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INTERSPECIFIC AND INTRASPECIFIC VARIATION IN CERCARIAE RELEASE

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ABSTRACT: Given the importance of temperature for the shedding of trematode infective stages (cercariae) from gastropod first intermediate hosts, we investigated the response to temperature increases of trematodes of the intertidal snail *Zeacumantus subcarinatus* collected from different latitudes (differing in mean annual summer temperature) on the South Island of New Zealand. We investigated whether shedding of cercariae at elevated temperatures differed both between species (interspecific variation) and among populations of each trematode species (intraspecific variation). The shedding of one trematode species, *Maritrema novaezealandensis* (Microphallidae), appears to decrease with increased temperature and differed among locations. In contrast, the shedding of a second species, *Acanthoparyphium* sp. (Echinostomatidae), increased at warmer temperatures. In particular, *Acanthoparyphium* sp.–infected snails from 1 location showed the greatest increase in the shedding of cercariae in response to elevated temperature. Our results demonstrate that different trematode species and populations may be dissimilarly impacted by temperature changes resulting from global warming. In addition, both interspecific and intraspecific variation may result in different impacts of trematodes on ecosystems at different locales.

The shedding of infective trematode larvae (cercariae) from their first intermediate hosts is often initiated in response to environmental cues. For example, both increased light and salinity can induce shedding of marine cercariae from an intertidal snail host (Mouritsen, 2002). Water level can also have an impact on cercariae shedding in intertidal systems (Fingerut et al., 2003). With the most favorable conditions, response to external cues may act to synchronize parasite shedding (Fingerut et al., 2003). This may be particularly advantageous if shedding corresponds with host availability (Combes et al., 1994; Pechenik and Fried, 1995), as cercariae generally have life spans of 24 h or less (McCarthy, 1999; Toledo et al., 1999). Trematodes play major roles in the structuring of animal communities, especially in intertidal ecosystems (Sousa, 1991; Mouritsen and Poulin, 2002), so it is important to identify external factors controlling cercariae shedding in order to understand trematode transmission and the maintenance of complex trematode life cycles.

Temperature is often the most important factor governing cercariae shedding. Many trematodes show a marked increase in cercariae shedding with increased temperature (e.g., Fried et al., 2002; Fredensborg et al., 2005); however, there is considerable variation among species. For example, more cercariae of the marine trematode *Maritrema subdolum* are shed at 25 C than at 20 C or 15 C (Mouritsen, 2002). This increase at 25 C was considerably beyond a generalized Q10-effect of temperature on enzyme-based metabolism, i.e., an expected 2- to 3-fold increase with a temperature increase of 10 C (Schmidt-Nielsen, 1997; Willmer et al., 2005). This suggests, in accordance with Ginetsinskaya (1988), that temperature directly or indirectly triggers the shedding of cercariae rather than just accelerating the cercaria maturation process (Mouritsen, 2002). In contrast, cercariae of another marine trematode, *Renicola roscovita*, have peak shedding at 20 C, with fewer shed from the gastropod host at both 10 C and 25 C (Thieltges and Rick, 2006). This suggests the existence of an upper temperature limit for cercarial shedding in *R. roscovita* (Thieltges and Rick, 2006) that may be associated with the upper temperature tolerance of its intermediate hosts, as in other trematode species (Erasmus, 1972; Lo and Lee, 1996).

While it is clear that there is variation among trematode species (interspecific variation) with respect to cercaria shedding in response to temperature, it is not as apparent whether variation among populations of a trematode species (intraspecific variation) is also common. Such variation has been reported for other aspects of cercaria shedding. For example, the cercariae of different schistosome species exhibit distinct circadian shedding patterns (Theron, 1989); however, intraspecific variation of cercariae shedding also occurs for *Schistosoma mansoni*, with distinct chronobiological variants documented (Theron et al., 1997).

The influence of temperature on cercariae shedding could show both interspecific and intraspecific variation for various reasons. It may be difficult to increase cercariae shedding in response to increased temperature if shedding is already high, given the constraints on maximal cercariae output that vary among trematode species and families (Galaktionov and Dobrovolskij, 2003). This would greatly influence how cercariae shedding responds to temperature (Poulin, 2006). For example, all else being equal, a trematode producing 100 cercariae per day at a given temperature would presumably have more host resources available to expand its production than would one already producing 5,000 cercariae of similar size daily at the same temperature (Poulin, 2006).

