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ORIGINAL PAPER

Reversed parasite-mediated selection in sticklebacks from eutrophied habitats

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Abstract Sexual selection is often assumed to increase the viability of populations by increasing the quality of offspring produced. Presently, human-induced environmental changes are altering the process of sexual selection by influencing male–male interactions and female mate choice. Here, we show that increased density of filamentous algae due to eutrophication reverses parasite-mediated selection during reproduction in threespine sticklebacks (*Gasterosteus aculeatus*). When we manipulated the density of artificial algae in a breeding area in the Baltic Sea, more males nested in dense than in sparse vegetation, but the males in dense vegetation were more parasitized. Interestingly, heavily parasitized males acquired more eggs than less parasitized males in dense vegetation but not in sparse vegetation. The higher probability of reproduction for parasitized males in dense algae growth could be due to impaired visibility relaxing male–male competition or reducing female choosiness. This could favour males in poor condition that often invest more in attracting females than males in good condition. In sparse vegetation, parasitized males may have a lower reproductive success due to intense male–male competition, careful female choice and high predation rate selecting against parasitized males. The results suggest that eutrophication could alter the fraction of the population that reproduces, which could have long-term evolutionary consequences.

Keywords Environmental change · Eutrophication · Male–male competition · Mate choice · Parasites · Sexual selection

Introduction

Humans are presently altering aquatic ecosystems worldwide through overfishing, pollution and nutrient discharge (Halpern et al. 2008). This can influence the demography of populations both directly, through the removal of individuals, and indirectly through cascading ecological effects (e.g. Estes and Duggins 1995). Another important pathway of human impact on populations, which has received surprisingly little attention, is human-induced changes of evolutionary processes (Palumbi 2001; Candolin and Heuschele 2008).

One of the main mechanisms of evolution is sexual selection, which drives the evolution of traits that increase mating and fertilisation success (Andersson 1994). Changes in the environment may influence the costs and benefits of sexually selected traits and, hence, alter the strength and target of sexual selection (Emlen and Oring 1977; Kokko and Rankin 2006). For example, changes in the spatial distribution of individuals can reduce mate encounter rate, which can increase the cost of mate choice and cause a relaxation of female mate choosiness (Real 1990; Shuster and Wade 2003). This can alter the number and quality of offspring produced in populations and, ultimately, influence the dynamics and viability of populations (Candolin and Heuschele 2008).

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Currently, aquatic ecosystems are changing due to eutrophication and increased growth of algae (Smith 2003). An area that is heavily affected is the Baltic Sea. Increased growth of both filamentous algae and phytoplankton is altering visibility and the structure of the habitats, particularly in shallow waters (Lehvo and Bäck 2001). Since the shallow benthic zone is an important breeding area for many fish species (Axenrot and Hansson 2004), human-induced eutrophication could alter the strength and direction of sexual selection operating in the fishes that spawn in the area, particularly fishes that rely on visual cues in mate choice (Seehausen et al. 1997; Järvenpää and Lindström 2004; Candolin et al. 2007; Heuschele and Candolin 2007; Wong et al. 2007).

Recent studies reveal that enhanced growth of filamentous algae increases the density of breeding threespine stickleback males *Gasterosteus aculeatus* L. in shallow waters of the Baltic Sea (Candolin and Voigt 2001a; Candolin 2004). Increased density of filamentous algae also correlates with a more even distribution of eggs among nests, which suggests that the strength of sexual selection is relaxed in dense vegetation (Candolin 2004). Experimental studies that have manipulated the density of filamentous algae (Candolin et al. 2007, 2008) and water turbidity (Engström-Öst and Candolin 2007; Wong et al. 2007) suggest that the relaxation could be due to impaired female choosiness and relaxed male–male competition under reduced visibility.

Stickleback males establish territories and build nests under intense male–male competition and develop a red nuptial coloration and perform a courtship dance to attract females (Wootton 1984). The size and condition of the males influence their success in the competition for territories and mates; big males in good condition dominate over smaller males (Rowland 1989; Kraak et al. 1999, Candolin 2000b; Candolin and Voigt 2001a, 2003). A relaxation of the strength of sexual selection in densely vegetated habitats could therefore influence selection on male condition. If condition correlates with individual fitness and how well the fish are adapted to prevailing conditions, then a relaxation in selection on condition could influence the viability of populations.

