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VERSITA

Temporal variation in prevalence and cercarial development of *Echinostephilla patellae* (Digenea, Philophthalmidae) in the intertidal gastropod *Patella vulgata*

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Abstract

The trematode *Echinostephilla patellae* is an abundant but scarcely investigated parasite found in coastal ecosystems of the British Isles. Redial and cercarial stages of the digenean occur in the digestive gland and gonads of common limpets *Patella vulgata*. Here, we present data on the temporal distribution of *E. patellae* infections in *P. vulgata* from an intertidal site on the Irish south coast as well as on the intramolluscan development of the cercariae over a period of one year. Prevalence of infection showed temporal variation with a distinct peak in September, possibly related to an increase in the abundance of bird final hosts coinciding with comparatively high temperatures at the study locality during the summer months. Maturation of cercarial stages was strongly correlated with water temperature. Whilst fully developed cercariae were present in the rediae from May to November, large numbers of infective stages occurred in the limpets' mantle blood vessels – where they accumulate prior to release – between June and September, suggesting this period of time to be the main transmission window for *E. patellae* cercariae.

Keywords

Trematodes, common limpet, cercarial development, seasonality, infection patterns

Introduction

Digenean trematodes are major parasitological components of coastal ecosystems (Thomas *et al*. 1997, Mouritsen and Poulin 2002), exploiting a wide range of marine organisms (e.g. Lauckner 1980, 1983; Sindermann 1990). Their life cycles typically include two intermediate and a final host, with gastropods being utilized as first intermediate host by the majority of digeneans. The common limpet *Patella vulgata* Linnaeus, 1758, occurring in rocky shore habitats throughout the coastal fringe of the British Isles, serves as host for four macroparasite species (Crewe 1951), of which the trematode *Echinostephilla patellae* (Lebour, 1911) is most common (Crewe 1951, James 1968). Redial and cercarial stages of this parasite develop in the gastropod's digestive gland and gonads, causing rapid degeneration of affected tissues (Rees 1934, Copeland *et al*. 1987). Prior to emergence from the host, cercariae congregate in the afferent branchial blood vessels of the limpet's mantle edge, appearing white and opaque against the surrounding translucent tissue (Crewe 1951), readily visible to the naked eye. On release, the free-swimming larvae seek to invade blue mussels *Mytilus edulis* Linnaeus, 1758, and encyst in the foot tissue following penetration (Prinz *et al*. 2009a), where they await ingestion by the avian final host, which is not specified yet. Kollien (1996) suggested the oystercatcher *Haematopus ostralegus* Linnaeus, 1758 as definitive host, without providing further evidence. However, this author succeeded in infecting young chickens with *E. patellae*. Hence, host specificity in this species is presumably rather low and various sea- and shorebirds might act as final host.

Although widespread and locally abundant, and thus probably of ecological relevance, comparatively little is known about the ecology of *E. patellae* infections to date. Previous studies dealt with pathological effects caused by the parasite in the first intermediate host (Rees 1934, Copeland *et al*. 1987), its life cycle (Kollien 1996, Prinz *et al*. 2009a) as well as with factors influencing cercarial transmission (Prinz *et al*. 2009a, b) and spatial distribution of *E. patellae* infections (Thomas 1965, James 1968, Copeland *et al*. 1987, Kollien 1996). So far, there is no information available on temporal infection patterns of this trematode in its gastropod host. Furthermore, the transmission window for *E. patellae* cercariae is

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not clarified yet. Experimental infections of the bivalve second intermediate host at different temperature regimes have shown a positive influence of temperature on infection success (Prinz *et al*. 2009a). This suggests that the main infection period is probably during the summer months, as observed in other trematode species (Køie 1975, Fingerut *et al*. 2003, Thieltges and Rick 2006) and as indicated by previous findings (Copeland *et al*. 1987, Kollien 1996). However, field data on seasonal development of cercarial stages supporting this assumption are missing.

