



# Human-induced eutrophication enhances reproductive success through effects on parenting ability in sticklebacks

Ulrika Candolin, Jonna Engström-Öst and Tiina Salesto

U. Candolin ([ulrika.candolin@helsinki.fi](mailto:ulrika.candolin@helsinki.fi)), Dept of Ecology and Evolution, Uppsala Univ., Box 573, SE-752 37 Uppsala, Sweden. – J. Engström-Öst, Finnish Institute of Marine Research, P.O. Box 2, FI-00561 Helsinki, Finland. JEÖ also at Aronia Coastal Research Team, Raseborgsvägen 9, FI-10600 Ekenäs, Finland. – T. Salesto, Dept of Biological & Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland.

Human-induced processes are altering habitats at an unprecedented rate and scale. This has changed the biodiversity and biomass in many areas, but also led to phenotypic and genetic alterations of populations. Here we investigated the effects of the ongoing eutrophication in the Baltic Sea on the reproductive success of threespine stickleback males *Gasterosteus aculeatus*, through effects on reproductive behaviour and parenting ability. We allowed males to complete breeding cycles in a competitive setting under increased macro algae cover or increased turbidity caused by phytoplankton growth. Both environmental factors improved the parenting ability of the males and enhanced reproductive output. Increased algal growth and turbidity reduced aggressive interactions between males during the parental phase, probably due to reduced visibility, which slowed down a deterioration of condition. This increased the reproductive lifespan of the males and enabled them to complete more breeding cycles, as found when males were allowed to complete as many breeding cycles as they could under increased algae cover. In addition, increased turbidity improved oxygen conditions, which enhanced hatching success and reduced the need for vigorous fanning behaviour. Increased turbidity, however, relaxed selection on male size. Together with earlier results on relaxed sexual selection under changed environmental conditions, this suggests that the effect of eutrophication on stickleback populations is complex. It increases the reproductive output of populations, since more individuals are spawning within eutrophicated areas and their hatching success is increased, but it relaxes sexual and natural selection at the reproductive stage. Whether this will shift selection and population regulation to other life stages, such as the juvenile stage, deserves further investigations.

Human induced eutrophication of waters is a serious problem in many lakes, bays and semi-enclosed seas. Increased inflow of nutrients, primarily phosphorous and nitrogen, increases the growth of certain algal species over others and forces a change in the species composition (Smith 2003). Of particular concern is turbidity caused by enhanced growth of phytoplankton, since it limits sunlight to bottom dwelling organisms, increases decomposition of organic material, and causes wide fluctuations in the level of dissolved oxygen in the water (Nielsen et al. 2002).

The consequences of human-mediated environmental changes for biodiversity and population dynamics are currently receiving much attention (Foley et al. 2005, Smart et al. 2006, Strayer et al. 2006). Less attention has been directed at the effects of environmental change on populations through effects on behaviours, although behavioural traits, like other traits, are adjusted to environmental conditions over evolutionary time (Endler 1987, McKinnon and Rundle 2002). Overall, the linkage between population dynamics and behavioural adaptations is not well understood (Sutherland 1996, Rankin and Kokko 2006). When environmental conditions change,

old behavioural patterns may become maladaptive and decrease the fitness of the population (Endler 1987, Forstmeier and Weiss 2004, Plath et al. 2005, Visser and Both 2005). Adjustments of behaviour may then be necessary, which could have equally strong effects on population output as changes in food supply or predation.

An area that is suffering heavily from human-induced eutrophication is the Baltic Sea (Raateoja et al. 2005, Råberg et al. 2005). Increased input of nutrients is enhancing the growth of filamentous algae and phytoplankton, resulting in changed habitat structure and turbid water (Cederwall and Elmgren 1990, Perttilä et al. 1995). These processes alter the species composition of the biotic communities, but the long-term effects are largely unknown (Bonsdorff et al. 1997, Bokn et al. 2002). A species that spawns in the affected coastal areas of the Baltic Sea is the threespine stickleback, *Gasterosteus aculeatus*. In spring, the fish migrate to shallow coastal waters where males build nests out of filamentous algae and court females for spawnings. Males alone care for the eggs and newly hatched juveniles for about two weeks. Both males and females may complete several breeding cycles in one season (Wootton 1976).