Here, we used artificial algae to investigate whether enhanced algae growth due to human activities influences the strength of selection on the condition of stickleback males during breeding under field conditions. We manipulated vegetation cover using artificial algae and recorded (1) the number and condition of males nesting in dense and sparse vegetation, and (2) the distribution of mating success among the males. To estimate the condition of the males, we calculated the Fulton's condition index (weight in relation to length) and determined parasite load, which usually reflects overall viability and health (Hamilton and Zuk 1982; Poulin and Vickery 1993).

Materials and methods

Habitat structure

At the start of the breeding season, ten sparsely and ten densely vegetated patches, 1.5×1.5 m, were distributed randomly within an open area in a shallow coastal bay of the Baltic Sea in southern Finland (59°50′N, 23°15′E). The patches mimicked areas with sparse or dense growth of filamentous algae. Each patch had tufts of 25 cm long, thin, green polypropylene strings attached to a 1.5×1.5 m metal garden fence with a mesh size of 10×6 cm. Dense patches contained 170 tufts of algae evenly distributed over the patch, whereas sparse patches contained 16 evenly distributed tufts. The patches were put out at a water depth of 70.6 cm ±10.5 (SE), following a checkerboard pattern. The distance between neighbouring patches was 2 m.

The patches were checked for territorial males every second day. In the present area, males usually collect eggs for about 2 days before they switch to the parental phase and accept no more eggs (Candolin, personal observation). Ten days after the first territory had been established in a patch, all males and their nests were collected from the patches. The eggs were separated from the nests, and the wet weight of the clutches was recorded. Since incubation takes 8–14 days, depending on water temperature, and the newly hatched fry stay by the nest for the first days, this should ensure that no eggs had hatched before collection. Immediately after removal of the males, accumulated detritus and algae were removed from the tufts, and the following experimental period was started by allowing new males to establish territories within the patches. Two sampling periods were completed in 2007. Later in the season, the number of successfully nesting males in sparse patches was too low for meaningful statistical analysis, and the data was excluded from the analysis. The same experimental procedures were repeated the following year, 2008, with the number of replicates increased to 11.

Assessment of male quality

Males were caught while snorkelling using a hand net that had a dummy female attached to the opening of the net. The males were transported to the laboratory, and their standard length and wet weight were measured. Male condition was estimated using Fulton's condition factor (weight/(standard length)^3, Ricker 1975). In addition, parasite prevalence, parasite species richness (PSR) and the intensity of parasite infection for common parasite species were estimated. We defined parasite *prevalence* as the number of infected individuals divided by the total number of individuals inspected, and PSR as the number of species per host (Bush et al. 1997). We assessed the intensity of infections, i.e. the mean number of parasites of a species per infected host, for the genera: *Diplostomum*, *Schistocephalus* and *Thersitina*. Microsporidia infections (*Glugea anomala*) were recorded by counting the number of xenomas in the body cavity and on the outside of the fish.

The fish were killed by decapitation and screened for external and internal parasites using a ×40 binocular microscope and a ×120 microscope. Eyeflukes (*Diplostomum* sp.) were counted by extracting the lens from the eye socket and screening the eye lens for metacercaria (Wall and Bjerkås 1999). The body surface, fins and all gill lamellae were inspected for external parasites, and the body cavity and the internal organs inspected for internal parasites (see Zander et al. 1999).

Statistical analysis

All statistical analyses were done using the statistical software R v2.9.2 (R Development Core Team 2009). We performed mixed-effect analyses of variance (ANOVAs) and analyses of covariance (ANCOVAs) using the lme-function for normally distributed data (nlme package, Pinheiro et al. 2007) and the lmer-function for Poisson and binomially distributed data (lme4 package, Bates 2007). We always included patch identity as a random factor and treatment, period and year as fixed factors. The models were subsequently reduced to the minimum adequate models using stepwise backward deletion. The effects of year and period are mentioned only when significant effects were detected. The distribution of the residuals was checked after each analysis, to confirm the reliability of the chosen test. Mann–Whitney's *U* test was used when residuals were not normally distributed.