In this study, we investigated (1) the temporal distribution of *E. patellae* infections in *P. vulgata* from an intertidal site on the south coast of Ireland over one year and (2) the intramolluscan development of the cercariae over the same period of time.

Materials and methods

Sampling and parasitological examination

Gastropod samples were taken monthly between April 2008 and March 2009 from Garrettstown Strand, Co. Cork, Ireland (51°38´N, 8°35´W). During each sampling session, 200 *Patella vulgata* were collected at low tide from exposed littoral rocks (excluding rock pools) at mid intertidal level from a comparatively homogeneous sampling area following a standardized sampling protocol. Since the determination of limpet age is quite complex involving several laboratory techniques (see Ekaratne and Crisp 1982), it is hardly feasible to follow a cohort of limpets over a year. Thus, it was decided to collect gastropods from a certain size class (40–50 mm shell length; standardized shell length composition of monthly samples), which was selected with regard to the probability of detecting mature infections (see Crewe 1951, Kollien 1996) and availability of hosts at the sampling site. All collected limpets were thoroughly inspected for the presence of cercariae in the mantle blood vessels and any positive observations were noted. To record water temperature over the year, a StowAway® TidbiT™ data logger was installed in the shallow sublittoral in close vicinity to the sampling site.

In the laboratory, gastropod shells were measured using a vernier caliper. The soft tissue was removed from the shell, dissected and screened for infections with *Echinostephilla patellae* under a stereomicroscope with incident illumination. To assess the maturity of cercarial stages, the visceral mass of five infected limpets, selected randomly from the sample, was transferred to separate dishes, broken down using dissection pins and diluted in seawater. Subsequently, ten rediae were taken haphazardly with a pipette, transferred to a glass slide and observed under a stereomicroscope with transmitted light. In November and March, when only three out of 200 limpets were found to be infected, 16–17 rediae were taken from the available individuals. Redial length was measured using an eyepiece micrometer. Numbers of developmental stages contained in the rediae were counted according to the following

