

Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Rencolidae)

David W. Thieltges*, Jennifer Rick

Alfred Wegener Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List, Germany

ABSTRACT: Marine bivalves harbour a diversity of trematode parasites affecting population and community dynamics of their hosts. Although ecologically and economically important, factors influencing transmission between first (snail) and second (bivalve) intermediate hosts have rarely been studied in marine systems. In laboratory experiments, the effect of temperature (10, 15, 20, 25°C) was investigated on (1) emergence from snails, (2) survival outside hosts and (3) infectivity in second intermediate hosts of cercariae of the trematode *Renicola roscovita* (Digenea: Rencolidae), a major parasite in North Sea bivalves. Emergence of cercariae peaked at 20°C (2609 ± 478 cercariae snail⁻¹ 120 h⁻¹) and was considerably lower at 10°C (80 ± 79), 15°C (747 ± 384) and 25°C (1141 ± 334). Survival time decreased with increasing temperature, resulting in 50% mortality of the cercariae after 32.8 ± 0.6 h (10°C), 26.8 ± 0.8 h (15°C), 20.2 ± 0.5 h (20°C) and 16.6 ± 0.3 h (25°C). Infectivity of *R. roscovita* cercariae in cockles *Cerastoderma edule* increased with increasing temperature and was highest at 25°C (42.6 ± 3.9%). However, mesocosm experiments with infected snails and cockle hosts in small aquaria, integrating cercarial emergence, survival and infectivity, showed highest infection of cockles at 20°C (415 ± 115 metacercariae host⁻¹), indicating 20°C to be the optimum temperature for transmission of this species. A field experiment showed metacercariae of *R. roscovita* to appear in *C. edule* with rising water temperature in April; highest infection rates were in August, when the water temperature reached 20°C. Since another trematode species (*Himasthla elongata*; Digenea: Echinostomatidae) occurring at the experimental site showed a similar temporal pattern, trematode transmission to second intermediate bivalve hosts may peak during especially warm (≥20°C) summers in the variable climate regime of the North Sea.

KEY WORDS: Trematoda · Transmission · Cercariae · Temperature · *Renicola roscovita* · *Himasthla elongata* · *Cerastoderma edule*

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INTRODUCTION

Marine molluscs are infected by a diverse assemblage of parasites with digenean trematodes being the dominant metazoan group (Lauckner 1980, 1983, Sindermann 1990). The adult stages develop in birds or fish, and larval stages utilise mostly snails as first, and bivalves, crustaceans or fish as second intermediate hosts. Marine trematodes exert various effects on their hosts and hence constitute an important population and community structuring factor in intertidal ecosystems (Lauckner 1984, Sousa 1991, Mouritsen & Poulin 2002a, 2005).

Although ecologically important, knowledge on transmission of trematode infective stages between first and second intermediate hosts in marine systems is limited. In freshwater systems, temperature is a major factor influencing emergence, survival and infectivity of the cercarial transmission stages of trematodes (e.g. Evans 1985, Shostack & Esch 1990, Pechenik & Fried 1995, Lo & Lee 1996, McCarthy 1999) and the few studies from marine systems indicate a similar trend. In *Maritrema subdolum*, which infects crustaceans as second intermediate host, temperature affected cercarial emergence and survival (Mouritsen 2002). In *Cryptocotyle lingua*, which infects fish as

*Email: dthieltges@awi-bremerhaven.de

second intermediate host, temperature influenced survival of cercariae (Möller 1978). However, the effect of temperature on infectivity has not been studied in marine cercariae. No information exists on the transmission ecology of marine trematodes utilising bivalves as second intermediate hosts.

One of the dominating trematode species in bivalves on tidal flats in the North Sea is *Renicola roscovita* (Digenea: Rencolidae) (Werding 1969, Lauckner 1983, Buck et al. 2005, Thieltges et al. 2006). It uses the gastropod *Littorina littorea* as first intermediate host and a variety of bivalves as second intermediate host with cockles *Cerastoderma edule* and blue mussels *Mytilus edulis* being dominant. Definitive hosts are gulls *Larus* spp. and common eiders *Somateria mollissima*. Metacercarial infections by *R. roscovita* can reduce growth in *M. edulis* (Thieltges 2006), a bivalve species with high ecological and economic value.

