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Increasing temperature counteracts the impact of parasitism on periwinkle consumption

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ABSTRACT: Parasites often have key structuring roles in natural communities. For instance, trematode infections significantly reduce consumption by the herbivorous gastropod *Littorina littorea*, in turn affecting the composition of coastal macroalgal communities on which the snail grazes. However, trematodes are extremely sensitive to temperature changes, in that production and release of infective stages (cercariae) from the snail host are strongly accelerated by increasing temperature. Hence, trematode-infected periwinkles may increase their rates of consumption under warmer conditions to support the additional energetic burden exerted through elevated cercarial shedding. We therefore hypothesized that the combined effect of higher temperatures and parasitism may neutralize the negative impact trematodes otherwise have on periwinkle consumption. To test this, we performed a microcosm experiment examining the combined effect of infection and temperature on the snails' consumption of the green macroalgae *Ulva lactuca*. Our results show an overall positive effect of temperature on consumption by larger periwinkles, but particularly so in trematode-infected specimens. Whereas infected snails consumed less than uninfected ones at 18°C, no difference was evident at 21°C. Hence, the synergy between parasitism and a relevant temperature increase, e.g. in lieu of expected global warming within this century (3°C), may indeed counteract the generally negative impact of trematodes on periwinkle grazing.

KEY WORDS: Trematodes · *Littorina littorea* · Global warming · Synergistic effect · Cercariae · Macroalgae

INTRODUCTION

Temperature affects many processes in natural systems, ranging from the performance of individual organisms (Schmidt-Nielsen 1997) to the distribution and abundance of species (Krebs 2001). Therefore, temperature changes associated with global climate change are expected to have broad ecological consequences in both marine and terrestrial environments (Parmesan & Yohe 2003, Root et al. 2003, Harley et al. 2006). Accordingly, considerable effort has been dedicated to understanding the ecological consequences of increasing temperature (e.g. Ottersen et al. 2001, Stenseth et al. 2002, 2003, Walther et al. 2002, Schiel et al. 2004, Rosenzweig et al. 2008).

Parasites have been recognised as major players in coastal ecosystems, as they commonly modify the phenotype of their host, often with ramifications to higher levels of ecological organisation (Sousa 1991, Thomas et al. 1998, 2005, Mouritsen & Poulin 2002a, 2005, Mouritsen & Haun 2008). In this context, recent studies have demonstrated potential indirect effects of trematodes on coastal alga communities. Wood et al. (2007) and Clausen et al. (2008) found trematode infections to reduce the consumption rate of the common periwinkle *Littorina littorea*, ultimately affecting the composition of the macroalgal community. This herbivorous snail is a potent regulator of the competitively dominant ephemeral algae and thus often controls the overall macroalgal structure in coastal habitats (Lubchenco 1978, Lein 1980, Bertness 1984, 1999, Wood et al. 2007). Hence, sites with a high proportion of trematode-infected periwinkles are likely to have a greater abundance of rapidly colonizing ephemeral algae rela-

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tive to sites with a high proportion of uninfected snails (Wood et al. 2007). Given that trematodes are thus indirectly capable of structuring the macroalgal community and given that snail–trematode associations are particularly sensitive to temperature (see below), it becomes imperative to elucidate the potential impact of e.g. climate warming on such host–parasite systems.

Trematodes are extremely sensitive to temperature change at a crucial step in their often complex life cycles. In the first intermediate host (primarily gastropods), the parasites' infective stages are produced asexually and periodically shed as short-lived, free-swimming cercariae (e.g. Werding 1969). Within the temperature range host and parasite can tolerate, a positive relationship generally exists between cercarial release from the snail and temperature (Kuntz 1947, Rojo-Vázquez & Simón-Martín 1985, Shostak & Esch 1990, Lo & Lee 1996, Umadevi & Madhavi 1997, Mouritsen 2002, Galaktionov et al. 2006, Poulin 2006). Higher temperatures also accelerate the production and maturation process of cercariae within the poikilotherm snail (Ataev 1991). Typically, the rate of physiological processes increases by a factor of 2 to 3 for every 10 degree rise in temperature (Q_{10}) (Schmidt-Nielsen 1997). Poulin (2006) reports a Q_{10} value of almost 8 in cercarial output from snails, and cercarial production thus responds much more markedly to temperature increases than expected from physiological processes in general. These findings emphasize the trematodes' extreme sensitivity to temperature and that cercarial production is not simply determined by the metabolic rate of the host.