Recent research shows that increased growth of algae has complex effects on reproductive behaviours and on sexual selection in sticklebacks. For example, increased growth of filamentous algae reduces predation risk and allows more courtship (Candolin and Voigt 1998), but relaxes sexual selection on visual traits, like courtship behaviour and red coloration (Candolin 2004, Candolin et al. 2007). Increased water turbidity caused by phytoplankton growth, on the other hand, induces selection for higher courtship activity (Engström-Öst and Candolin 2007), but compromises socially enforced signals of male quality, which allows more cheating in the signalling of individual quality (Wong et al. 2007). These changes are probably due to reduced visibility under increased algae growth, which reduces both the number of mate encounters (Candolin and Voigt 2001a) and the ability of females to evaluate males using visual traits (Candolin et al. 2007). Overall, increased algal growth appears to reduce the importance of visual cues in mate choice, while possibly increasing the importance of olfactory cues (Heuschele and Candolin 2007).

Here, our aim is to determine the effect of eutrophication on reproductive output in sticklebacks, through effects on male parental care behaviour and on hatching success. We consider both increased algae cover and increased turbidity caused by heightened growth of phytoplankton. The quality of parental care is of crucial importance for reproductive success, since the male alone cares for the eggs by defending the nest against potential egg predators and by fanning water into the nest and so over the eggs for about two weeks. Changes in the ability to defend the eggs, or in the effort needed to raise a clutch of eggs, could have a large impact on the reproductive output of populations.

Eutrophication most likely influences reproductive output and population viability through a multitude of interacting factors, such as food availability, competition and predation. By focusing on effects on parental behaviour, we single out one factor that affects population output. Together with research on other factors, such as the number of breeding adults, predation pressure, food availability and growth conditions for juveniles, this should give insights into the different pathways in which environmental changes influence the populations, as well as the short term and long term consequences this may have for the persistence of the populations.

## Material and methods

We performed two experiments to investigate the effects of habitat changes due to eutrophication on parental care behaviour and reproductive output. The first experiment determined the effects of increased growth of filamentous algae and the second the effects of algae-induced turbidity.

The sticklebacks were caught with Plexiglas traps (Candolin and Voigt 2001b) from Vindskär bay close to Tvärminne Zoological Stn (60°N, 23°E), before the breeding season. The fish were housed in flow through aquaria under natural light and water temperature conditions and fed frozen chironomid larvae. Male fish, as determined by the development of blue eye colour, were transferred to separate holding aquaria. A lack of suitable nesting materials in the aquaria discouraged breeding

behaviour. The subsequent transfer to the experimental aquaria, described below, corresponds to the change fish experience when migrating from clear water into bays with varying algae growth, where they will breed. The males were measured for standard length to the nearest mm and weighed to the nearest 0.01 g before being used in the experiments. All experiments were performed under natural light and temperature conditions in outdoor facilities.

### Increased vegetation cover

To determine the effect of increased algal cover on parental care behaviour, males were transferred to individual 20-l flow through aquaria that differed in percentage of algal cover. All males were given a nesting dish (Ø 14 cm), filled with sand, filamentous green algae (*Cladophora glomerata*) for nest construction, and one artificial plant for hiding (Candolin 1997). Half of the males experienced an open habitat, containing only the nesting dish at one end of the aquarium. The remaining males experienced a vegetated habitat with bunches of 15 cm long, thin, green polypropylene strings distributed over approximately 75% of the bottom, up to a height of 15 cm. The artificial algae mimicked filamentous algae, and the density represented the density of algae found in nature, with the dense vegetation treatment corresponding to a high density of algae in the field (Candolin and Salesto 2006). Each male was fed frozen chironomid larvae once every second day.

One day after a male had completed nest building, a female was introduced into the aquarium and allowed to spawn with the male. She was removed immediately after spawning and the male was left to care for the eggs. The mass of eggs spawned was determined by weighing the eggs about 2 h after spawning when the eggs had hardened. To weigh the eggs, the nesting dish was lifted from the aquarium and the eggs carefully removed with forceps and dried on absorbent paper. The egg mass was weighed in a bowl of water and then returned to the nest (Candolin 2000c). Males always accepted the eggs and repaired the nest entrance and any other parts that had been damaged. This procedure has no significant influence on egg survival (Kraak et al. 1997, Candolin 2000b).