This study was designed to investigate the influence of water temperature on (1) emergence from the first intermediate host, (2) survival between first and second intermediate hosts and (3) infectivity of cercariae of *Renicola roscovita* to the second intermediate host. This was done by laboratory experiments under 4 different temperature regimes (10, 15, 20, 25°C) using *Littorina littorea* as first and cockles *Cerastoderma edule* as second intermediate hosts. In addition, a field experiment was designed to detect seasonal patterns of infection.

MATERIALS AND METHODS

Parasite and host material. To obtain periwinkles *Littorina littorea* infected with *Renicola roscovita*, snails were randomly collected from the upper intertidal zone near the Wadden Sea Station Sylt, in the List tidal basin, in the northern Wadden Sea in April 2004. In the laboratory, collected periwinkles were screened for *R. roscovita* infections by exposing them in bowls filled with aerated seawater (approx. 20°C) to intense light for several hours, and subsequently analysing the seawater for the presence of emerged cercariae. *R. roscovita*-infected periwinkles were isolated and kept in aerated aquaria (60 l) until the start of experiments. As second intermediate host for infection experiments, common cockles *Cerastoderma edule* were collected from a site in the lower intertidal zone in the List tidal basin where no trematode infections occurred. Cockles were kept in a large flow-through aquarium (3 m diameter, water height 50 cm) with water temperature according to ambient conditions (approx. 10 to 15°C).

Emergence of cercariae. Periwinkles were individually placed in small plastic jars (50 mm diameter) with 100 ml aerated seawater, covered with a clear plastic

lid and exposed to artificial daylight (5500 K, 5000 lux). For each treatment, 10 periwinkles were incubated in a constant temperature chamber, at 4 temperatures: 10, 15, 20 and 25°C. Every 12 h the seawater was exchanged with fresh, aerated seawater of the same temperature. The exchanged water was fixed with 10% formalin and the cercariae were counted in a zooplankton chamber (Bogorov chamber) under a dissection microscope. Experiments lasted for 5 d (120 h).

Survival of cercariae. At each temperature, 300 cercariae of *Renicola roscovita* (average age of 2 h) taken from a pool of first intermediate hosts were distributed in 10 small Petri dishes (60 mm diameter), filled with 50 ml aerated seawater and exposed to artificial daylight (5500 K, 5000 lux). The Petri dishes (10 with 30 cercariae each) were incubated in constant temperature chambers at 4 temperatures: 10, 15, 20 and 25°C. At intervals of 2 h, dead cercariae were counted until all cercariae were dead. The criterion for cercarial death was their failure to respond to a mechanical stimulus with a fine needle (Anderson & Whitfield 1975, Evans 1985, McCarthy 1999).

Infectivity of cercariae. At each temperature, 30 cercariae (maximum age of 1 h) from a pool of first intermediate hosts were placed in a Petri dish (85 mm diameter) filled with 100 ml aerated seawater and exposed to artificial daylight (5500 K, 5000 lux). 15 Petri dishes per temperature treatment (10, 15, 20 and 25°C) were incubated in constant temperature chambers. The experiment was started by addition of 1 small *Cerastoderma edule* (11 to 12 mm shell length) to each dish. After 24 h all cockles were put into fresh aerated seawater for another 24 h to allow full encystment of metacercariae. Finally, the cockleshells were removed, the tissue placed between 2 large glass slides and encysted metacercariae counted under a dissection microscope.