When analysing for differences between parasite prevalence, we used a generalised mixed-effect ANOVA based on residual maximum likelihood with egg possession (1/0) in addition to treatment, period and year as fixed factors. Differences in the intensity of parasite infections of nesting males were analysed using a Kruskal–Wallis test, using the average value of each patch. When analysing for differences in the number of males with eggs in their nests, we used a generalised mixed-effect model with binomial distribution (egg possession (1/0) and treatment, period and year as fixed factors). When analysing for effects of male characteristics on amount of eggs in nests, we included all nesting males and used a mixed-effect ANCOVA with PSR, body length and male condition as covariates, and treatment, period and year as fixed factors.

Results

Demographic data

More males nested in densely vegetated patches than in sparsely vegetated patches (Fig. 1, 84 patches, Mann–Whitney *U* test: W=1,255, P<0.001). Males did not differ in condition between dense and sparse vegetation ($F_{1,59}$= 0.10, P=0.75), but males were in slightly better condition during the second year ($F_{1,56}$=10.69, P=0.002). Males in the two vegetation treatments did not differ in mean body length ($F_{1,59}$=0.53, P=0.47), but males were shorter during the second year ($F_{1,61}$=7.59, P=0.008).

Parasite infections

PSR of males was higher in dense vegetation, increased over the breeding season and was higher during the second year (Fig. 2 and Table 1). PSR was not significantly correlated with the condition factor of the males, but a higher sample size is required to gain a more reliable result (Pearson's product-moment correlation, r=−0.174, t_{106}= 1.82, P=0.07). The intensity of parasite infections was higher in dense vegetation for *Apatemon* sp., *Thersitina* sp., *Schistocephalus* sp. and *G. anomala* (Table 3).

Regarding the occurrence of different parasite species, the prevalence of *Diplostomum* sp. depended on vegetation and period; males in sparse vegetation had a lower prevalence than males in dense vegetation, but across habitats, the prevalence increased over the season (Table 2). No habitat-dependencies in prevalence were found for the other taxa (Table 2). PSR and the intensity of infection were positively correlated for all parasite species for which

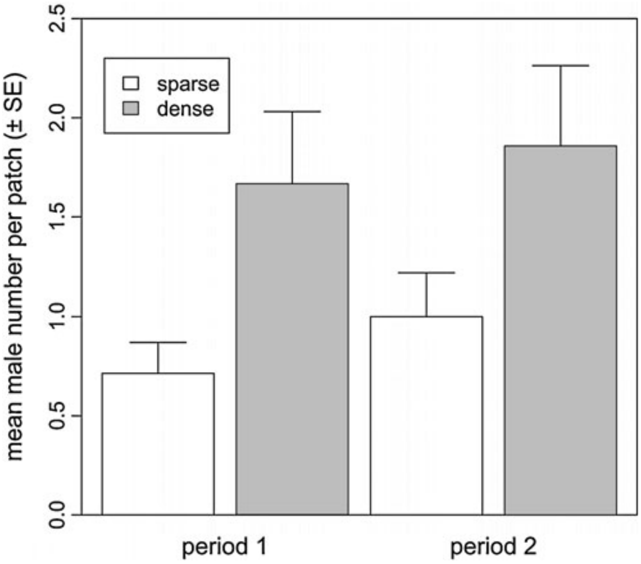

Fig. 1 Mean number of nesting males (±SE) during the two periods in sparse and dense vegetation

