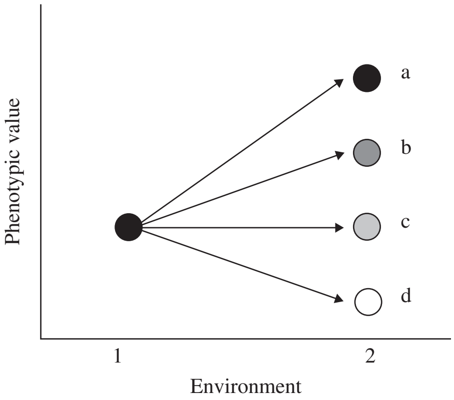

Fig. 1. The benefit of phenotypic plasticity in a new environment depends on how close to the optimum the population is moved. ●, the optimum phenotypic value in each environment; a, perfect adaptive plasticity; b, incomplete adaptive plasticity; c, canalization or no plasticity; d, maladaptive plasticity.

survive and reproduce in the new environment, and maladaptive plasticity could frequently result in extinction. Alternatively, maladaptive plasticity could increase the expression of genetic variance, that is, reveal cryptic genetic variation in the phenotypes. This could promote adaptive evolution if enough genotypes express beneficial phenotypes (Rutherford, 2003; Grether, 2005).

In *G. aculeatus*, an example of incomplete adaptive plasticity that could have triggered genetic differentiation is the phenotypic plasticity in trophic morphology found in many lake populations. When two species of a recently diverged limnetic-benthic species pair in a lake in British Columbia were raised on diets that represented the natural diet of the other species, each species came to resemble the other species in morphology (Day *et al*., 1994). The two species hence exhibited morphological plasticity in an adaptive direction. There was also genetic variation for plasticity, which demonstrates that plasticity has an evolutionary potential in the species. This result suggests that incomplete adaptive plasticity may have played an important role in the divergence of the species pair in the lakes (Day *et al*., 1994).

Several lines of research indicate that *G. aculeatus* is an ecologically flexible species that harbours much phenotypic plasticity in traits such as morphology (Day *et al*., 1994; Sharpe *et al*., 2008), resource use (Svanbäck & Bolnick, 2007), physiology (Schaarschmidt *et al*., 1999), life-history traits (Baker & Foster, 2002), mating behaviour (Candolin *et al*., 2007; Engström-Öst & Candolin, 2007; Delcourt *et al*., 2008), nuptial colouration (Candolin, 1999*a*; Boughman, 2007) and parental care (Candolin *et al*., 2008). This plasticity could be one explanation for why *G. aculeatus* have been able to rapidly adapt to a range of different freshwater conditions from their marine origin (McKinnon & Rundle, 2002). Plasticity may initially have allowed the species to survive and reproduce in a new environment and thereby given the population time to accrue genetic changes and genetically adapt to the new conditions. This plasticity could now help the species to adapt to anthropogenic disturbance.

GENETIC CHANGES AND CONSTRAINTS

When plasticity does not result in a perfect match with the adaptive peak in the altered environment, directional selection can move the population towards the new peak through genetic change. This response requires that standing variation in the right direction exists, or that new beneficial mutations arise, or that gene flow provides the population with beneficial alleles. Since human-induced changes are usually rapid, mutations may play a minor role and genetic adaptation may primarily rely on standing genetic variation and gene flow.

Research on *G. aculeatus* in natural, undisturbed conditions suggests that there is often sufficient univariate additive genetic variation for responses to directional selection (Schluter *et al*., 2004). Selection targets individuals, however, who are made up of traits can be genetically correlated. Genetic variance and covariance for multivariate trait combinations could, therefore, be lower and limit multivariate responses to selection and constrain adaptive evolution (Schluter, 1996; Blows *et al*., 2004). In support of this view, Schluter (1996) found negative and positive genetic covariation among several morphological and meristic traits for 10 populations of *G. aculeatus*. The direction of evolution was in the direction of maximum genetic variance, which suggests that limited variation for other combinations of traits biased evolution. Similarly, suites of body shape traits in *G. aculeatus* have consistently evolved together across environmental gradients (Walker & Bell, 2000), and the colonization of fresh water has resulted in consistent phenotypic changes, that is, parallel evolution (Schluter *et al*., 2004; Cresko *et al*., 2007). Hence, some changes appear to be more likely than others, due to similarly biased production of genetic variation in different populations and similar constraints due to correlated traits (Schluter *et al*., 2004). These biases in genetic variation and covariation could facilitate adaptation to some environmental changes while hindering adaptation to others.