Models presented by the Intergovernmental Panel on Climate Change (IPCC 2007) predict increases in average global surface temperature of 1.1 to 6.4°C during the 21st century, which are also bound to affect near-coastal waters. In addition to increasing the consumption rate of periwinkles in general (Newell et al. 1971), such elevated ambient temperatures can also be expected to exert an additional energy drain on trematode-infected snails through accelerated cercarial production, further increasing consumption rates. It can therefore be hypothesized that such temperature–parasitism synergy may neutralize the negative impact trematode infections would otherwise have on periwinkle consumption, or may even reverse it into increased consumption, everything else being equal.

To explore this hypothesis, we investigated the combined effect of temperature and parasitism on the consumption of the green macroalga *Ulva lactuca* by the common periwinkle *Littorina littorea* in a laboratory microcosm experiment. Such small-scale experimentation has increasingly been recognized as a useful approach for elucidating ecosystem responses to climate change (Benton et al. 2007).

MATERIALS AND METHODS

Experimental design. The microcosm experiment was performed at Rønbjerg Marine Biological Station, Limfjorden, Denmark (56° 53′ 27″ N, 9° 9′ 57″ E) from 8 January to 7 Febuary 2008. Two temperature treatments were established in 4 similar-sized water tanks (100 × 100 × 45 cm length × width × height) generated by flow-through thermostats allowing for diurnal temperature treatments (2 tanks for each temperature rather than 1 to achieve a higher level of replication). The latter was introduced to approach temperature conditions experienced by snails *in situ*. One treatment aimed at the decadal mean summer (June to August) surface temperature of 1990 to 2006 in Limfjorden (18°C). The other treatment aimed at a water temperature 3°C above the present level (21°C), corresponding to the predicted rise in temperature in Denmark within this century (Christensen et al. 1998, 2001). During experimentation, the water temperature was measured every 30 min by submerged temperature loggers and was 17.9 ± 0.04 and 21.2 ± 0.08°C (mean ± SE) in the 2 treatments, respectively. Each tank was supplied with seawater (25 to 28‰) at a flow rate of 1 l min^{-1}, corresponding to a retention time of approximately 3.3 h (water depth: 20 cm). This relatively high flow rate served to achieve the required temperature treatments and to ensure well-oxygenated microcosms.

A plastic cup (250 ml, 8.5 cm high) served as the experimental unit in which green algae and the herbivorous snails were established. A total of 560 such cups were submerged (i.e. water in tanks covered the tops of cups) and arranged evenly in the 4 water tanks, i.e. 280 cups at each experimental temperature and 140 in each tank.

Collection of experimental organisms. *Ulva lactuca* collected at a nearby locality was rinsed and prepared for each cup by a standardised draining procedure in which the thallus was placed and dabbed between 2 tea towels. The drained wet weight was then determined to the nearest 0.01 g, and a known amount (2.50 to 2.70 g) was added to each of the 560 cups. Statistically, the offered amount of macroalgae in the 2 temperature treatments, and among trematode-infected and uninfected snails eventually added, was not different at the start of the experiment (1-way ANOVA, $F_{3,418} = 0.371$, $p = 0.774$). The overall mean initial algal wet weight in microcosms was 2.59 ± 0.05 and 2.58 ± 0.05 g at 17.9 and 21.2°C, respectively.

Specimens of *Littorina littorea* were randomly collected according to the natural size distribution on a stone jetty inside of Rønbjerg Harbour at the beginning of November 2007. Prior to the experiment, the snails were stored in the laboratory and acclimatized for 7 wk in well-aerated, running seawater at approximately

18°C and with access to unlimited green macroalgae as a food source. Snails planned for the 21°C treatment were not acclimatized in the same manner, because the relatively small temperature increase of a further 3°C was judged to be insignificant to these poikilothermic organisms, which may experience much higher *in situ* temperature changes on a daily basis. This lack of acclimation, however, may have contributed to the higher snail mortality observed in the high temperature treatment (see 'Data analyses').