Mesocosm experiments. Five glass bowls (90 mm diameter) were filled with approximately 3 cm deep sediment taken from the field. The bowls were filled with 400 ml seawater, equipped with an air pump and exposed to artificial daylight (5500 K, 5000 lux). Five bowls each were incubated in constant temperature chambers at 4 temperatures: 10, 15, 20 and 25°C. To each bowl, 10 *Cerastoderma edule* were added. After 6 h, when the cockles were buried, 3 infected *Littorina littorina* and pieces of sea lettuce *Ulva* spp. as food were added to each bowl. After 3 d, the cockles were removed and left in seawater of the same temperature for another 24 h to allow full encystment of metacercariae. Following this, cockle tissues were screened for encysted metacercariae as described above.

Infection in the field. In January 2004, 1500 non-infected 1 yr old *Cerastoderma edule* (13 to 15 mm) were placed within an area of 2 m². A fence of mesh wire (1 cm mesh size) of 5 cm height was set up to pre-

vent cockles from dislodging and to mark the experimental area. Until December, in the middle of each month, 20 cockles were randomly chosen and examined for infection with metacercariae as described above. In addition to *Renicola roscovita*, metacercariae of *Himastha elongata* (Digenea: Echinostomatidae) (also occurring in cockles at this site) were counted. Data on average water temperature of the water body in the basin were obtained from a long-term monitoring programme in the List tidal basin (provided by J. E. E. van Beusekom).

Statistical analysis. Differences in emergence, infectivity and intensity of *Renicola roscovita* in mesocosm experiments at the 4 temperatures were analysed using analysis of variance (1-way ANOVA). After testing for normality and homogeneity, data transformation was necessary for intensity data, which were log-transformed, and for infection success data, which were arcsine-transformed. Post-hoc calculations were performed with Tukey's HSD test (Day & Quinn 1989). Survival of cercariae at the 4 temperatures was analysed using repeated-measurement ANOVA, since cercariae were subsequently counted in the same dish several times, resulting in non-independence of the data. Prior to analysis, these data were arcsine-transformed.

RESULTS

Emergence of cercariae was significantly different at the 4 temperatures (Fig. 1; 1-way ANOVA; $F_{3,36} = 9.28$, $p < 0.001$) and peaked at 20°C (2609 ± 478 cercariae snail⁻¹ 120 h⁻¹). There was a significant difference in emergence between 20 and 10°C (80 ± 79), 15°C (747 ± 384) and 25°C (1141 ± 334) (Tukey's HSD-test; $p < 0.001$, $p < 0.01$, $p < 0.05$ respectively).

The survival time of cercariae decreased with increasing temperature (Fig. 2). A repeated-measure-

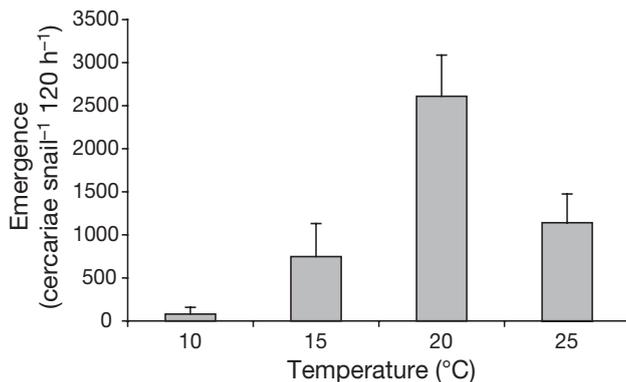


Fig. 1. *Renicola roscovita*. Mean (+SE) emergence of cercariae from snail first intermediate host *Littorina littorea* at 44 different temperatures. $n = 10$ snails at each temperature