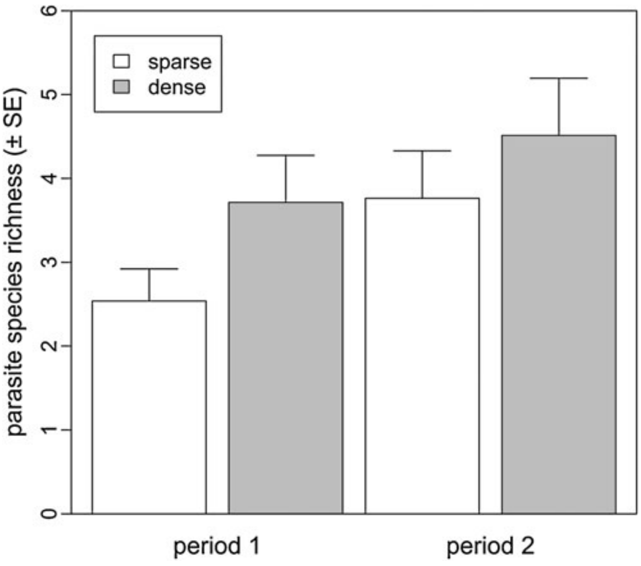

Fig. 2 Mean parasite species richness (±SE) during the two periods in sparse and dense vegetation

intensity was measured (Table 3). Thus, males harbouring many parasite species had severer infections.

Mating success

The total amount of eggs deposited in each patch was higher in dense vegetation (Mann–Whitney *U* test, 84 observations, W=1,093, P=0.033; Fig. 3). The amount of eggs deposited in each nest was also higher in dense vegetation ($F_{1,45}$=6.22, P=0.0016) but varied with time and was higher in the first period in each year ($F_{1,53}$=7.21, P=0.0097) and in the second year of the experiment ($F_{1,53}$=20.72, P<0.0001). The probability that an individual nesting male had eggs in his nest did not depend on vegetation (102 observations in 61 patches, mixed model ANOVA with a binomial link function, z=−0.98, P=0.32) but was higher during the first period (z=−2.45, P=0.014) and during the second year of the experiment (z=4.71, P<0.001).

When inspecting the effect of male characteristics on the number of eggs in each male's nest, the amount of eggs was found to depend on PSR of the male, with the pattern differing depending on vegetation density; the amount of eggs in the nest increased with PSR in dense vegetation but decreased with PSR in sparse vegetation (Fig. 4a, interaction between PSR and treatment $F_{1,38}$=6.56, P=0.015), independent of period and year. Across vegetation treatments, the effect of PSR on the amount of eggs in a nest varied over time, with heavily parasitized males receiving more eggs early in the season and less parasitized males receiving more later in the season, when the proportion of parasitized males had increased (Fig. 4b, interaction between PSR and period $F_{1,38}$=8.25, P=0.007). The amount of eggs received did not depend on the condition of the male ($F_{1,36}$=2.36, P=0.13) or his body length ($F_{1,35}$=0.6, P=0.44), but males received more eggs in the second year ($F_{1,57}$=19.81, P<0.001). Qualitatively similar results are obtained when only males with eggs are included in the model.

Males with eggs had a significantly lower prevalence of *Thersitina* sp. and *Schistocephalus* sp. than males without eggs, but a higher prevalence of Digenia species (*Diplostomum* sp. and *Apatemon* sp.; Table 2).

Discussion

More males established territories and built nests in densely vegetated compared to sparsely vegetated patches. This could be due to more males choosing densely vegetated nesting sites or to the rate of predation on nesting males being lower in dense vegetation. Sticklebacks generally prefer vegetated and concealed areas as nesting sites and feeding grounds, probably due to a lower predation risk (Kynard 1978, 1979; Sargent and Gebler 1980; Kraak et al. 2000). However, males are reluctant to nest in heavily vegetated habitats where visibility and mate encounter rate is low (Candolin and Salesto 2006). Since dense vegetation allows a higher density of territories, due to poor visibility reducing territory size (Mori 1993; Candolin and Voigt 2001a; Candolin 2004) and relaxing male–male interactions (Sargent and Gebler 1980; Sargent 1982; Candolin et al. 2008), more males could have been able to choose the vegetated patches. Moreover, the finding that males received more eggs in dense than in sparse vegetation suggests that the vegetation was not too dense for attracting females.