When the male had repaired the nest and resumed normal parental behaviour, an additional male was added to the aquarium to serve as a potential egg predator and competitor (Hyatt and Ringler 1989). Egg cannibalism by other sticklebacks is the main source of egg predation in the brackish water of the Baltic Sea, where species diversity is low and insect predators are largely lacking. The tip of one of the dorsal spines of the intruding male was cut so the he could be separated from the nest owner. The intruding male was 4–8 mm smaller than the nest holding male, to prevent that the intruder would take over the nest. A stone was added to the aquarium to serve as a hiding place for the intruding male, in order to reduce fights between the males. If the condition of the intruding male deteriorated, due to attacks from the nesting male, he was replaced by another male of the same size.

Once a day, between 9 and 11 a.m., the parental behaviour of the parenting male and his aggressive interactions with the intruder were recorded for 10 min. The male drives water over the nest by fanning, so the number and duration of fanning bouts were recorded, together with the number of attacks on the rival male. After 7–10 days, depending on water temperature, when the eggs were almost ready to hatch, the eggs were removed from the aquarium and weighed to determine the percentage of eggs that had survived. Developed, healthy eggs are easily distinguished from dead eggs, as the dark embryo moves inside the eggshell. Dead eggs could therefore be removed before weighing the egg mass. Hatching success is thus given as the percent of the mass of eggs that survived until the hatching stage. The weight of an egg may change during development, but the change should be similar over replicates and not confound the results (Candolin 2000a, 2000b, 2000c).

The male was weighed to the nearest 0.01 g to determine the reduction in body condition. Thereafter, the male was given fresh filamentous algae (*C. glomerata*) and allowed to build a new nest and begin a new breeding cycle. The males were allowed to complete as many breeding cycles as they could until they died or stopped breeding (Candolin 2000a). Since males in the present area only breed during one year, and then die (Candolin unpubl.), the total number of hatched eggs represents the lifetime reproductive success of the males.

The means of the time spent fanning the nest, the number of fanning bouts, and the number of attacks on the intruding male were calculated for each breeding cycle. The values were averaged over the cycles, so that a mean value for each male was obtained. In the analyses, both mean values and values during the first breeding cycle were used. Qualitatively similar results were gained and only the results for the mean values of the males are presented. All data were checked for normality and homogeneity of variances before analyses. Time spent in aggressive interactions and number of attacks were log transformed before analyses. Fifteen replicates of each treatment were performed.

### Increased turbidity

To determine the effect of turbidity, caused by phytoplankton growth, on parental care behaviour, males with no prior breeding experience were transferred to 20-l aquaria that differed in phytoplankton density. Half of the males experienced clear seawater ( $1.5 \pm 0.09$  NFU, nephelometric formazine unit), whereas the remaining males experienced turbid water ( $8.7 \pm 0.9$  NFU) caused by adding the unicellular planktonic chlorophyte *Brachiomonas submarina*. The aquaria were aerated for 10 min every morning, after the behavioural measurements. All aquaria contained a nesting dish with sand and filamentous algae (*C. glomerata*) and an artificial plant for hiding at one end of the aquarium, and a stone at the other end of the aquarium to serve as a hiding place for the intruding male, as described for the algal cover experiment.

*Brachiomonas submarina* algal cultures were grown outdoors under natural light conditions in 45-l uncovered

containers, using 10  $\mu\text{m}$ -filtered seawater and aquatic fertilizer (Kemira) at a concentration of 0.75%. The culture was diluted daily and nutrients added to favour rapid algal growth. The cultures were supplied with air continuously. Turbidity was measured daily with a nephelometer.

The same procedures as described for the increased algal cover experiment were followed. One female was allowed to spawn in the nest of the male and an intruding male was added. The parental behaviour of the nesting male was observed until the eggs reached the hatching stage. The hatching success and change in body weight of the nesting male was determined at the end of the experiment, using the same methods as described above. In contrast to the algal cover experiment, the males were allowed to complete only one breeding cycle due to time constraints. The oxygen level and turbidity of the water were measured every second afternoon. Oxygen was measured with a portable oxygen meter, and turbidity with the portable nephelometer. New *B. submarina* algal solution was added as soon as the turbidity values started to decrease.