In order to ascertain whether a sufficient proportion of the collected periwinkles harboured mature trematode infections, snails from a haphazardly chosen subsample were placed individually in small glass jars with seawater at 25°C under illumination. Under these conditions trematode-infected snails normally start shedding cercariae within a few hours (authors' pers. obs.). We confirmed that cercariae were in fact released by some of the snails, and 3 types of infections were identified: *Cryptocotyle lingua*, *Himasthla elongata* and *Renicola roscovita* (see Werding 1969 for life cycles). Screened snails were not included in the experiment.

Establishment of experiment. Periwinkles, initally of unknown infection status, sex, weight and shell height, were placed individually in 530 of the 560 experimental cups. The remaining 15 cups at each experimental temperature without periwinkles, served as controls to determine macroalgal growth in the absence of grazing. These controls were distributed as evenly as possible among the 4 water tanks. All cups were individually covered with mesh (2 mm mesh size) to ensure that *Ulva lactuca* and snails remained in their respective cups during the experiment. In addition, a small stone of terrestrial origin (i.e. free of snail food sources) was placed in each cup as a stabilizing element, ensuring that all cups remained submerged. During the entire experiment the microcosms were exposed to a 19:5 h day (525 µE m^{-2} s^{-1}):night cycle, which ensured optimum light conditions for green macroalgal growth (de Casabianca et al. 2002). Microcosms were well oxygenated throughout the experiment, as evidenced by the presence of air bubbles caught below the mesh mounted at the top.

The experimental period ranged between 21 and 28 d, which ensured that none of the snails had depleted their available food sources. The staggered termination of the 560 microcosm experiments was necessary due to the labour associated with the post-experimental protocol. Remaining sea lettuce in each experimental unit was drained, and the wet weight was determined according to the procedure described above. The shell height (apex to aperture) of the snails was measured to the nearest 0.1 mm. The shell was then removed from each periwinkle to determine the soft-tissue wet weight to the nearest 0.01 g, the snail's gender, and the presence and identity of primary larval trematode infections in the gonad-digestive gland complex. Shell height and sex were included in the present study because these variables, aside from infection status, have previously been shown to affect the snails' macroalgal consumption (Clausen et al. 2008). The soft-tissue wet weight of periwinkles was measured in order to quantify their condition.

The microcosms were submerged in a common water body and, thus, cannot be considered entirely independent. We do not consider, however, that this experimental condition compromised our analysis, as we cannot envisage any realistic factor — communicated between microcosms through the water body — that might have influenced the qualitative outcome of the investigation. Moreover, periwinkles are obviously connected by a common water body in nature, and the present experimental set-up therefore reflects greater realism.

Data analyses. Statistical analyses were performed using SPSS for Windows (Version 14.0). Prior to all main analyses, tests for the assumptions of homogeneity of variance and normal distribution were conducted. Because each of the 2 temperature treatments were established in 2 separate tanks (i.e. 2 blocks of 2 temperature treatments), the data were analysed for a potential block effect. Hence, a preliminary full-model ANCOVA, including block together with all other fixed factors and shell height as covariable, showed no significant effect of block on consumption ($F_{1,405}$ = 1.139, p = 0.286). Hence, the 2 blocks were pooled at each temperature prior to further analysis.

Height–weight relationships of uninfected and infected snails were analysed by ANCOVA on ln-transformed height–weight data. To evaluate the combined effect of temperature and status of infection (uninfected or infected by larval trematodes) and potentially confounding variables (size and sex) on the consumption of *Ulva lactuca* by *Littorina littorea* we used full-factorial ANOVA. In all analyses, the consumption rate was corrected for the effect of temperature on algal growth (see final paragraph). Variation in the association with recorded mean values is given as the standard error (±SE) throughout. Experimental units in which snails died during the experiment (13 individuals at 17.9°C and 95 individuals at 21.2°C) were removed from the water tanks during the experiment and excluded from the final analysis. In addition, 1 control unit at 21.2°C was excluded from further analysis, as the thallus was partly decomposed. This reduced the effective sample size in the ANOVAs accordingly.