Males that nested in dense vegetation were more parasitized than males that nested in sparse vegetation. There are several possible non-exclusive explanations for the pattern. It could arise from parasitized males choosing dense vegetation, from predation removing parasitized males from sparse vegetation or from the transmission of parasites being higher in dense vegetation and, hence, increasing the level of parasite infections. Earlier studies have found male–male competition to be more intense in sparser vegetation (Candolin and Voigt 2001b; Candolin et al. 2008). Male–male competition could

Table 1 The effects of vegetation, period and year on parasite species richness of nesting males

Factor	Estimate	SE	$F_{1,59}$	P
Vegetation	−0.96	0.27	12.78	0.0007
Period	1.06	0.26	17.07	0.0001
Year	0.76	0.27	8.92	0.0041

Based on a mixed effect analysis of variance with patch as random factor and vegetation, period and year as fixed factors

Table 2 Mean parasite prevalence for different parasite species during the two periods

Class	Dense		Sparse		Statistics (generalised mixed model)				
	All males	Males with eggs	All males	Males with eggs	Factor	Estimate	SE	z	P
Ciliata									
Trichodina sp.	0.92	0.97	0.88	0.85	TRE	−1.06	1.05	−1.01	0.31
					EGG	0.61	1.11	0.54	0.59
					PER	4.42	1.77	2.49	0.013
					YEAR	4.20	1.78	2.37	0.018
Monogenea									
Gyrodactylus sp.	0.8	0.85	0.74	0.69	TRE	−0.76	0.57	−1.33	0.18
					EGG	0.15	0.62	0.22	0.83
					PER	2.22	0.64	3.46	<0.001
					YEAR	1.96	0.65	3.23	0.003
Digenia									
Diplostomum sp.	0.69	0.75	0.5	0.46	TRE	−1.01	0.49	−2.05	0.040
					EGG	1.06	0.51	2.06	0.039
					PER	1.69	0.53	3.22	0.002
Apatemon sp.	0.19	0.34	0.09	0.15	TRE	−0.67	0.73	−0.92	0.36
					EGG	2.42	0.81	3.010	0.003
Crustacea									
Argulus foliaceus	0.46	0.5	0.44	0.31	TRE	−0.03	0.43	−0.07	0.94
					EGG	−0.12	0.4	−0.30	0.76
Caligus sp.	0.09	0.04	0.06	0	TRE	−0.48	0.86	−0.56	0.58
					EGG	−1.31	1.17	−1.12	0.26
					YEAR	−2.18	1.07	−2.02	0.043
Thersitina gasterosteus	0.53	0.38	0.35	0.15	TRE	−0.93	0.58	−1.59	0.11
					EGG	−1.57	0.53	−3.00	0.003
Cestoda									
Schistocephalus solidus	0.24	0.22	0.08	0	TRE	−1.48	0.89	−1.66	0.097
					EGG	−1.84	0.76	−2.41	0.016
					PER	−2.55	0.82	−3.13	0.002
Oomycetes									
Saprolegnia spp.	0.08	0.15	0.06	0	TRE	0.32	11.9	0.03	0.98
					EGG	2.57	3.00	0.86	0.39
Microsporidia									
Glugea anomala	0.14	0.13	0.09	0.08	TRE	−0.62	0.79	−0.79	0.43
					EGG	0.66	0.69	0.94	0.34

All statistical results were derived by backward deletion from a generalised mixed model including *year*, *period* (PER), *treatment* (TRE) and *eggs in nest* (EGG) as fixed factors and parasite prevalence as dependent variable. The table includes the non-significant values for *eggs* and *treatment* before they were removed from the model

therefore have prevented heavily parasitized males from establishing nests in sparse vegetation, forcing the males to choose densely vegetated sites. Moreover, predation risk is usually higher in exposed areas than in concealed areas (Kynard 1978; Sargent and Gebler 1980). Since heavily parasitized males can be more vulnerable to predation due to, for instance, altered behaviour or impaired vision (Milinski 1985; Owen et al. 1993), high predation risk in sparse vegetation could have removed parasitized males that succeeded in nesting in the habitat.