The means of the time spent fanning, the number of fanning bouts, and the number of attacks on the intruding males were calculated. Hatching success was arcsine square root transformed before analyses. Twenty-five replicates of each treatment were performed.

## Results

### Increased vegetation cover

Vegetation cover reduced aggressive interactions between the nesting male and the intruding male, but had no effect on parental care behaviour: males nesting under dense algae cover spent less time in aggressive interactions ( $t$ -test,  $t_{28} = 3.64$ ,  $p = 0.001$ , Fig. 1a) and attacked the intruder less often than males nesting in the open habitat (number of attacks  $\pm$  SE in vegetated habitat:  $8.1 \pm 5.3$  and in open habitat:  $20.3 \pm 15.8$ , log-transformed values:  $t_{28} = 4.35$ ,  $p < 0.001$ ). There was no significant effects of vegetation cover on fanning behaviour ( $t_{28} = 0.42$ ,  $p = 0.68$ , Fig. 1a) or on the percentage of eggs hatching ( $t_{28} = 1.02$ ,  $p = 0.32$ , Fig. 2a).

Males under vegetation cover lost less weight at each breeding cycle than males nesting in the open habitat ( $t_{28} = 2.31$ ,  $p = 0.028$ , Fig. 3a). However, there was no significant difference in weight loss over the whole season ( $t_{28} = 0.73$ ,  $p = 0.47$ , Fig. 3a), since males under vegetation cover were able to complete more breeding cycles ( $t_{28} = 2.17$ ,  $p = 0.039$ , Fig. 4a). Males nesting under vegetation cover hatched more eggs than males nesting in the open, when the mass of eggs hatched over the whole season was calculated ( $t_{28} = 2.19$ ,  $p = 0.037$ , Fig. 4b). There was no difference between the treatments in the amount of eggs received ( $t_{28} = 1.15$ ,  $p = 0.15$ ).

Hatching success showed a non-significant tendency to increase with male body length ( $r = 0.12$ ,  $F_{1,28} = 3.77$ ,  $p = 0.062$ ), independent of treatment (ANCOVA: interaction factor:  $F_{1,26} = 1.13$ ,  $p = 0.30$ ).

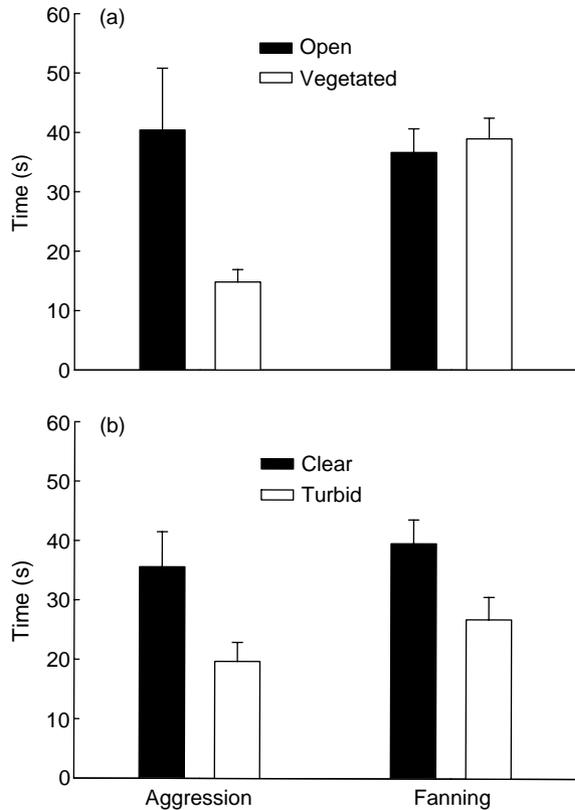


Fig. 1. Time (+SE) spent in aggressive interactions with the rivalling male and time spent fanning the eggs in (a) open and vegetated habitats, and (b) clear and turbid water. Untransformed values are shown for aggression.