Although temperature-mediated changes in cercariae shedding vary widely among trematode species, the geometric mean derived from a meta-analysis suggests an almost 8-fold increase in response to a 10-C rise in temperature (Poulin, 2006). However, the effect of increased temperature would appear to be affected by geography, as the latitude of origin of the snail-trematode association is correlated negatively with temperature-mediated increases in cercariae shedding. Within the 20–55° latitude range, trematodes from lower/lesser latitudes, i.e., closer to the equator, show more pronounced temperature-driven increases in cercariae shedding compared with trematodes at higher/greater latitudes, i.e., further from the equator (Poulin, 2006).

Here, we examine whether cercariae shedding by 2 different trematode species, using the intertidal mudsnail *Zeacumantus subcarinatus* collected from different latitudes on the South Island of New Zealand, shows interspecific and/or intraspecific

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variation in response to increased temperature. In a previous study, a lack of migration among bays within the Otago Harbor of the South Island (scale 5–15 km) was inferred from ecological data on these snails, with populations highly reliant on local reproduction (Fredensborg et al., 2005). Genetic isolation of both host and parasite should be even greater at a larger geographic scale, thus providing opportunity for intraspecific variation with respect to cercarial shedding. It was also found that cercariae of *M. novaezealandensis*, which use *Z. subcarinatus* as intermediate host, exhibited a positive temperature-dependent shedding pattern (Fredensborg et al., 2005). However, this applies to snails collected from locations within the Otago Harbor, which may not provide a large enough scale to observe intraspecific variation in response to increased temperature.

Given the temperature differences among our sampling sites at different latitudes and the correlation between latitude and the extent of temperature-dependent increases in cercarial shedding (Poulin, 2006), we hypothesized that there might be intraspecific variation with respect to temperature response. We also expected that both trematode species were likely to increase the number of cercariae shed when exposed to warmer temperatures, not exhibiting interspecific variation in this respect.

MATERIALS AND METHODS

Trematode species used

We chose to examine the 2 trematode species found to be most common while screening for infected snails (see below). The first, *M. novaezealandensis* (Microphallidae), uses the intertidal mudsnail *Z. subcarinatus* as the first intermediate host, various crabs and amphipods as second intermediate hosts, and red-billed gulls as a definitive host (Martorelli et al., 2004). The second, *Acanthoparyphium* sp. (Echinostomatidae), uses *Z. subcarinatus* or *Z. lutulentus* as its first intermediate host, a species of cockle as a second intermediate host, and likely uses oystercatchers as final hosts (Martorelli et al., 2006).

Sampling and screening

Approximately 500–800 *Z. subcarinatus* individuals were collected from tidal mudflats from 3 locations on the South Island of New Zealand (Fig. 1): McCormacks Bay (43°33′S, 172°44′E), Lower Portobello Bay (45°47′S, 170°42′E), and Greenpoint Domain Reserve (46°36′S, 168°21′E) from December 2006 to February 2007. Mean annual temperatures for these locations, using data available from the National Institute of Water and Atmospheric Research of New Zealand for 1971–2000, are as follows: McCormacks Bay, 12.2 C ± 3.9 SD; Lower Portobello Bay, 11.1 C ± 3.1 SD; and Greenpoint Domain Reserve, 9.9 C ± 3.2 SD (www.niwascience.co.nz/edu/resources/climate). For the summer months (December–March), during which shedding of cercariae should be concentrated, mean temperatures for 1971–2000 are as follows: McCormacks Bay, 16.5 C ± 0.9 SD; Lower Portobello Bay, 14.1 C ± 0.8 SD; and Greenpoint Domain Reserve, 13.4 C ± 0.7 SD (www.niwascience.co.nz/edu/resources/climate).