The reason for the substantially higher snail mortality in the high temperature treatment remains unknown, but may be related to the additional temperature stress imposed on the snails acclimated only to

18°C. An acclimation to 21°C of snails planned for the high temperature treatment would probably have reduced the mortality, as weak snails would have been eliminated prior to the experiment. However, because the consumption rates of snails dying during the experiment were excluded from the analyses, the different mortality rates between treatments do not invalidate our analysis or the conclusion drawn. The differential mortality could also be envisaged to result from a higher mortality rate of particularly infected snails at the higher temperature. This scenario is, however, unlikely because the prevalence of infection in snails at the end of the experiment was similar in the 2 temperature treatments (17.9°C: 27.0%; 21.2°C: 29.4%).

Because snail consumption of algae was measured as the difference between algal mass added at the start and retrieved at the end of the experiment, and because the growth rate of *Ulva lactuca* is temperature dependent (Wang et al. 2007), consumption was corrected for algal growth at both experimental temperatures. This was done by multiplying the average amount of algal mass present during the experiment (g) and the average growth rate of controls (g g^{-1} start weight d^{-1}), and adding this number to the observed daily consumption to get a corrected consumption total (i.e. average change in algal mass per day). The average amount of algae present was obtained by assuming (as the simplest model) a linear decline in algal mass during the experiment (i.e. half the sum of start and end weights). This number equalled 1.75 g at both 17.9 and 21.2°C. The growth rate of controls was on average –0.00150 g g^{-1} d^{-1} at 17.9°C (not different from zero, 1-sample *t*-test, $t_{14} = -1.169$, p = 0.262) and 0.00364 g g^{-1} d^{-1} at 21.2°C (significantly different from zero, $t_{13} = 2.589$, p = 0.022), which demonstrates the relevance of correcting consumption for different algal growth rates at different experimental temperatures.

RESULTS

In accordance with the pre-experimental screening, 3 different trematode species were found to infect the experimental snails. The most frequently occurring species were *Renicola roscovita* (20.4% of the snails infected) and *Himasthla elongata* (6.6%), whereas infections by *Cryptocotyle lingua* were rare (0.5%). Two snails were found infected by both *R. roscovita* and *H. elongata*.

Infection and snail condition

Across temperature treatments the soft-tissue wet weight and shell height of the periwinkles *Littorina littorea* were positively correlated both among uninfected ($r^2_{302} = 0.82$, $p < 0.001$) and infected ($r^2_{116} = 0.74$, $p < 0.001$) individuals (Fig. 1). An analysis of covariance on snail wet weight showed, aside from significant effects of shell height and infection status (uninfected individuals weighed on average 8% more than infected snails), a significant interaction between infection status and shell height (Table 1, Fig. 1). Hence, the difference in overall condition (weight at a given shell height) between uninfected and infected snails was particularly evident for larger individuals (Fig. 1). Because the analysis was not corrected for the wet weight of parasite tissue, the observed negative effect of infection on snail condition is conservative: the difference between infected and uninfected snails would be larger had parasite tissue been removed prior to analysis.

The above analysis was performed on all types of infections combined. An ANCOVA carried out solely

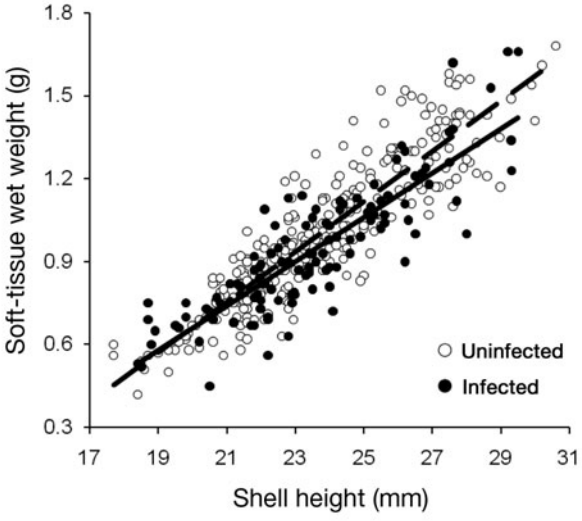

Fig. 1. *Littorina littorea*. Shell height–soft-tissue wet weight relationship of uninfected (○, broken line, n = 304) and trematode-infected (●, continuous line, n = 118) snails

Table 1. *Littorina littorea*. Summary statistics of the ANCOVA, including the status of infection (uninfected or infected by larval trematodes) as the fixed factor and shell height as covariable on the soft-tissue wet weight of the periwinkles *L. littorea* as the dependent variable (ln-transformed data)