### Increased turbidity

Males nesting in turbid water spent less time in aggressive interactions with the intruding male ( $t_{48} = 2.34$ ,  $p = 0.023$ , Fig. 1b) and attacked the intruder less often than males nesting in clear water (number of attacks  $\pm$  SE in turbid water:  $9.3 \pm 1.4$  and in clear water:  $21.5 \pm 3.9$ ,  $t_{48} = 2.93$ ,  $p = 0.005$ ). The turbidity treatment influenced the time spent fanning the eggs; males in the turbid water treatment spent less time fanning the eggs than males in clear water ( $t_{48} = 2.30$ ,  $p = 0.026$ , Fig. 1b). Still, they had a higher

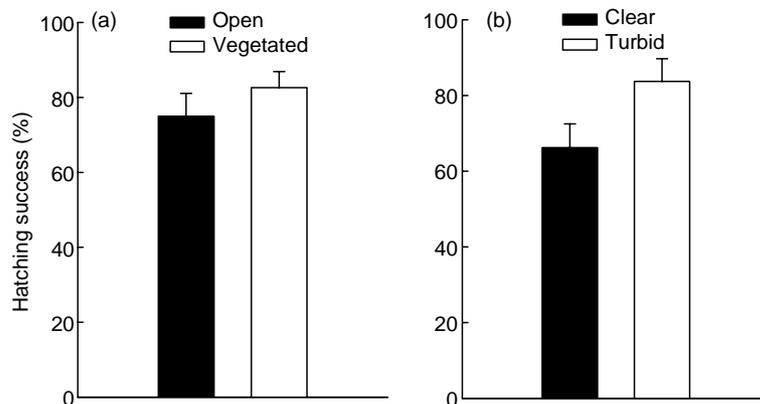


Fig. 2. Hatching success (+SE) of males nesting in (a) open and vegetated habitats, and (b) clear and turbid water. Untransformed values are shown.

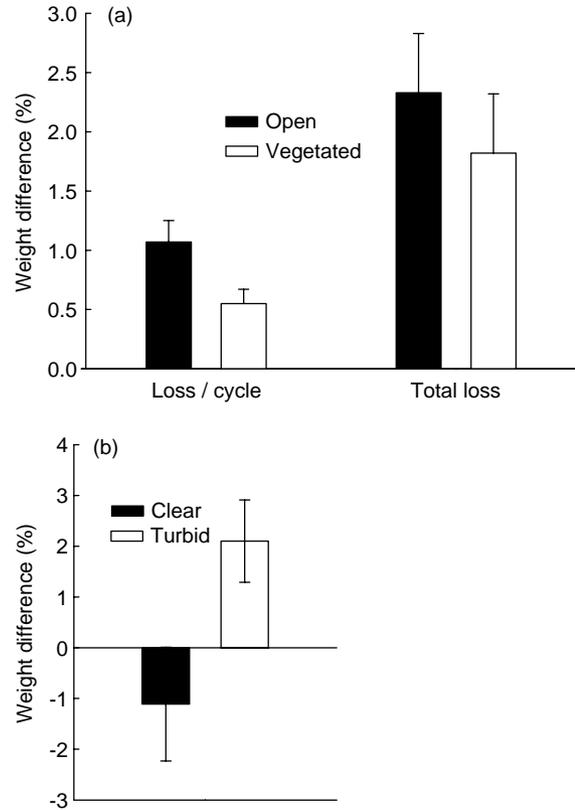


Fig. 3. Wet weight loss (+SE) during each breeding cycle and over all cycles of males nesting in (a) open and vegetated habitats, and (b) in clear and turbid water.

hatching success than males in clear water ( $t_{48} = 2.11$ ,  $p = 0.040$ , Fig. 2b). The oxygen levels and water turbidity were higher in turbid water (Table 1). Males in turbid water gained some weight whereas males in clear water lost weight ( $t_{48} = 2.23$ ,  $p = 0.030$ , Fig. 3b).

Larger males had a higher hatching success than small males in clear water ( $r^2 = 0.19$ ,  $F_{1,23} = 6.74$ ,  $p = 0.016$ ), but not in turbid water where all males had a high hatching success independent of body size ( $r^2 = -0.04$ ,  $F_{1,23} = 0.10$ ,  $p = 0.76$ , interaction term in ANCOVA:  $F_{1,46} = 2.88$ ,  $p = 0.097$ , Fig. 5).