Snails were randomly collected by hand at low tide from the low tide water line to approximately 3/4 of the way toward the high tide margin. After transportation to the University of Otago (Dunedin), snails were kept in the laboratory in 2-L plastic containers filled with artificial seawater at 35 practical salinity units (PSU), with each containing 200–300 individuals. Snails were kept at ambient temperature (15–23 C) with a natural photoperiod and were supplied sea lettuce (*Ulva reticulata*) collected from Otago Harbor.

To screen for infected individuals, groups of 5 snails were placed in individual wells of cell-well plates containing 3 ml of artificial seawater (35 PSU) each and kept in an incubator overnight at 28 C before being examined the next morning for the emergence of cercariae. Individuals found to be infected were then kept in separate containers in the same conditions as described above.

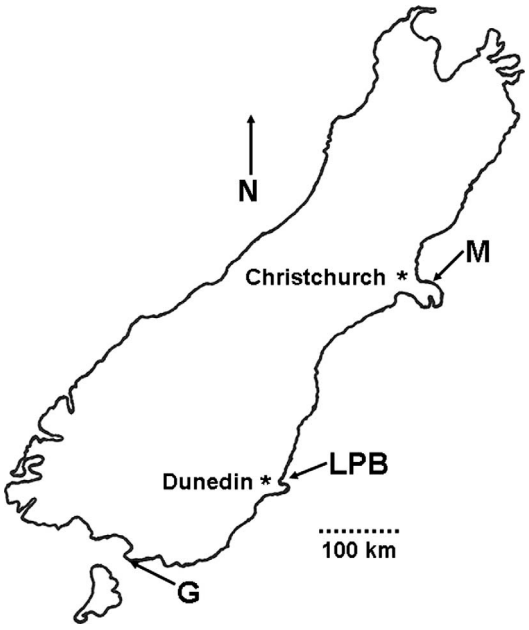

FIGURE 1. Snail collection locations on the South Island of New Zealand. M, McCormacks Bay; LPB, Lower Portobello Bay; G, Greenpoint Domain.

Experimental procedure

The experiment was conducted in an environmental chamber set at 15 C with a 14:10-hr light:dark cycle. In addition, 2 incubators were used within the chamber. Both had glass doors to allow exposure to the light conditions. One was set at 20 C, and the other was set at 25 C. Given the relatively low prevalence of infection of both trematode species from certain sites, 12 *M. novaezealandensis*–infected individuals from each of the 3 sites were used for the first trial with this species, while 13 *Acanthoparyphium* sp.–infected individuals from McCormacks Bay and Lower Portobello Bay, respectively, were used for the first trial with this species. *Acanthoparyphium* sp.–infected individuals from Greenpoint Domain Reserve were not found until additional screening in March; thus, the first 2 trials for this species were conducted with individuals from only 2 sites.

Cell-well plates consisting of 12 wells (6 ml each) were used. Each well was filled with 3 ml of artificial seawater (35 PSU). Experiments were run separately for the 2 trematode species. For each species, snails from different sites were randomly assigned to wells, resulting in 3–4 full plates. The experiment using *M. novaezealandensis* began at the end of January 2007, with the plates kept at 15 C for 24 hr. After this time period, snails were individually transferred into new cell-well plates in which the water was pre-warmed to 20 C. Cercariae left in the wells of the initial plates were then counted, using a dissection microscope. Given the small size of *M. novaezealandensis* and the large numbers of cercariae typically shed by this species, 1-ml aliquots were used as subsamples after agitation of the wells. After 24 hr at 20 C, snails were transferred to new plates containing water pre-warmed to 25 C, with the same counting procedure. The snails were actually moved into new plates containing freshwater prewarmed/cooled to the appropriate temperature. At that time, snails were measured using callipers and returned to their original containers.