Source of variation	df	*F*	p
Status of infection	1	5.21	0.023
Shell height	1	1636.50	<0.001
Status of infection × shell height	1	5.72	0.017
Error	418		

on infected snails, entering the 2 most frequently occurring infections (*Renicola roscovita* and *Himasthla elongata*) as fixed factors, showed no 2-way interaction ($F_{1,111}$ = 0.820, p = 0.367). Moreover, removing the few *Cryptocotyle lingua* and double infections from the group of infected snails in the main ANCOVA did not influence the results qualitatively. This justified that the different types of infection were pooled into 1 group (infected) in the main analysis.

Infection, temperature and consumption

The periwinkles' rate of macroalgal consumption was positively related to the soft-tissue wet weight of the snails, although the residual variation was large (r^2_{418} = 0.065, p < 0.001; Fig. 2). Irrespective of infection status, this relationship was particularly evident for specimens of <1.1 g soft-tissue wet weight (r^2 = 0.05, p < 0.001), but tended to disappear in larger individuals (r^2 = 0.012, p = 0.214; Fig. 2). Together with the fact that the larger periwinkles were also affected the most in terms of overall condition by the infections (Fig. 1), this prompted us to analyse small (<1.1 g soft-tissue wet weight) and large (≥1.1 g soft-tissue wet weight) snails separately. Across temperature treatments, the daily average removal of algal mass was 0.069 ± 0.001 g for small and 0.076 ± 0.001 g for large snails, corresponding to a 9% higher consumption rate in the latter group of periwinkles.

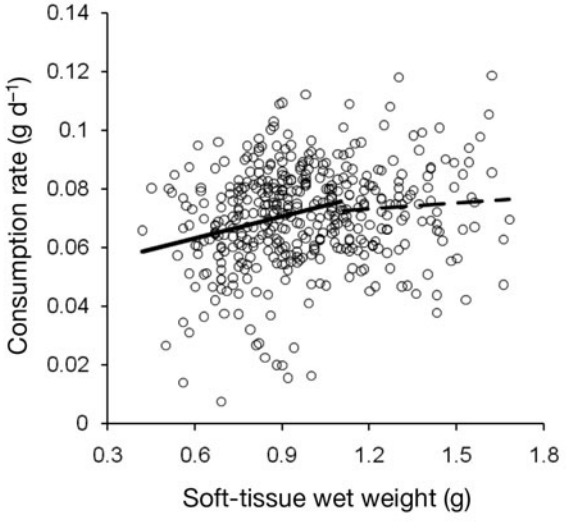

Fig. 2. *Littorina littorea*. Consumption rate (g *Ulva lactuca* [wet weight] removed per day) as a function of the soft-tissue wet weight (g) of uninfected and trematode-infected periwinkles combined (n = 422). Periwinkles <1.1 g soft-tissue wet weight (continuous line, n = 295) and ≥1.1 g soft-tissue wet weight (broken line, n = 127)

Large periwinkles

For the larger snails (≥1.1 g soft-tissue wet weight), a full-factorial ANOVA showed that second- and third-order interactions were non-significant and thus excluded in a subsequent reduced model (Table 2). This analysis showed that status of infection, shell height and sex did not independently affect the consumption rate significantly (although infection status was marginally significant; p = 0.057; Table 2). In contrast, temperature had an overall positive influence on consumption, and a statistically significant interaction could be demonstrated between temperature and infection status (Table 2, Fig. 3). At 17.9°C, uninfected snails grazed 19% more macroalgal biomass per day than infected snails, whereas infected periwinkles had a slightly higher average consumption rate (3.3%) than uninfected at 21.2°C (Fig. 3). The latter was, however, non-significant. Irrespective of infection status, snails grazed more rapidly at the higher temperatures: the daily removal of algal mass was, on average, 0.072 g at 17.9°C and 0.079 g at 21.2°C, corresponding to a 10% increase in consumption.