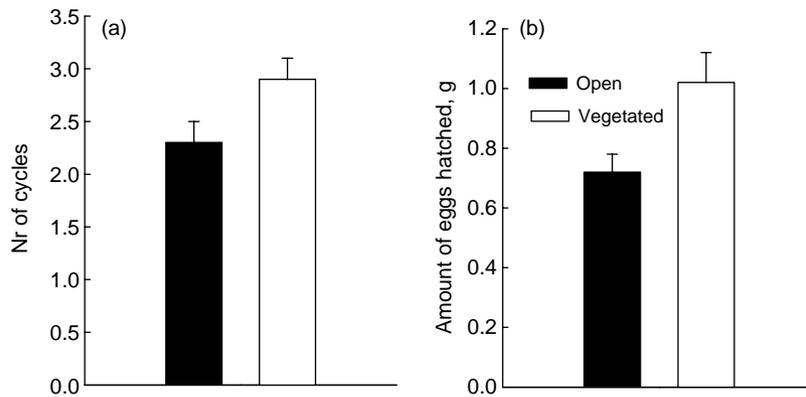


Fig. 4. (a) Number (+SE) of breeding cycles completed and (b) the total mass of eggs hatched (+SE), summed over all breeding cycles, for males nesting in open and vegetated habitats.

## Discussion

Two major consequences of eutrophication, increased macro algae cover and increased turbidity due to growth of phytoplankton, had positive effects on male parenting success and on reproductive output of sticklebacks. Both environmental factors reduced aggressive interactions between the nesting male and the intruder, which saved energy and possibly reduced injuries. This made it possible for the nesting male to complete more breeding cycles and increase lifetime reproductive output, as found in the vegetation treatment where males were allowed to complete as many breeding cycles as they could. The reduction in aggressive interactions was probably due to reduced visibility, which made it possible for the nesting male to care for the eggs without being seen by the intruder, and for the intruder to hide unseen.

In addition to this indirect effect of increase algal growth on reproductive success, enhanced turbidity had a direct effect on fanning behaviour and on reproductive success; it reduced the need for fanning while it increased hatching success and reproductive output. This was most likely a consequence of augmented oxygen levels in the water due to photosynthesis by the algae. High oxygen content of water is known to reduce the need for fanning in sticklebacks (van Iersel 1953, Reebbs et al. 1984), and has been found to reduce fanning behaviour and the loss of body weight in common gobies *Pomatoschistus microps* (Jones and Reynolds 1999). Since the summer nights are light in the study area, the algae were able to photosynthesize for most of the day and keep the oxygen levels high. Thus, stickleback males nesting in phytoplankton rich water incurred a double advantage in that they suffered fewer intrusions from rival males and needed to spend less effort fanning the eggs.

This, in turn, saved resources for future breeding cycles, which should augment lifetime reproductive output.

Increased turbidity caused by phytoplankton growth reduced selection for large male size, by equalizing the parenting success of males of different sizes; large males had a higher hatching success than smaller males in clear water, but this size advantage disappeared under increased growth of phytoplankton. Apparently the oxygen conditions were so good in turbid water that even small males could keep the eggs aerated. Under clear water conditions, on the other hand, only the largest males were able to reach a high hatching success, through high fanning rate or less cannibalism. This suggests that selection for large male size at the parenting stage is relaxed in turbid water. If large body size correlates with good condition and indicates high genetic quality, which is possible according to the condition-dependent theory of sexual selection (Andersson 1986, Rowe and Houle 1996) and has been demonstrated for many species (Johnstone 1995, David et al. 2000, Kotiaho 2002), then size-independent hatching success could result in an improved reproductive success of poor condition males of low genetic quality. However, selection on size arises also at other stages of the reproductive cycle, such as in the competition for territories (Candolin and Voigt 2001a). The relative importance of relaxed selection on body size at the parenting stage is therefore unknown.

Several earlier laboratory studies show that sexual selection on visual cues is relaxed under eutrophic conditions (Candolin et al. 2007, Engström-Öst and Candolin 2007, Wong et al. 2007). Moreover, field studies suggest that the opportunity for sexual selection is reduced in areas with a dense growth of filamentous algae, since the variation among males in the mass of eggs in their nests decreases when the density of algae increases (Candolin 2004). This relaxation of sexual selection could be due to reduced mate

Table 1. Water turbidity and oxygen levels (mean  $\pm$  SE) in clear and turbid water.