The same procedure was used for *Acanthoparyphium* sp.–infected snails at the end of February, with 1 exception. As these cercariae are larger, with typically fewer shed per day, no subsampling was required. The experiment was repeated for both trematode species at the end of March, using the same individuals. However, dead snails were substituted with individuals later found to be shedding cercariae after a second round of screening. Six *M. novaezealandensis*–infected snails were substituted (1 from Greenpoint Domain, 3 from Lower Portobello Bay, 2 from McCormacks Bay), as well as 6 *Acanthoparyphium* sp.–infected snails (1 from Lower Portobello Bay, 2 from McCormacks Bay). As

more snails were found to be shedding cercariae after additional screening, we were also able to add 1 snail from each location for each of the 2 species, for a total of 13 *M. novaezealandensis* and 14 *Acanthoparyphium* sp. for the second experimental trial. A third trial for *Acanthoparyphium* sp. only was conducted in April, using 13 individuals from each of the 3 sampling sites. The same *Acanthoparyphium* sp.–infected snails used in the second trial from McCormacks Bay and Lower Portobello Bay were used in this third trial as well.

Statistical analyses

The following procedure was performed separately for the 2 trematode species, as well as for each experimental trial. Snails that shed cercariae during screening but not during the experiment were excluded from the analysis. A linear regression, with snail size as the independent variable and number of cercariae shed as the dependent variable, was performed for each of the 3 temperatures used. A 1-way analysis of variance (ANOVA) or *t*-test was used to determine whether snails differed in size among/between sites, with *t*-tests used when only 2 sites were being compared. Based on the results obtained (see below), we did not correct the numbers of cercariae shed to account for snail size, although this potentially can have an effect on the number of cercariae shed (Poulin, 2006). A value of 1 was added to the number of cercariae shed by each snail at each temperature to allow a ln-transformation of the data in order to meet the assumption of normality. These data were then entered into a general linear model analysis, using a repeated-measures ANOVA. Site latitude was used as the between-subjects factor to determine whether cercariae shedding differed between/among sites, while temperature was used as the within-subjects factor to determine whether temperature had an influence on the number of cercariae shed by each snail.

A 1-way ANOVA was used to determine whether sites differed in their mean annual temperature, as well as in their mean summer temperature. All analyses were performed using SPSS 15.0.

RESULTS

Snail size

The size of *M. novaezealandensis*–infected snails used in the first trial was not related to the number of cercariae shed at 15 C ($R^2 = 0.024$, $F_{1,33} = 0.814$, $P = 0.373$), 20 C ($R^2 = 0.014$, $F_{1,33} = 0.454$, $P = 0.505$), or 25 C ($R^2 = 0.012$, $F_{1,33} = 0.393$, $P = 0.535$). The same result was seen for *M. novaezealandensis*–infected snails used in the second trial for the number of cercariae shed at 15 C ($R^2 = 0.058$, $F_{1,33} = 2.037$, $P = 0.163$), 20 C ($R^2 = 0.078$, $F_{1,33} = 2.784$, $P = 0.105$), and 25 C ($R^2 = 0.090$, $F_{1,33} = 3.283$, $P = 0.079$). Snails from the 3 sites did not differ significantly in size for both the first trial ($F_{2,32} = 1.04$, $P = 0.365$) and the second trial ($F_{2,32} = 2.397$, $P = 0.107$).

The size of *Acanthoparyphium* sp.–infected snails used in the first trial was related to the number of cercariae shed at 15 C ($R^2 = 0.289$, $F_{1,21} = 8.532$, $P = 0.008$), but not at 20 C ($R^2 = 0.162$, $F_{1,21} = 4.247$, $P = 0.051$) or 25 C ($R^2 < 0.0001$, $F_{1,21} = 0.002$, $P = 0.968$). The same result was seen for *Acanthoparyphium* sp.–infected snails used in the second trial for the number of cercariae shed at 15 C ($R^2 = 0.272$, $F_{1,22} = 8.240$, $P = 0.009$), 20 C ($R^2 = 0.141$, $F_{1,22} = 3.617$, $P = 0.070$), and 25 C ($R^2 = 0.103$, $F_{1,22} = 2.521$, $P = 0.127$), as well as the third trial for the number of cercariae shed at 15 C ($R^2 = 0.171$, $F_{1,30} = 6.207$, $P = 0.018$), 20 C ($R^2 = 0.062$, $F_{1,30} = 1.971$, $P = 0.171$), and 25 C ($R^2 < 0.0001$, $F_{1,30} = 0.011$, $P = 0.917$). The significant relationship at 15 C is likely the result of very few snails shedding this trematode species at this low temperature, and this was not considered to be indicative of the general relationship between cercariae output and snail size; thus, no size correction was used for numbers of cercariae shed. Snails from the 2 sites used did not significantly differ in size for the first trial ($t_{21} = -1.595$, $P = 0.126$) or second trial ($t_{22} = -1.746$, $P = 0.095$), nor did they differ significantly for the third trial in which 3 sites were used ($F_{2,29} = 1.964$, $P = 0.158$).