Full-model ANOVAs carried out on the 2 most frequent types of infections (*Renicola roscovita* and *Himasthla elongata*) separately, generally reached conclusions similar to those above on combined infections. For *R. roscovita*, a 2-way interaction between the status of infection and temperature was clearly evident (ANOVA, $F_{1,115}$ = 4.468, p = 0.037). For *H. elongata*, this interaction was non-significant according to the 5% default level (ANOVA, $F_{1,99}$ = 2.297, p = 0.133). However, Underwood (1981) suggested retaining

Table 2. *Littorina littorea*. Periwinkles of ≥1.1 g soft-tissue wet weight. Summary statistics of the reduced-model ANOVA, including the status of infection (uninfected or infected by larval trematodes), sex and temperature as fixed factors and shell height (apex to aperture) as covariable on the consumption of the green alga *Ulva lactuca* by large periwinkles as the dependent variable. A preceding full model demonstrated a lack of significant 2- and 3-way interactions: status of infection × sex ($F_{1,120}$ = 1.988, p = 0.161), temperature × sex ($F_{1,118}$ = 0.143, p = 0.706), status of infection × temperature × sex ($F_{1,118}$ = 0.574, p = 0.450). Associated sums of squares and degrees of freedom are included in the error variation in the present analysis. Partial η^2 for the reduced model = 0.136

Source of variation	df	*F*	p
Status of infection	1	3.71	0.057
Shell height	1	0.33	0.569
Sex	1	2.43	0.122
Temperature	1	12.52	0.001
Status of infection × temperature	1	6.77	0.010
Error	121		

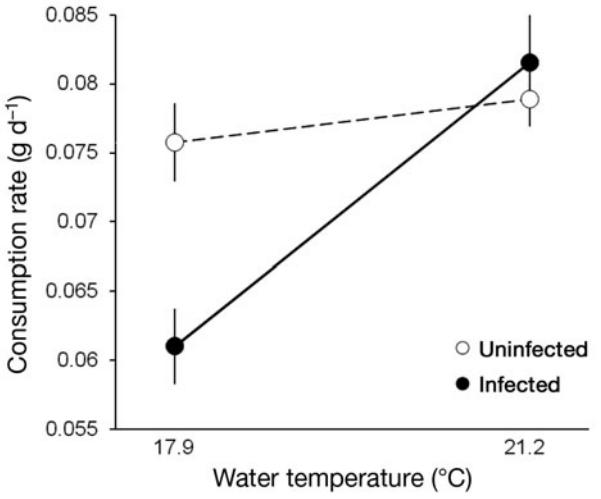

Fig. 3. *Littorina littorea*. Periwinkles of ≥1.1 g soft-tissue wet weight. Consumption rate of the green alga *Ulva lactuca* by large uninfected (○, broken line) and trematode-infected (●, continuous line) snails at water temperatures of 17.9 and 21.2°C. Sample sizes: uninfected (n = 41) and trematode-infected (n = 14) at 17.9°C; uninfected (n = 59) and trematode-infected (n = 13) at 21.2°C. Values are means ± SE

interactions that meet a 15% significance level and, thus, we may consider the interaction significant. Hence, the 2 types of infections tend to affect consumption in a similar manner.

Small periwinkles

As opposed to large snails, a full-factorial ANOVA carried out on smaller snails (<1.1 g soft-tissue wet weight) revealed a significant overall positive relationship between consumption rate and shell height (r^2_{293} = 0.04, p = 0.001). Hence, in order to correct for the effect of size and thereby make the data comparable to those on large snails (Fig. 3), consumption–shell height residuals were used as the unit of analysis. A full-model ANOVA on residual consumption demonstrated a lack of significant 2-way interaction between the status of infection and temperature; this interaction was thus excluded in the reduced model (Table 3). Other 2-way interactions were close to being significant and were therefore kept in the reduced model (sensu Underwood 1981). The reduced model showed non-significant main effects (status of infection, temperature and sex), but significant or close to significant 2- and 3-way interactions between infection status, temperature and sex (Table 3, Fig. 4). Hence, the analysis indicated a rather complicated picture for the smaller snails' consumption in relation to the 3 interacting predictors — status of infection, temperature and sex