	Clear, n=25	Turbid, n=25	t	p
Water turbidity NFU	1.47 $\pm$ 0.09	8.66 $\pm$ 0.92	7.76	<0.001
Oxygen saturation (%)	115 $\pm$ 2	145 $\pm$ 5	5.36	<0.001
Oxygen mg l <sup>-1</sup>	11.4 $\pm$ 0.1	14.6 $\pm$ 0.7	4.71	<0.001

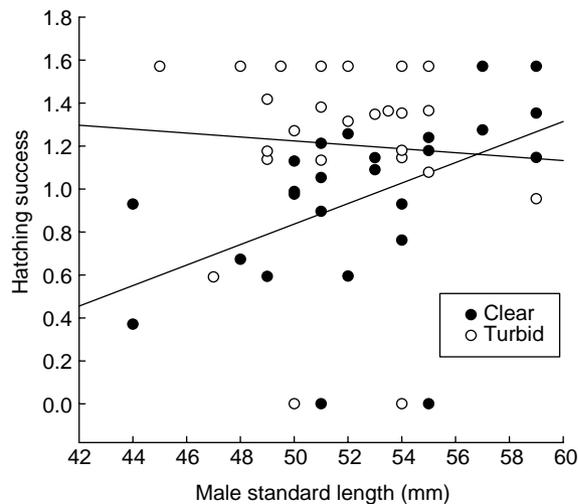


Fig. 5. Dependence of hatching success (arcsine square root transformed) on male size in clear and turbid water.

encounter rate or to hampered mate evaluation under reduced visibility, which would decrease the possibility of adaptive mate choice. Together with the present results of reduced selection on body size, these studies suggest that selection during the reproductive stage is relaxed under the new conditions. Whether this will shift selection to other life stages, or if increased importance of olfactory cues in mate choice could counteract this effect and enhance adaptive selection (Heuschele and Candolin 2007), deserves further investigations.

The density of nesting males is generally higher in densely vegetated areas (Candolin and Voigt 2001a, Candolin 2004). An increase in lifetime reproductive success in these areas, as suggested by this study, would then increase the reproductive output of the populations through an augmented number of eggs hatching within an area. Whether this will occur depends on the effect of eutrophication on several other factors, such as the fecundity of the females, the number of females that spawns and on egg predation. The effect of eutrophication on female fecundity and the probability of spawning have not been directly determined. Earlier field studies suggest, however, that the amount of eggs spawned do not differ depending on algae growth, even though mate encounter rate is reduced in dense algae growth (Candolin and Voigt 2001a, Candolin 2004). Apparently, reduced mate encounter rate reduces only the variation among males in the amount of eggs they receive, probably due to reduced female mate choosiness, not the amount of eggs spawned (Candolin 2004).

For an increased number of hatching juveniles to survive until adulthood and enlarge the population, the environmental conditions should be favourable also for juveniles and adults. Otherwise natural selection against the increased number of offspring should strengthen, through food limitation, predation or parasite infections, in which case juvenile or adult mortality would keep the population size down. Whether the population size of sticklebacks is increasing or not under the changing conditions is presently unknown, since natural annual fluctuations are high and

data from multiple years are required to determine the trend.

To summarize, increased algal growth in the form of increased algal cover and increased turbidity enhanced the reproductive output of sticklebacks. This arose through reduced aggressive interactions with intruding males and improved oxygen conditions, which improved hatching success and the general condition of the males and, thus, augmented lifetime reproductive success. However, selection on male size was reduced in turbid water. Together with an overall reduction in sexual selection under eutrophic conditions, this suggests that selection and population regulation at the reproductive stage could be relaxed under the new conditions. Whether the population size of sticklebacks will increase as a result of enhanced reproductive output, or if the regulation of population growth and the strength of selection for individuals adapted to the new environment will increase at other life stages, such as the juvenile stage, warrant further investigations.

A multitude of factors, other than behaviour and oxygen conditions, such as food availability and predation risk, will probably also change under eutrophication, through changes in species diversity and biomass. Further, the amount of decaying organic material increases with higher production, which consumes substantial amounts of oxygen. Here, we have studied only a few isolated factors that determine reproductive output under eutrophic conditions. A challenge of future work will be to consider multiple factors and their interaction to determine both the proximate and ultimate effects of eutrophication on stickleback populations.

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