Although sufficient genetic variation could exist under natural conditions for a response to changed selection, and though adaptive radiation to new conditions has occurred over evolutionary time, adaptation to rapid human-induced environmental changes can be more challenging. Anthropogenic disturbances often reduce genetic variation, such as the fragmentation of habitats that reduces gene flow between populations and enhances genetic drift within populations (Saccheri *et al*., 1998). Freshwater habitats are particularly vulnerable to human-induced fragmentation. Recent studies on human disturbance of riverine landscapes in Belgium show that anthropogenic constructions that fragment rivers create migration barriers for *G. aculeatus* populations (Raeymaekers *et al*., 2008, 2009). This alters the balance between gene flow and genetic drift and reduces genetic diversity, which could limit the potential for genetic adaptation.

RESPONSES OF *G. ACULEATUS* TO A CHANGING ENVIRONMENT

Aquatic environments are currently changing due to human activities, such as emission of municipal, agricultural and industrial wastewater, fishing, increased boat traffic, water diversion and introduction of new species. This causes eutrophication, pollution with toxic chemicals (*e.g.* heavy metals and endocrine disrupters) and changes in the structure of the environment and in flow regimes, to mention just a few effects.

Gasterosteus aculeatus is an evolutionarily flexible species that originated in the ocean and subsequently radiated into postglacial lakes and streams throughout much of the northern hemisphere (Bell & Foster, 1994; Schluter, 2000; McKinnon & Rundle, 2002). Several lines of research show that it can adapt relatively rapidly to different environmental conditions through phenotypic and genetic changes in morphology, physiology and behaviour (McKinnon & Rundle, 2002; Cresko *et al*., 2007). These adaptive shifts appear, at least for body shape, to result from a few genes with large effects and multiple genes of smaller effect (Albert *et al*., 2008).

How *G. aculeatus* react to rapid human disturbances is currently gaining attention. Effluents from industrial and municipal sources contain compounds that interfere with the endocrine system of *G. aculeatus* and influence physiological functions (Scholz & Mayer, 2008). In particular, chemicals with oestrogenic or antiandrogenic action lessen the production of spiggin, a glue protein used in nest-building (Sebire *et al*., 2009). This reduces nest-building and courtship behaviour of *G. aculeatus* and could lower the reproductive output of populations. Human-induced environmental changes can also alter species interactions and augment the risk of extinction of populations. In British Colombia, the introduction of an exotic catfish *Ameiurus* *nebulosus* (Lesueur) into a lake has caused the extinction of a pair of sympatric *G. aculeatus* species, a limnetic and a benthic species (Hatfield, 2001). In several other lakes, the *G. aculeatus* species pairs are hybridizing and collapsing into swarms of hybrids through reversed speciation (Taylor *et al*., 2006). This effect is most probably due to the introduction of an exotic crayfish *Pascifasticus leniscululus* (Dana) and increased nutrient load from urban runoff, which changes the environment from clear water with abundant littoral vegetation to turbid water devoid of macrophytes. These changes apparently remove the fitness disadvantage of hybrids and breaks down premating isolation by influencing mate choice (Taylor *et al*., 2006).

All responses to anthropogenic disturbance may not be as dramatic. Due to high phenotypic flexibility, *G. aculeatus* may frequently be able to react with phenotypic adjustments to altered conditions. This might give the species time to gradually evolve genetic adaptations under directional selection in altered environments. In the following section, the responses of *G. aculeatus* to the deterioration of their breeding habitats, due to human-induced eutrophication, will be discussed. The change is happening rapidly and serves as a model system for investigation of behavioural responses to eutrophication.

RESPONSES TO EUTROPHICATION

Gasterosteus aculeatus breed in shallow water. Shallow water is also the habitat that is most severely affected by eutrophication. Increased input of nutrients due to human activities enhances primary production, which reduces visibility and can change the oxygen content and pH of the water. Since vision is an important sensory channel during mate choice, and as oxygen content influences hatching rate and parental effort, eutrophication may alter both sexual selection and reproductive output in *G. aculeatus* populations.

The effects of eutrophication on reproduction in *G. aculeatus* have been investigated in the Baltic Sea. Studies show that the density of nesting males is higher in denser growth of filamentous algae, but that the distribution of eggs among males is more equal (Candolin, 2004). The increased density of males could be due to impaired visibility in dense algal cover reducing male interactions and the size of the territory that a male can defend and, hence, allowing more males to nest within an area. This is supported by studies that record smaller territories and fewer aggressive interactions in denser vegetation (Candolin & Voigt, 2001; Candolin *et al*., 2008). The number of males reproducing thus increases with the degree of eutrophication, which could decrease the strength of selection at this life-history stage.