Table 3. *Littorina littorea*. Periwinkles of <1.1 g soft-tissue wet weight. Summary statistics of the reduced-model ANOVA, including the status of infection (uninfected or infected by larval trematodes), sex and temperature as fixed factors on the consumption–shell height residuals of the green alga *Ulva lactuca* by small periwinkles as the dependent variable. A preceding full model demonstrated a lack of significant 2-way interaction between status of infection and temperature ($F_{1, 287}$ = 0.153, p = 0.696). Associated sums of squares and degrees of freedom are included in the error variation in the present analysis. Partial η^2 for the reduced model = 0.038

Source of variation	df	*F*	p
Status of infection	1	0.12	0.731
Sex	1	0.35	0.554
Temperature	1	0.16	0.689
Status of infection × sex	1	3.30	0.070
Temperature × sex	1	2.91	0.089
Status of infection × temperature × sex	2	3.14	0.045
Error	287		

(Fig. 4). Whereas small males roughly followed the pattern seen for the larger snails (Fig. 3), small infected females tended to consume less than uninfected ones at the higher temperature. However, the sample sizes were rather low for this 3-way interaction (see legend to Fig. 4), which might have contributed to this somewhat inconsistent pattern. In any case, the amount of variation explained in the reduced-model ANCOVA was quite low (η^2 = 0.038; Table 3), and similar to the isolated effect of shell height (see above).

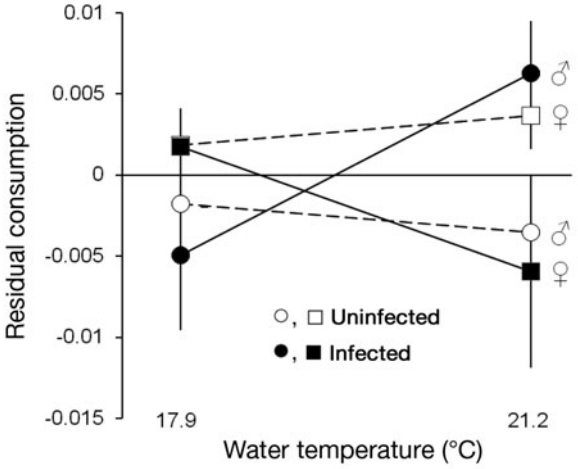

Fig. 4. *Littorina littorea*. Periwinkles of <1.1 g soft-tissue wet weight. Consumption–shell height residuals of the green alga *Ulva lactuca* by small snails at 17.9 and 21.2°C. Sample sizes: uninfected males (○, broken line, n = 73) and females (□, broken line, n = 70) at 17.9°C; trematode-infected males (●, continuous line, n = 14) and females (■, continuous line, n = 40) at 17.9°C; uninfected males (○, broken line, n = 31) and females (□, broken line, n = 30) at 21.2°C; trematode-infected males (●, continuous line, n = 18) and females (■, continuous line, n = 19) at 21.2°C. Values are means ± SE

DISCUSSION

The implications of climate warming — and other phenomena leading to variation in ambient temperature — on the ecologically important parasite–host associations in marine environments have received only limited attention (Marcogliese 2001, Mouritsen & Poulin 2002b, Mouritsen et al. 2005, Khan & Chandra 2006, Poulin & Mouritsen 2006), and, to our knowledge, no experimental study has hitherto considered the synergistic effect of parasitism and temperature on host consumption rates. However, the present results demonstrate that such synergy may significantly alter the consumption rate of common periwinkles *Littorina littorea* in a manner different from the 2 factors (temperature and parasitism) in isolation.

Our results also provide novel evidence that trematode infections compromise the periwinkles' general condition, evident particularly in larger/older individuals (Fig. 1). Because these long-lived littorinoids rarely lose their trematode infection once infected (Rothschild 1942, Robson & Williams 1970, Curtis 2003), this phenomenon may be related to the continued stress experienced by older hosts that have often been infected for a considerable time. Moreover, as opposed to smaller/younger snails, larger individuals showed no positive relationship between consumption rate and size (Fig. 2). Together, this justified a separation between small and large snails in the analyses of factors affecting snail consumption of algae.

The analysis of large snails clearly showed synergism between temperature and infection status, evidenced by the significant interaction between these 2 factors (Fig. 3). In accordance with previous studies (Wood et al. 2007, Clausen et al. 2008), trematode infections depressed periwinkle consumption at about 18°C, which presently is a common coastal seawater temperature in many temperate regions during summer, including Denmark. However, whereas increasing temperature generally increased consumption, this effect was particularly strong in infected snails, and at 21°C the consumption by infected and uninfected periwinkles could no longer be distinguished statistically.