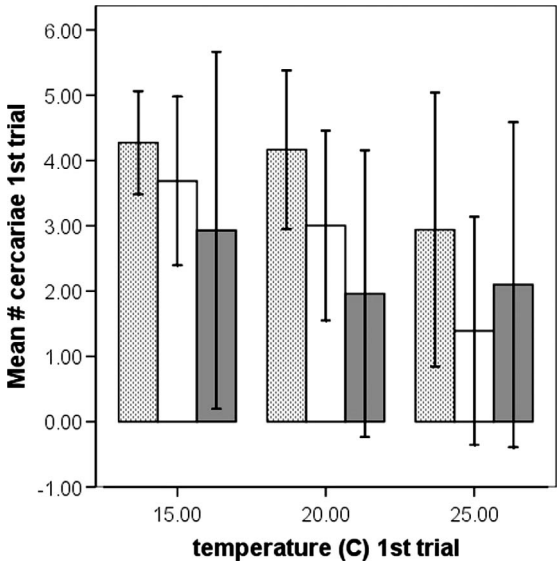

FIGURE 2. Mean cercariae output of *M. novazealandensis* in response to temperature increases for the first trial. Greenpoint Domain, stippled bars; Lower Portobello Bay, white bars; McCormacks Bay, grey bars. Means of ln-transformed number of cercariae shed are given ± SD.

Site temperature

The mean annual temperature (1971–2000) did not differ significantly among the 3 sampling sites ($F_{2,33} = 1.317$, $P = 0.282$); however, the mean summer temperature (December–March, 1971–2000) did show a significant difference among sites ($F_{2,9} = 15.714$, $P = 0.001$), with Tukey Honestly Significant Difference (HSD) post-hoc tests indicating a significant difference between Greenpoint Domain and McCormacks Bay ($P = 0.001$), as well as between Lower Portobello Bay and McCormacks Bay ($P = 0.015$), with mean summer temperature being highest at McCormacks Bay.

Maritrema novaezealandensis

Multivariate tests indicated a significant effect of temperature on cercariae output for the first trial (Wilks' $\lambda = 0.731$, $F_{2,31} = 5.693$, $P = 0.008$), but not for the second trial (Wilks' $\lambda = 0.856$, $F_{2,31} = 2.602$, $P = 0.09$), as the number of cercariae shed decreased with increasing temperature in the first trial (Figs. 2, 3). Multivariate tests also showed no significant interaction of temperature and latitude for either the first trial (Wilks' $\lambda = 0.85$, $F_{4,62} = 1.311$, $P = 0.276$) or the second trial (Wilks' $\lambda = 0.794$, $F_{4,62} = 1.894$, $P = 0.123$).

Tests of within-subjects effects indicated a significant effect of temperature for the first trial ($F_{1.638,54.409} = 8.373$, $P = 0.001$), but no significant interaction of temperature and latitude ($F_{3.276,52.409} = 1.333$, $P = 0.273$). The Greenhouse-Geisser correction was used for the first trial as the assumption of sphericity was violated, i.e., that all variances of the differences were equal in the populations sampled. Tests of within-subjects ef-