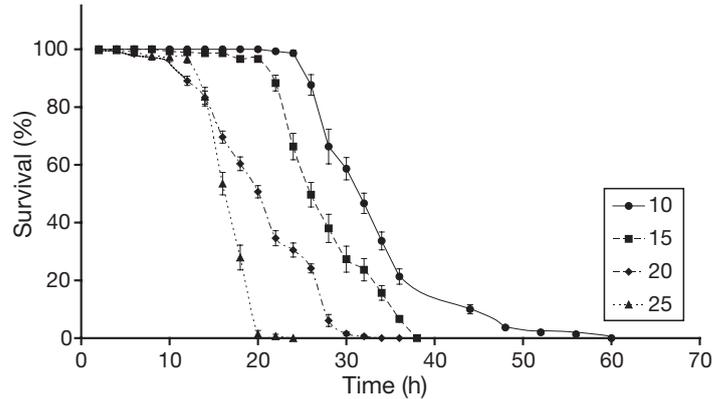


Fig. 2. *Renicola roscovita*. Mean (\pm SE) survival percent of cercariae over 60 h at 4 different temperatures (°C). $n = 10$ Petri dishes with 30 cercariae each

ment ANOVA revealed significant effects of temperature and time on survival and significant interactions (Table 1). The mean half life of cercariae (50% dead) was 32.8 ± 0.6 h (10°C), 26.8 ± 0.8 h (15°C), 20.2 ± 0.5 h (20°C) and 16.6 ± 0.3 h (25°C).

Infection success of cercariae increased with increasing temperature and showed significant differences among temperature regimes (Fig. 3; 1-way ANOVA; $F_{3,56} = 20.73$; $p < 0.001$). This was due to significant differences in infection success between the 10°C treatment and all other treatments (Tukey's HSD-test; $p < 0.001$ each).

The infection intensity of metacercariae in the mesocosm experiment was significantly different among the temperature treatments (Fig. 4; 1-way ANOVA; $F_{3,16} = 33.16$; $p < 0.001$). This was due to statistical differences in intensity between the 10°C treatment and the 15, 20, 25°C treatments (Tukey's HSD-test; $p < 0.05$ for 15°C and $p < 0.001$ for the other temperatures) and differences among the 15°C treatment and the 20 and 25°C treatments ($p < 0.001$).

In the field, infection of *Cerastoderma edule* with *Renicola roscovita* started in April and reached its

Table 1. *Renicola roscovita*. Results of repeated-measurement ANOVA testing survival of cercariae over 60 h at 4 different temperatures (10, 15, 20, 25°C). $n = 10$ small dishes with 30 cercariae each

	df	MS	F	p
Between subjects				
Temp.	3	16.9	638.9	< 0.001
Error	36	0.03		
Within subjects				
Time	29	14.4	2593.2	< 0.001
Temp. \times Time	87	0.6	103.7	< 0.001
Error (Time)	1044	0.006		

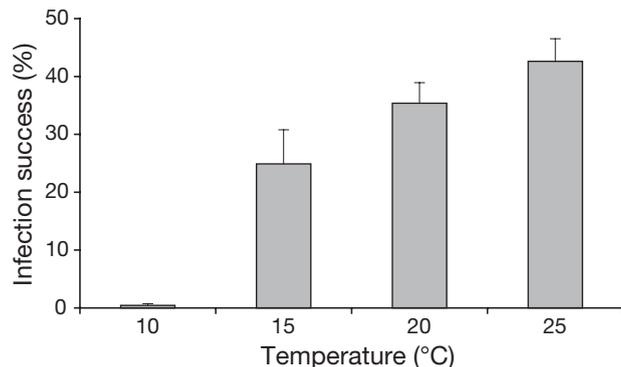


Fig. 3. *Rencicola roscovita*. Mean (+SE) infection success percent of cercariae in cockle second intermediate hosts *Cerastoderma edule* at 4 different temperatures. n = 15 cockles exposed to 30 cercariae each