MATE CHOICE AND COURTSHIP BEHAVIOUR

Sexual selection arises from the variation among individuals of one sex in mating and fertilization success (Andersson, 1994). Consequently, the equal distribution of eggs among males in dense algal growth suggests that the strength of sexual selection on male traits is relaxed. To investigate whether this could be due to changed female choosiness, the density of algae was manipulated under laboratory conditions, and effects on the behaviour of pairs of spawning *G. aculeatus*, when no male–male competition occurred, were noted. When the density of vegetation was high, females spent more time inspecting a male before spawning, indicating that the evaluation of males was impaired and required a larger effort (Candolin *et al*., 2007). *Gasterosteus aculeatus* males attract females with a conspicuous courtship dance combined with bright colours; a red ventral side and blue eyes (Wootton, 1976). The evaluation of these visual traits should be more difficult under impaired visibility and increases the cost of mate choosiness for females. Females may therefore attempt to lower mate choice costs by being less choosy, which could explain the equalized distribution of mating success among males.

Males reacted to increased algae growth with an intensification of courtship activity (Candolin *et al*., 2007). The interest of the females in the males, however, did not increase with courtship effort. Males hence increased the cost of courtship without gaining any benefits. This effect suggests that the increased courtship effort was maladaptive, and that phenotypic flexibility moved the individuals further from the optimum for courtship. When the experiment was repeated under augmented water turbidity, caused by the growth of phytoplankton, however, increased investment in courtship did pay off and males that courted the most intensely gained most attention from females (Engström-Öst & Candolin, 2007). Since turbidity only reduces visibility while dense vegetation can completely prevent detection, this result suggests that the way in which visibility is reduced determines its influence on mate choosiness. Thus, whether phenotypic flexibility in courtship in *G. aculeatus* is adaptive or not depends on the exact nature of environmental conditions.

MALE–MALE INTERACTIONS

Gasterosteus aculeatus males often nest in aggregations, and male–male interactions determine which males will be able to establish a territory and build a nest. Male interactions also influence mating success of males by forcing males to adjust both courtship activity and red colour expression of their dominance status; dominant males becoming brighter and courting more than subdominant males (Candolin, 1999*b*, 2000*a*, *b*). This social control of signalling can facilitate the evaluation of males and thereby female mate choice, since dominance reflects condition and viability (Candolin, 2000*a*) and predicts paternal success with dominant males being better at defending their nest (Candolin, 2000*b*).

When two males that differed in condition were allowed to court a female in clear water, the males adjusted their colour expression and courtship activity to each other so that the male in good condition, who usually dominated over the poor condition male, expressed larger signals than the poor condition male (Candolin 1999*b*). When the turbidity of the water was increased through the growth of phytoplankton, however, the social control of signalling relaxed. Poor condition, subdominant males were then able to court females vigorously and express bright colours despite the presence of males in better condition (Wong *et al*., 2007). Consequently, females are less able to tell the condition and dominance status of males in turbid water and could end up mating with poor condition males, who are often poor fathers (Candolin, 2000*b*). Increased water turbidity could thus result in non-adaptive female choice, which could influence the genetic quality of the population and slow down adaptation to the new conditions.

SWITCH TO OTHER CUES?

When visual traits decrease in importance in mate choice and mate competition, due to impaired visibility, the importance of other traits could increase and compensate for the reduction in information. In support of this, the use of olfactory cues increased under turbid water conditions. Females were allowed to choose between two males in clear and turbid water and had access to only visual cues, olfactory cues or both cues under laboratory conditions (Heuschele *et al*., 2009). Interestingly, the use of only olfactory or only visual cues resulted in different mate choices, which suggests that visual and olfactory cues give different information (Candolin, 2003). A eutrophication-induced switch in the use of cues could hence influence mate choice and change the fraction of the population that reproduces.

For a switch in the use of cues to be adaptive and move the population towards the phenotypic and genotypic optimum in the new environment, the individuals that are chosen should be those that are best adapted to the new conditions. If the new cues facilitate adaptive mate choice, then genetic adaptation to the new conditions could accelerate. If the new cues do not indicate the viability of the males in the new environment, however, then their use could result in non-adaptive choices and retard adaptation, increasing the cost of directional selection which could decrease population viability. Whether the environment-dependent switch in the use of cues is adaptive in *G. aculeatus* is unknown but appears possible. Olfactory cues could provide fish with important information about the health and viability of individuals under eutrophic conditions when the honesty of visual cues as indicators of male dominance, condition and parental ability is reduced (Reusch *et al*., 2001; Wong *et al*., 2007).