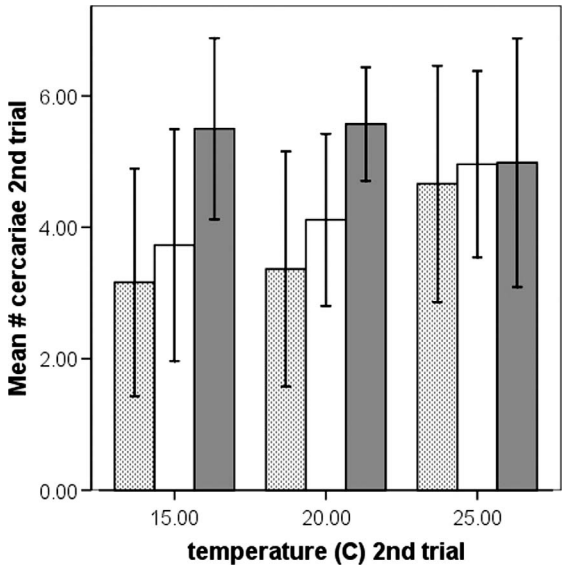

FIGURE 3. Mean cercariae output of *M. novazealandensis* in response to temperature increases for the second trial. Greenpoint Domain, stippled bars; Lower Portobello Bay, white bars; McCormacks Bay, grey bars. Means of ln-transformed number of cercariae shed are given ± SD.

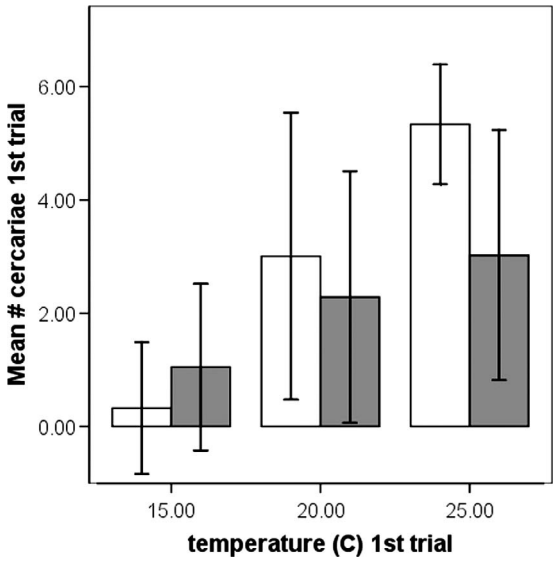

FIGURE 4. Mean cercariae output of *Acanthoparyphium* sp. in response to temperature increases for the first trial. Lower Portobello Bay, white bars; McCormacks Bay, grey bars. Means of ln-transformed number of cercariae shed are given ± SD.

fects for the second trial indicated no significant effect of temperature ($F_{2,64}$ = 2.804, P = 0.068), as well as no significant interaction of temperature and latitude ($F_{4,64}$ = 2.391, P = 0.06).

Tests of between-subjects effects indicated a significant effect of latitude on cercariae output for both the first trial ($F_{2,32}$ = 3.384, P = 0.046) and second trial ($F_{2,32}$ = 6.158, P = 0.005). However, the trend for the first trial indicated that the greatest number of cercariae were shed by snails from Greenpoint Domain, followed by Lower Portobello Bay, and then McCormacks Bay, whereas the trend for the second trial was the exact opposite.

Acanthoparyphium sp.

Multivariate tests indicated a significant effect of temperature for the first trial (Wilks' λ = 0.327, $F_{2,20}$ = 20.617, $P < 0.0001$), second trial (Wilks' λ = 0.123, $F_{2,21}$ = 74.918, $P < 0.0001$), and third trial (Wilks' λ = 0.346, $F_{2,28}$ = 26.443, $P < 0.0001$), as a greater number of cercariae were shed with increased temperature (Figs. 4–6). There was also a significant interaction of temperature and latitude for both the first trial (Wilks' λ = 0.721, $F_{2,20}$ = 3.866, P = 0.038) and third trial (Wilks' λ = 0.693, $F_{4,56}$ = 2.817, P = 0.034), but not for the second trial (Wilks' λ = 0.777, $F_{2,21}$ = 3.005, P = 0.071).