The degree to which a higher transmission of parasites in dense vegetation could have increased parasite infections during the 12 days that the experiment was running is unknown. The fact that most of the internal parasites were at later developmental stages suggests that most infections had taken place before the choice of breeding site. For instance, all recorded cestodes of *Schistocephalus* sp. were longer than 1 cm and of white colour, which indicates that the infections had taken place at least 1–2 weeks earlier (Hammerschmidt and Kurtz 2005, 2009). The eyefluke

Table 3 Mean intensity of infection by different parasite species and correlations with parasite species richness

	Mean parasite intensity					Correlation between parasite species richness and intensity			
Class	Dense	Sparse	*df*	χ^2	*P*	*t*	*df*	cor	*P*
Monogenea									
Gyrodactylus sp.	10.74	8.7	1	0.002	0.97	2.55	93	0.26	0.012
Digenia									
Diplostomum sp.	2.53	2.47	1	1.93	0.16	4.25	106	0.38	<0.001
Apatemon sp.	3.07	1	1	3.95	0.048	2.26	106	0.21	0.026
Crustacea									
Argulus foliaceus	1.71	1.6	1	0.88	0.34	4.76	106	0.42	<0.001
Caligus sp.	1.14	1	1	1.79	0.18	2.69	106	0.25	0.008
Thersitina gasterosteus	2.41	1.83	1	5.15	0.023	3.66	106	0.36	<0.001
Cestoda									
Schistocephalus solidus	1.11	1	1	4.74	0.029	3.12	106	0.29	0.002
Microsporidia									
Glugea anomala	3.3	1.67	1	3.23	0.072	2.02	106	0.19	0.046

Kruskal–Wallis test was used to test for effect of vegetation on the intensity of parasite infections, using average values of each patch and including all nesting males. To test whether parasite species richness and mean intensity of infection were correlated, Pearson's product-moment correlation was used

Diplostomum sp., which was more common in dense vegetation, is able to reach its final destination in the eye within 24 h (Chappell et al. 1994). Infections could therefore have taken place at the nesting site. However, we found a wide size range of metacercaria in the lens, which suggests that some infections could have taken place prior to choosing the nesting site.

A prevalence of parasitized males in dense vegetation could also be due to intrinsic habitat preferences of males. If males that chose densely vegetated nesting sites had preferred more vegetated habitats also outside the breeding season, then a correlation between the degree of parasite infections and the choice of habitat could developed for parasites with a high transmission rate in dense vegetation, such as *Argulus foliaceus* (Poulin and Fitzgerald 1989).

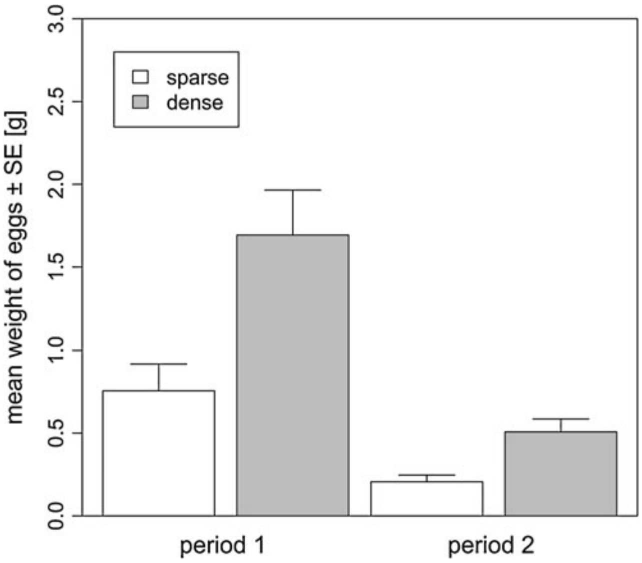

Fig. 3 Mean weight (±SE) of all eggs in a patch during the two periods in sparse and dense vegetation

Although the cause of the high infection levels in dense vegetation cannot be determined in this study, the results show that male–male competition is unable to remove severely parasitized males from the pool of reproducing males and that females apparently do not avoid mating with parasitized males in dense vegetation. Selection for healthy males, who can deal with the energetically demanding tasks of breeding (Chellappa et al. 1989), such as the defence of a territory, the oxygenation of the eggs and the avoidance of predation, could therefore be relaxed. Furthermore, the higher prevalence of eye flukes *Diplostomum* sp. in dense vegetation suggests that selection for good vision is reduced (Owen et al. 1993; Seppälä et al. 2004).