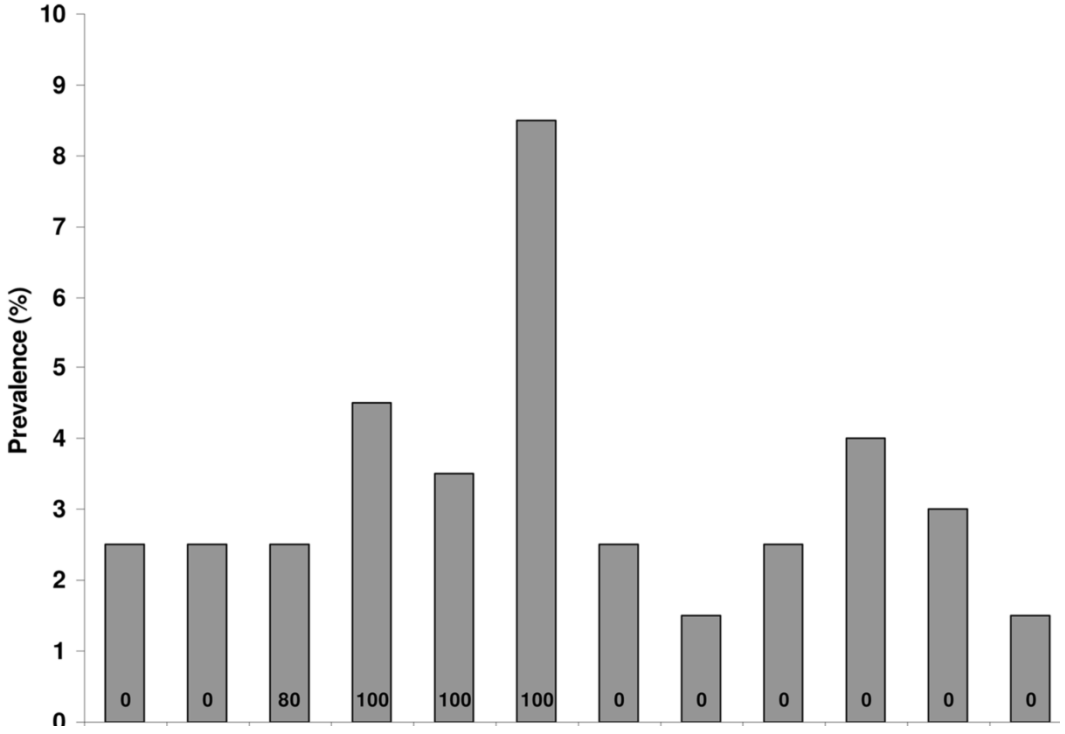

Fig. 1. Annual variation in prevalence of *Echinostephilla patellae* infections in *Patella vulgata* and percentage of infected limpets showing cercariae in the mantle blood vessels (values given inside bars; n = 200 limpets per month)

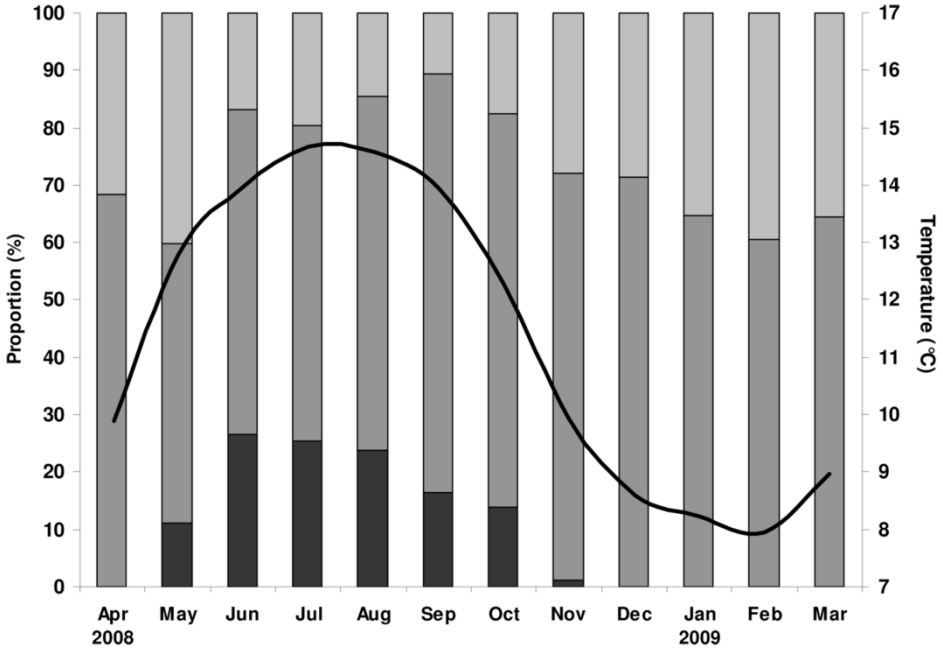

Fig. 2. Annual variation in water temperature (—) and proportion of germinal balls (□), cercarial embryos (■), and fully developed cercariae (■) in *Echinostephilla patellae* rediae recovered from *Patella vulgata* (n = 50 rediae per month)

categories: (1) germinal balls, (2) cercarial embryos in various developmental stages, and (3) fully developed cercariae, exhibiting prominent lateral excretory canals and actively moving in the rediae.

Statistical analysis

Data analysis was carried out in SPSS and results were considered as significant at $p<0.05$. All tests were preceded by formal evaluation of assumptions and data were transformed if necessary. A chi-square test was performed to compare the prevalence of infection (see Bush *et al*. 1997) in *P. vulgata* between months. To analyze differences in redial length as well as number of developmental stages in the rediae between months, one-way analysis of variance (ANOVA) was used. The relationship between monthly mean water temperature and the proportion of fully developed cercariae was assessed using linear regression, after arcsine-transformation of percentage data. Potential differences in shell length between monthly gastropod samples were evaluated with a one-way ANOVA.