ALTERNATIVE REPRODUCTIVE BEHAVIOURS

All *G. aculeatus* males do not reproduce by attracting females to a nest that they have built; some attempt to parasitize the courtship effort of others. They sneak into the nest of territorial males and attempt to fertilize at least part of the eggs that females spawn in the nest (van den Assem, 1967). These males can be males that have no territory themselves, or nesting males that attempt to increase their mating success by siring some offspring in the nests of others (van den Assem, 1967).

The success of sneaking depends on the ability of the sneaker to detect spawning pairs and on the ability of spawners to detect the sneaker and chase him away. The importance of vision in detection suggests that eutrophication and reduced visibility could influence sneaking. When *G. aculeatus* were allowed to spawn in wading pools, increased vegetation cover reduced the occurrence of sneaking (U. Candolin & L. Vlieger, unpubl. data), while increased turbidity under aquarium conditions reduced sneaking (Vlieger & Candolin, 2009). Since sneaking was often performed by nesting males and this skews mating success towards fewer males (U. Candolin & L. Vlieger, unpubl. data), a reduction in sneaking decreases the variation among males in mating success and, hence, the strength of sexual selection on male traits (U. Candolin & L. Vlieger, unpubl. data).

The effects of eutrophication on the opportunity for sexual selection consequently depend on whether it is territorial or non-territorial males that sneak. If it is non-territorial males, then eutrophication increases the opportunity for sexual selection. If sneaking is mainly carried out by territorial males, however, then eutrophication reduces the opportunity for sexual selection. In the Baltic Sea, where much of the sneaking is carried out by territorial males, and eutrophication increases the number of territorial males, increased eutrophication could reduce the strength of sexual selection.

PARENTAL CARE

In *G. aculeatus* the male alone cares for the offspring in the nest, while the female abandons her eggs immediately after spawning. The survival of the offspring depends on the ability of the male to defend the eggs against a range of predators and on his efforts in fanning oxygen-rich water into the nest. Laboratory studies show that increased growth of phytoplankton augments the oxygen level in the water, which reduces the required fanning effort of males and improves egg hatching success (Candolin *et al*., 2008). This applies to high latitudes where summer nights are short and phytoplankton are able to photosynthesize for most of the day. In addition, increased water turbidity reduces aggressive interactions among males, which gives the males additional time for parental care, lowers energy expenditure and reduces the risk of injuries (Candolin *et al*., 2008).

Phytoplankton-induced turbidity can hence be favourable in reducing required parental effort. This can increase male survival, the proportion of eggs that hatch and the number of reproductive cycles that a male can complete, which could influence population growth. It is possible, however, that selection at other stages, such as the juvenile stage, strengthens when more offspring are hatching and that this limits population growth.

WHAT DO *G. ACULEATUS* IN EUTROPHIED WATERS INDICATE ABOUT ADAPTATION TO ANTHROPOGENIC DISTURBANCE?

The research on the effects of human-induced eutrophication on the reproductive behaviour of *G. aculeatus* shows that the fish respond to sudden changes with plastic alterations of their behaviour (Fig. 2). They adjust their nesting behaviour, mate search behaviour, courtship behaviour, choosiness, sneaking attempts and parental behaviour to the prevailing conditions. The reaction norms along which the individuals adjust their behaviour have evolved under earlier conditions, however, before humans drastically increased the degree of eutrophication. The behaviours are, therefore, adjusted to the expected costs and benefits in the old environment, where the water was clearer and the growth of filamentous algae sparser. Although some behavioural adjustments to eutrophication are adaptive, like the reduction in the use of visual cues that are less honest under the new conditions, other changes appear maladaptive, such as the increase in male courtship activity. The effect that these adaptive and maladaptive adjustments have on population viability and genetic adaptation to new conditions is unknown and requires further investigation.