The choice of densely vegetated nesting sites was beneficial for parasitized males. While the males had a lower mating success than healthier males in sparse vegetation, the pattern was the opposite in dense vegetation, where infected males received more eggs. The higher mating success of healthy males in sparse vegetation is in line with earlier work on sticklebacks (Blais et al. 2004; Kraak et al. 1999; Milinski and Bakker 1990) and other species (e.g. Ehman and Scott 2002; Rantala et al. 2002; Worden et al. 2000). It agrees with the predictions of the hypothesis of parasite-mediated sexual selection, which postulates that females should choose males based on traits that reflect parasite load (Hamilton and Zuk 1982).

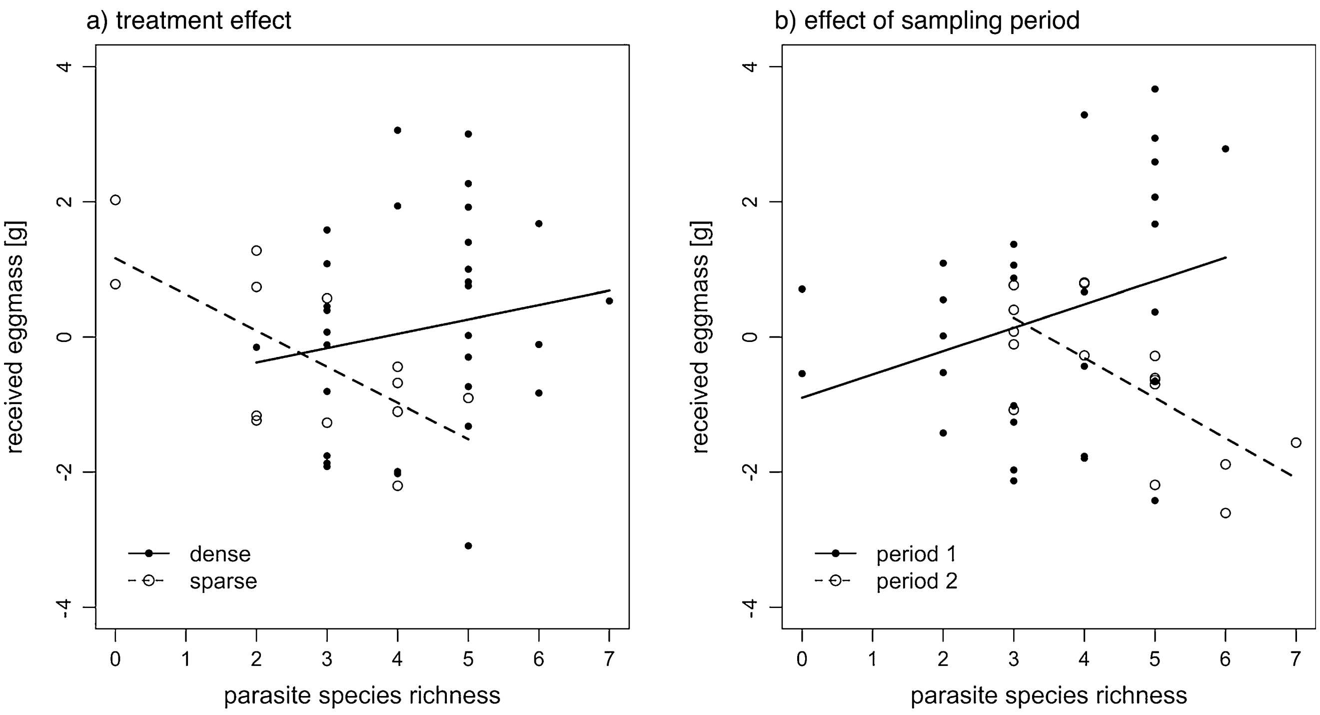

Fig. 4 The relationship between amount of eggs received and parasite species richness of territorial males in different (**a**) vegetation treatments and (**b**) periods. *Lines* are based on model estimates from mixed effects analyses of covariance with residual egg mass as dependent factor, parasite species richness as covariate and (**a**) treatment or (**b**) period as fixed factor. We corrected for the effects of (**a**) treatment and (**b**) period by running a full model with either period or treatment as fixed factor, together with year, and then using the residuals as dependent factor in the final model