Tests of within-subjects effects indicate a significant effect of temperature for the first trial ($F_{2,42}$ = 21.069, $P < 0.0001$), second trial ($F_{2,44}$ = 54.827, $P < 0.0001$), and third trial ($F_{2,58}$ = 28.894, $P < 0.0001$). There was also a significant interaction of temperature and latitude for both the first trial ($F_{2,42}$ = 3.973, P = 0.026) and third trial ($F_{4,58}$ = 2.97, P = 0.027), but not for the second trial ($F_{2,44}$ = 2.205, P = 0.122). Cercariae shedding increased with greater temperature for all 3 locations; however, cercariae shedding by snails from Lower Portobello Bay showed the greatest increase at the warmest temperature used in the first and third trials. Although the interaction was not significant for the second trial, a similar trend of proportionately greater increase in shedding by snails from Lower Portobello Bay at 25 C was observed.

Tests of between-subjects effects indicated no significant effect of latitude on cercariae shedding for trial 1 ($F_{1,21}$ = 2.757, P = 0.112) and trial 2 ($F_{1,22}$ = 0.039, P = 0.846). However, there was a significant effect of latitude in the third trial ($F_{1,22}$ = 6.721, P = 0.004). Tukey HSD post hoc tests indicated that this was driven by a significant difference in the number of cercariae shed between snails from Greenpoint Domain and

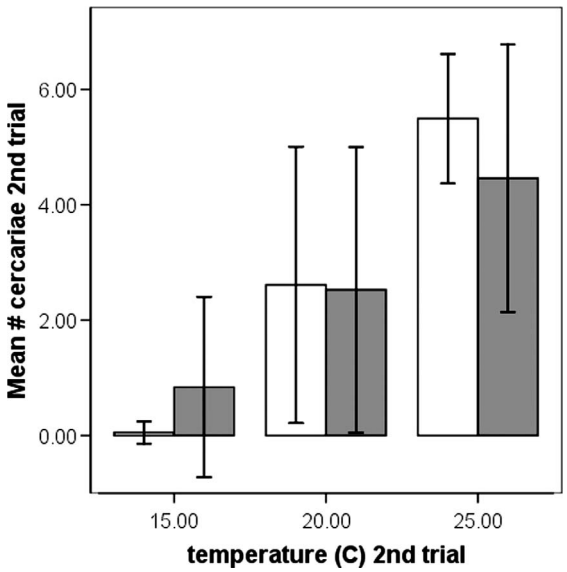

FIGURE 5. Mean cercariae output of *Acanthoparyphium* sp. in response to temperature increases for the second trial. Lower Portobello Bay, white bars; McCormacks Bay, grey bars. Means of ln-transformed number of cercariae shed are given ± SD.

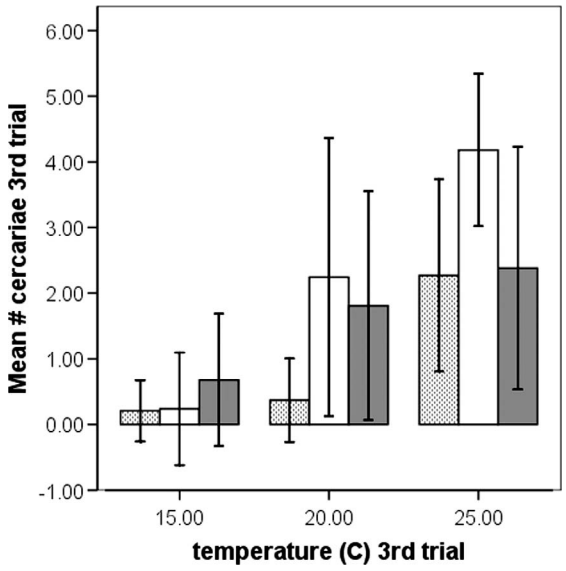

FIGURE 6. Mean cercariae output of *Acanthoparyphium* sp. in response to temperature increases for the third trial. Greenpoint Domain, stippled bars; Lower Portobello Bay, white bars; McCormacks Bay, grey bars. Means of ln-transformed number of cercariae shed are given ± SD.

those from Lower Portobello Bay ($P = 0.003$); the general trend for all 3 trials was such that the greatest number of cercariae was shed by snails from Lower Portobello Bay, followed by McCormacks Bay, and then Greenpoint Domain.