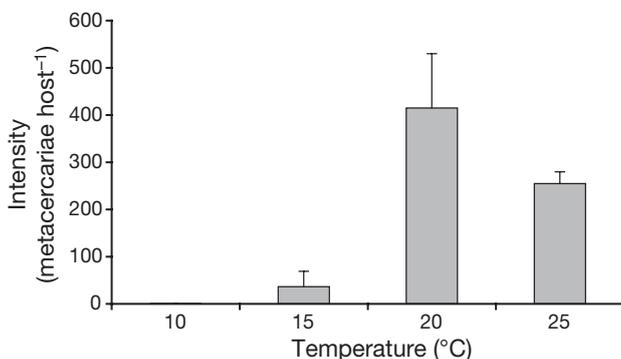


Fig. 4. *Rencicola roscovita*. Mean (+SE) infection intensity (metacercariae per host) of cercariae in *Cerastoderma edule* in mesocosm experiments at 4 different temperatures. n = 5 mesocosms, each containing 3 *Littorina littorea* (infected with *R. roscovita*) and 10 *C. edule*

highest intensity at the end of the summer (Fig. 5). In autumn and winter no new infections occurred. A similar pattern was observed for *Himasthla elongata*. Water temperature peaked in August at a maximum of 21.5°C (mean 19.6 ± 0.3°C) and was generally highest over the summer months (Fig. 5).

DISCUSSION

Water temperature had a strong effect on emergence, survival and infectivity of cercariae of *Rencicola roscovita*. This indicates that transmission success may vary between years, depending on the North Atlantic climate regime.

Emergence of cercariae was highest at 20°C. Since all snails were collected from the field at the same time (thus representing an average developmental condition of sporocysts within the population), temperature seems to trigger the emergence of cercariae and not

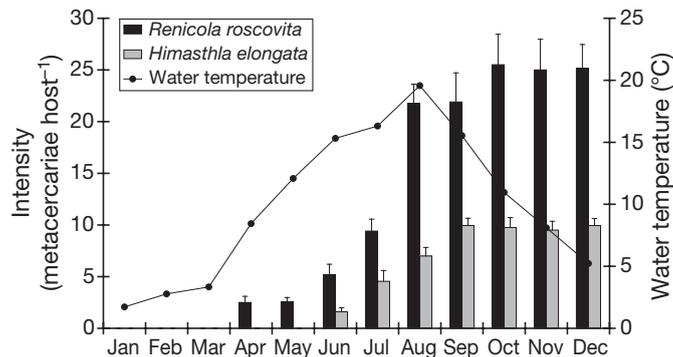


Fig. 5. *Rencicola roscovita* and *Himasthla elongata*. Mean (+SE) infection intensity of metacercariae in *Cerastoderma edule* in an experimental enclosure on a temperate tidal flat (bars) and mean monthly seawater temperature (°C) (data points and lines) in List tidal basin from January to December 2004

just accelerate cercarial maturation (Ginetsinskaya 1988, Mouritsen 2002). Increase in emergence with increasing temperature has also been observed in other trematode–host systems (Lo & Lee 1996, Lyholt & Buchmann 1996, Mouritsen 2002). However, since emergence was considerably lower at 25°C than at 20°C, there seems to exist an upper temperature limit for cercarial emergence in *Rencicola roscovita*. In other trematode species such an upper limit has been suggested to be associated with an upper temperature tolerance of the intermediate hosts (Erasmus 1972, Lo & Lee 1996). However, for *R. roscovita*, the upper temperature limits for the first intermediate host *Littorina littorea* and the 2 dominant second intermediate hosts *Cerastoderma edule* and *Mytilus edulis* are beyond 25°C (Hamby 1975, Newell 1979, Ansell et al. 1981, Gosling 1992). Hence, the observed emergence temperature optimum of 20°C for *R. roscovita* cercariae should result from advantages for the parasite's transmission success rather than host physiology.

The survival time of *Rencicola roscovita* cercariae decreased with increasing temperature. Cercariae are assumed to have a restricted energy reserve in the form of glycogen (Anderson & Whitfield 1975) which is presumably used up faster at high temperatures due to higher rates of cercarial activity (Pechenik & Fried 1995). Decreased survival with increasing temperature was also shown for other trematode cercariae from marine (Möller 1978, Mouritsen 2002) and freshwater (e.g. Evans 1985, Shostack & Esch 1990, Lyholt & Buchmann 1996, McCarthy 1999) systems and seems (with a few exceptions (e.g. Lo & Lee 1996) to be a universal phenomenon in trematode cercariae. The mean time until 50% mortality of *R. roscovita* cercariae ranged from 16.6 h (25°C) to 32.8 h (10°C). However, for the actual infection success of cercariae their functional longevity (time until cercariae, although still alive, are