Why did dense vegetation then allow parasitized males to collect more eggs than healthier males? It could be due to parasitized males having a higher mating success, a lower egg mortality rate or a higher egg stealing success than healthier males in dense vegetation. Males in poor condition are known to invest more than good condition males in courtship and in red nuptial coloration (Candolin 1999). However, under intense male competition, poor condition males are not able to maintain their high investment, due to a social control of signalling (Candolin 2000b, c). This could explain the lower reproductive success of parasitized males in sparse vegetation. Moreover, parasitized males that managed to invest much in courtship in sparse vegetation could have suffered high predation rates and been removed from the population. In dense vegetation, on the other hand, male–male competition is less intense and the social control of signalling relaxed due to poor visibility (Wong et al. 2007). This could have allowed parasitized males to maintain a high investment into courtship, resulting in ‘dishonest’ signalling of condition (Candolin 1999), as found in earlier studies where visibility has been manipulated (Wong et al. 2007).

In addition, relaxed female choosiness in dense vegetation could have allowed parasitized males that invested much in courtship to realise a high mating success. Under good visibility, stickleback females prefer less parasitized males (Milinski and Bakker 1990), and these males have a high mating success (Blais et al. 2004), as found in sparse vegetation in the present study. However, when visibility is reduced, the ability of females to compare males based on visual cues is hampered (Candolin et al. 2007; Engström-Öst and Candolin 2007). This could have increased the mating success of parasitized males.

The possibilities that parasitized males had more eggs in their nests than healthier males in dense vegetation due to a lower egg predation rate or a higher egg stealing success appear unlikely, but cannot be excluded. Parasitized males are usually poor competitors (e.g. Barber and Ruxton 1998), but if they are better at defending their offspring or are more successful in stealing eggs in dense vegetation is unknown.

Whether females benefit or not from mating with parasitized males in dense vegetation depends on the fitness of their offspring and, hence, on the parental ability and the genetic quality of the males. If parasitized males are of high genetic quality, which can occur under some circumstances (Getty 2002), or have superior parental ability, then a preference for parasitized males could be beneficial. Parasitized males could face a low probability of future reproduction and therefore invest more into current reproduction and parental care than males with more future reproductive opportunities (Candolin 1999). On the other hand, if parasitized males are of low genetic quality and father offspring with a low probability of survival, then an increased mating success of parasitized males could lower the viability of the population.

The production of offspring appears to be high in densely vegetated habitats, as more eggs are laid in dense than in sparse vegetation (present study and Candolin 2004), hatching success is higher (Candolin et al. 2008) and the habitat offers shelter for fry (Foster et al. 1988) and reduces the risk of nest raids (Moodie 1972; Kynard 1978, 1979, but see Mori 1993). This high offspring production could compensate for the reduction in the strength of selection at the nesting stage in dense vegetation and shift selection to later life history stages, such as the juvenile stage. This could contribute to the maintenance of viable populations under eutrophied conditions.

The high mating success of parasitized males decreased with time when all males, irrespective of vegetation, were inspected. Early in the season, heavily parasitized males received more eggs, while later in the season healthy males had a higher success. Since the degree of parasite infections increased over the season, the preference of females for healthy males could have strengthened with time or male–male competition intensified (Candolin 2000a). If increased selection on condition later in the season will influence population, viability depends on the survival of the offspring that hatch late in the season and on their contribution to the following generation.

To summarise, heavily parasitized males acquired more eggs than less parasitized males in areas with dense algae cover, but less eggs in areas with sparse algae cover. The improved reproductive success of parasitizes males in dense vegetation could be due to high investment into reproduction combined with relaxed male–male competition and hampered female choice. Whether mating with parasitized males is beneficial or not for females and if it will influence population viability depends on the parental ability of the males and their genetic quality.

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