DISCUSSION

As expected, greater numbers of *Acanthoparyphium* sp. cercariae were shed in response to increased temperature, as has been found in the majority of studies examining temperature-mediated cercariae shedding. However, *M. novaezealandensis* did not appear to respond to temperature increases in this manner. Rather, a significant pattern of decreased cercariae shedding with increased temperature was observed for snails in the first trial, whereas there was no significant effect of temperature in the second trial. This is in contrast to a previous study that showed a significant increase in cercariae shedding for this species collected from Lower Portobello Bay at 25 C (Fredensborg et al., 2005). For this species, the large variation in the number of parasites shed across temperatures is likely to preclude any generalizations regarding the general response to increased temperature. Nonetheless, it would appear as though interspecific variation in the response of trematodes to increased temperatures does occur, given the consistently highly significant effect on *Acanthoparyphium* sp.

While we did not find a significant interaction of latitude and temperature for *M. novaezealandensis*, there appears to be intraspecific variation in the response to elevated temperature, as there was a significant effect of the latitude from which snails were collected. Once again, the large variation in the number of parasites shed across temperatures is likely to preclude any generalizations, as the general response to increased temperature in *M. novaezealandensis*–infected snails from the 3 sampling locations was not consistent between the 2 trials. Snails from the lowest latitude in 1 trial shed the most cercariae, whereas snails from the highest latitude in the other trial shed the most cercariae. The large variation among snails within sites and relatively small sample sizes used may limit the statistical power to elucidate among site differences.

Intraspecific variation was also seen among *Acanthoparyphium* sp.–infected individuals from different sites, but this was due to an interactive effect with increased temperature. The greatest increase in cercariae shedding was observed for individuals from Lower Portobello Bay at 25 C, in both the first and third trials. This interaction was not significant for the second trial; however, a similar trend is evident. Thus, while there is not an exact correlation between temperature-mediated cercariae shedding and latitude, there is significant variation among populations of snails infected with either *Acanthoparyphium* sp. or *M. novaezealandensis*. Such intraspecific variation may simply be the result of genetic drift occurring in isolated populations, or it could be due to parasite or snail adaptation to local climatic conditions. If the variation is the result of the latter factor, this is unlikely to be the result of temperature differences only, as the number of cercariae shed in response to elevated temperature did not appear to follow a strict latitudinal gradient for either of the species used in this study.

It has been suggested that humans might be unknowingly selecting for rapid changes in pathogen biology through habitat fragmentation, climate shifts, and environmental pollution (Altizer et al., 2003). With respect to the current study, trematode populations with a more advantageous response to elevated temperatures may be selected for, with the possible consequent spread of those genotypes to other geographic locations. As such, there may be microevolutionary processes that will allow for certain local parasite populations to flourish under global warming.

It is then difficult to generalize about the potential effects of elevated temperatures on cercariae shedding and subsequent parasite transmission, given that populations in different locales will likely show different responses. These responses may also be dependent on the intermediate host species used. It is also important that, based on our present findings, different trematode species are likely to be impacted differently. For example, while the Lower Portobello Bay population of *Acanthoparyphium* sp. may have increased production and transmission at 25 C compared to the other 2 populations studied, it would appear that none of the *M. novaezealandensis* populations in this study disproportionately increased cercariae shedding at elevated temperatures compared to the others, and in fact showed decreased shedding at times.

Parasites have been shown to be ubiquitous components of intertidal communities, able to regulate host population density, influence the diversity of the benthic community, and affect the structure of intertidal food webs (Poulin and Mouritsen, 2006). As such, climate-mediated changes in local parasite transmission and abundance will have significant implications for intertidal ecosystems (Poulin and Mouritsen, 2006), with possible collapses of certain host populations (Mouritsen et al., 2005). Given our finding of population variation in the short-term response of trematodes to elevated temperature, it is likely that the intertidal communities at different locations of the South Island of New Zealand will not be impacted in the same manner.

Of course, parasite-mediated biological effects due to climate

change are not predictable solely in terms of temperature response (Marcogliese, 2001). It is essential to also explore how aquatic parasites may be affected by such factors as water levels, acidification, oceanic currents, and stratification, as well as many others (Marcogliese, 2001). As there is likely to be variation both among and within parasite species in response to such factors, further investigations of the interspecific and intraspecific variation among parasites are needed.

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