For the group of smaller periwinkles, the pattern was more complex. Whereas males tended to follow the same pattern as larger snails (strong increase in consumption with temperature among infected individuals), small infected females consumed the least at the higher temperature (Fig. 4). The reason for this inconsistency among sexes in smaller infected periwinkles remains unknown. Nevertheless, considering that (1) small infected females constitute only 19% of the present haphazardly sampled experimental population of adult periwinkles, (2) the average consumption rate of larger snails is significantly greater than that of smaller snails, and (3) large snails constitute 30% of the sampled population, a temperature increase from 18 to 21°C will generally tend to eliminate the otherwise negative influence of trematode infections on the snail population's consumption of ephemeral algae. Moreover, the fact that several species of trematodes tend to produce similar effects on snail consumption (Wood et al. 2007, Clausen et al. 2008, present study) also suggests that the phenomenon is not parasite specific, but probably general to cercaria-shedding trematode infections.

As discussed by Wood et al. (2007) and Clausen et al. (2008), the reduced consumption rate of infected snails at current temperate summer temperatures (~18°C) may be the result of reduced energy demands due to parasitic castration and/or compromised digestive capacity stemming from a damaged digestive gland. However, the latter is not supported by the present results, because infected snails were able to launch a disproportionately large increase in consumption at a higher temperature. Nevertheless, this disproportionate temperature-dependent increase in consumption among larger/older infected snails is likely governed by elevated cercarial production and release. Increasing environmental temperatures generally accelerate the production of cercariae within the snail host gonad-digestive gland complex, as well as triggering their release (Kuntz 1947, Rojo-Vázquez & Simón-Martín 1985, Shostak & Esch 1990, Lo & Lee 1996, Umadevi & Madhavi 1997, Mouritsen 2002, Poulin 2006). This positive relationship is also evident for the most frequently occurring species in the present experiment (*Renicola roscovita* and *Himasthla elongata*) (Fingerut et al. 2003, Thieltges & Rick 2006). In addition, Galaktionov et al. (2006) have demonstrated that this temperature effect is not a momentary phenomenon, in that the temperature-elevated asexual production and release of cercariae can be maintained over time. Hence, the processes may thus neutralize the negative influence trematode infections otherwise have on periwinkle consumption by exerting an additional energy drain on the snail host, in turn, increasing the amount of edible macroalgal food consumed to meet this demand.

As opposed to large snails, the analysis carried out on smaller periwinkles demonstrated a lack of 2-way interaction between temperature and infection status on the consumption of *Ulva lactuca*. Reasons for this inconsistency between the 2 size-specific groups of snails remain unknown. It is likely, however, that the group of smaller/younger infected snails, on average (as compared to larger/older infected specimens), harboured younger — not yet fully developed — infections, ultimately lowering the energetic drain on the snail host through constrained cercarial output.

Periwinkles are indeed significant regulators of near-coastal algal communities (Lubchenco 1978, Lein 1980, Bertness 1984, 1999), and trematodes evidently have the potential to mitigate this structuring role (Wood et al. 2007, Clausen et al. 2008, present study). Wood et al. (2007) also managed to confirm this *in situ*, by demonstrating a relatively greater abundance of ephemeral macroalgae among populations of periwinkles with a high trematode prevalence relative to populations with a high proportion of uninfected snails. The present results suggest that ongoing global warming will tend to counteract this indirect positive effect trematodes are currently having on ephemeral algae, everything else being equal. However, the processes governing macroalgal abundance and diversity in the coastal zone are complex, and a multitude of quantitatively more important factors than snail parasitism may ultimately determine the balance between ephemeral and more grazer resistant algae under the future climate scenario. For instance, present results also suggest that increasing temperature directly favours ephemeral macroalgae (the growth rate of *Ulva lactuca* was greater at the higher temperature), aside from decreasing snail abundance and thereby overall grazing pressure (if the higher snail mortality in the higher temperature treatment is taken as indicative). It is, however, questionable whether the last process will be operational *in situ*. *Littorina littorea* has a pelagic larval stage, and individuals lost from the local population may be replaced by immigration of recruits.

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