Research also suggests that human-induced eutrophication relaxes the opportunity for sexual selection in *G. aculeatus*, through hampered female choice, relaxed male–male competition and reduced sneaking. It might even cause slightly maladaptive sexual selection through a reduction in the social enforcement of the honesty of sexual signals. This effect is in line with results from other studies that have found

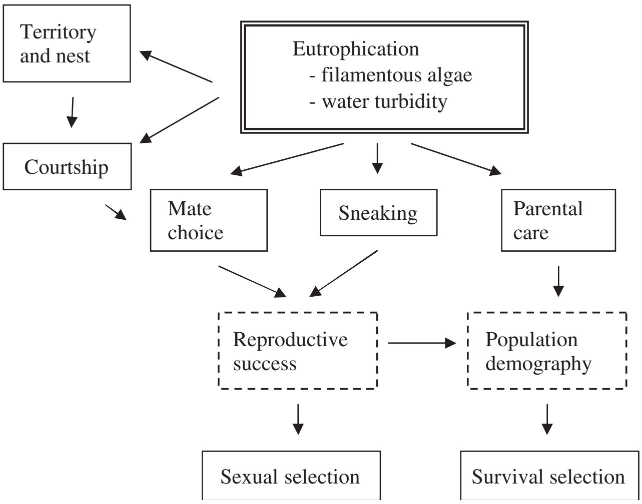

FIG. 2. The pathway of effects of eutrophication on different reproductive behaviours and selection forces in *Gasterosteus aculeatus*.

sexual selection to be unimportant or maladaptive in new environments (Holland, 2002; Rundle *et al*., 2006). Generally, the role of sexual selection in adaptation to new conditions is controversial, with some studies finding the occurrence of sexual selection to accelerate adaptation, while other studies find it to retard or to have no effect (Candolin & Heuschele, 2008). In *G. aculeatus*, a relaxation of sexual selection together with an increase in the number of offspring hatching could strengthen natural selection at later life-history stages. The relaxation could hence be beneficial and allows the direction and strength of natural selection to change in an adaptive direction, ultimately resulting in a population that is better adapted to the eutrophied conditions. Relaxed sexual selection due to impaired mate choice can increase hybridization among closely related species, which can reverse speciation and reduce biodiversity, as found for *G. aculeatus* in human disturbed Canadian lakes (Taylor *et al*., 2006).

Theoretical studies suggest that the role of sexual selection in adaptation depends on the stage of change (Thibert-Plante & Hendry, 2009). At the initial stages of adaptation, sexual selection may retard adaptation if females have preferences that are adaptive in the old environment but not under the changed conditions. At later stages of adaptation, when male traits have started to evolve towards new adaptive peaks, favourable female preferences that increase the fitness of the offspring can increase in frequency. Sexual selection can then shift female preferences and male traits in an adaptive direction, which can accelerate adaptation (Servedio, 2004). This influence of the stage of adaptation on the role of sexual selection is supported by work on *G. aculeatus* that find sexual selection to be relaxed during initial adjustments to anthropogenic disturbance, such as eutrophication (Candolin *et al*., 2007), but to play a major role in more stable environments and to reinforce ecological speciation through reduced gene flow at later stages of adaptation (Boughman, 2001). For sexual selection to play a facilitating role in the adaptation of *G. aculeatus* to human-induced environmental change, the environment must consequently reach a state where female preferences and male traits have had time to adapt genetically to the new conditions.

When phenotypic adjustments do not move the population all the way to the new adaptive peak, then directional selection will strengthen. This requires standing genetic variation in the right direction. Whether *G. aculeatus* harbour enough genetic variation, and if the changes can occur rapidly enough, is unclear. Some studies suggests that much genetic variation exists (Schluter *et al*., 2004), which should facilitate genetic adaptation to drastic environmental disturbances, but particularly reduction in genetic connectivity among populations could reduce genetic variation and the potential for adaptation (Raeymaekers *et al*., 2008). More research is clearly needed.

Gasterosteus aculeatus has provided much information about adaptation to new conditions through its radiation to different freshwater habitats from its marine origin. Currently, research on this fish is increasing the knowledge of responses to rapid human-induced environmental change. An increasing number of studies show that there is much phenotypic plasticity in fitness-linked traits, and that the species reacts to rapid and dramatic anthropogenic disturbances with adaptive adjustments of their phenotypes. There can also be non-adaptive changes that could reduce population viability, and reduced genetic connectivity among populations could decrease genetic variation and limits the potential for genetic adaptation to new conditions.

The work on *G. aculeatus* in eutrophic environments also suggests that the strength of sexual selection can be relaxed under anthropogenic disturbance. This could increase the relative importance of survival selection in adaptation, which could be a stronger force and more rapidly cause adaptive genetic alterations under new conditions. The strongest responses to selection may take place at the initial stages of change when selection is strongest and there is still much genetic variation (Kinnison & Hendry, 2001). Relaxed mate choosiness and sexual selection, however, can increase hybridization and cause the merging of species, with negative effects on biodiversity. Since human disturbances can be dramatic, the resolution of the limit of flexibility, the possibility of genetic adaptation to rapid environmental alterations and the consequences of impaired mate choosiness are important lines of future research.

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