no longer available to infect a host) rather than their total survival time is important. This functional longevity is usually only 20 to 50% of the total survival time, since cercarial infectivity decreases with increasing age (Evans 1985, Lowenberger & Rau 1994, Pechenik & Fried 1995, McCarthy 1999). Hence, the mean functional longevity of *R. roscovita* is probably between 8 and 16 h, depending on ambient temperature.

Infectivity of *Renicola roscovita* cercariae was highest at 25°C, presumably due to a temperature dependent increase in cercarial swimming activity resulting in a corresponding increase in the number of contacts between cercariae and host per unit time (Evans 1985). Additional to temperature mediated effects on cercarial behaviour, host behaviour is certainly also important. Bivalve activity and filtration intensity increases with rising temperature (Newell 1979) and since infections are mainly caused by inhaled cercariae (Montaudouin et al. 1998, Wegeberg et al. 1999) temperature dependent host behaviour should also increase infection success.

Although infectivity of cercariae of *Renicola roscovita* was highest at 25°C, the mesocosm experiments, integrating emergence, survival and infectivity of cercariae at different temperatures, indicated that 20°C is an optimum temperature for transmission of *R. roscovita*. Besides potential synergistic effects of emergence, survival and infectivity at different temperatures in mesocosms, the presence of bivalve intermediate hosts might also have influenced the emergence of cercariae and thus have led to differential infectivity of cercariae: Mouritsen (2002) showed that second intermediate host exudates enhanced emergence of cercariae of *Maritrema subdolum*. A similar effect could occur in the *R. roscovita*-cockle system, but this remains to be investigated.

That 20°C is the optimal temperature for transmission of *Renicola roscovita* cercariae is supported by observations in the field experiment. Intensity of *R. roscovita* metacercariae in cockles was highest in August when the water temperature reached 20°C. Hence, summer should be the main infective season for *R. roscovita* cercariae due to (1) temperature dependent development of sporocysts in the first intermediate hosts of snails (Möller 1978, Fagbemi 1984, Ataev 1991) and (2) a strongly temperature dependent emergence, survival and infectivity of cercariae when mature, as shown in our experiments. Another trematode species occurring at the experimental site, *Himasthla elongata*, showed a similar temporal pattern. This suggests that transmission of cercariae on temperate tidal flats generally peaks during summer. In contrast, the mean temperature of the water body is considerably lower in spring and autumn. However, in

shallow waters and water remaining, at low tide (tide pools) temperature can strongly increase during sunny and calm days (Thieltges pers. obs.). Hence, shallow waters and tide pools should be hotspots for trematode infections on temperate tidal flats, where appropriate temperatures for transmission are regularly attained. This was also inferred from laboratory studies by Mouritsen (2002), and field experiments showed a higher trematode load in cockles in tidal pools compared to those in surrounding hummocks (Thieltges & Reise 2006).

Summer temperatures in the vicinity of the North Atlantic vary considerably between years, largely depending on the North Atlantic climate oscillation (NAO) (Stenseth & Ottersen 2004). The NAO is calculated as the deviance from the average sea level pressure difference between Iceland and the Azores. A positive NAO index results in high temperatures, strong winds and high precipitation in northern Europe and low temperatures in North America. A low NAO index has opposite effects. The NAO index fluctuates between years, resulting in different summer conditions. Hence, trematode transmission to second intermediate bivalve hosts may peak during particular warm summers under highly positive NAO conditions. Such conditions are predicted to arise more frequently in northern Europe under various climate change scenarios (Stenseth & Ottersen 2004). Hence, a warming trend may lead to enhanced transmission on temperate tidal flats with a multitude of potential subsequent effects on host populations and communities (Margaroli 2001, Mouritsen & Poulin 2002b).

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