Results

Overall prevalence of *Echinostephilla patellae* infection in *Patella vulgata* was 3.3 ± 1.9% (mean ± SD). Statistical analysis revealed a significant difference in numbers of infected limpets between months (χ^2 test; $p = 0.01$), with a distinct peak in September (Fig. 1). Redial length as well as number of developmental stages in the rediae (Table I) did not vary between months (ANOVA; $p>0.05$). Monthly mean water temperature (calculated from hourly recordings) ranged between 7.9°C in February and 14.7°C in July (Fig. 2). Maturation of *E. patellae* cercariae showed pronounced seasonality (Fig. 2). Germinal balls and cercarial embryos were present year round. Fully developed cercariae first appeared in the rediae in May and were observed until November. Cercariae were found to congregate in the gastropods' mantle blood vessels from June to September (Fig. 1). Numbers of fully developed cercariae were strongly positively correlated with water temperature ($r^2 = 0.951$, $p<0.001$). No differences in limpet shell length were detected between months (ANOVA; $p>0.05$).

Table I. Length (mean ± SD) of *Echinostephilla patellae* rediae recovered from *Patella vulgata* and number (mean ± SD) of developmental stages per redia from April 2008 to March 2009

Month	Redial length (mm)	No. of stages per redia
April 2008	3.40 ± 0.68	28.74 ± 7.77
May	3.57 ± 0.93	30.28 ± 10.20
June	3.77 ± 0.95	30.32 ± 9.91
July	3.49 ± 0.76	28.56 ± 8.75
August	3.81 ± 0.73	30.10 ± 9.52
September	3.48 ± 0.72	27.46 ± 8.34
October	3.64 ± 0.81	30.78 ± 9.63
November	3.54 ± 0.85	28.26 ± 10.08
December	3.42 ± 0.85	27.90 ± 8.02
January 2009	3.48 ± 0.81	26.20 ± 8.05
February	3.58 ± 0.76	29.90 ± 8.30
March	3.81 ± 0.71	30.38 ± 9.15
Total	3.58 ± 0.81	29.07 ± 9.04

Discussion

Seasonal fluctuations in prevalence of infection in first intermediate hosts have been reported from various marine host-trematode systems. Whilst in short-lived (< 2 years) gastropods the observed dynamics are largely attributable to life history characteristics of the host (Esch and Fernandez 1994, Field and Irwin 1999, Kube *et al*. 2002), temporal patterns in long-lived hosts are often inconsistent and causes of variation in the frequency of infection are less clear (Sindermann and Farrin 1962, Esch and Fernandez 1994, Ngo and Choi 2004). Similar to the findings of previous investigations (Robson and Williams 1970, Lang and Dennis 1976, Sannia and James 1978, Hughes and Answer 1982), which revealed an increase in infection rates during the warmer months of the year, our study showed prevalence of *Echinostephilla patellae* infections in *Patella vulgata* to peak in September, suggesting recent miracidial invasions. Two major factors, which are known to considerably influence infection rates in intermediate hosts, might have contributed to the observed pattern at the studied locality, namely temperature and abundance of upstream hosts. Ambient temperature is an important parameter regulating the transmission of miracidia in marine (Vanoverschelde 1982) as well as freshwater trematodes, with higher temperatures generally leading to an increase in infection success (Upatham 1973, Christensen *et al*. 1976, see Pietrock and Marcogliese 2003 for review). Secondly, density of bird final hosts is a significant and possibly even more decisive external factor determining infection rates in downstream hosts by impacting the numbers of infective propagules in the system (Hechinger and Lafferty 2005, Fredensborg *et al*. 2006). Numbers of sea- and shorebirds roosting and defecating on the littoral rocks outside the breeding territories are presumably comparatively low during the breeding season and larger congregations of birds do not recur at the shore until July. At the sampling site, a rise in water temperature probably coincides with elevated numbers of final hosts during midsummer, resulting in an increase in prevalence of infection in September (see Robson and Williams 1970, Hughes and Answer 1982). Since redial lengths as well as numbers of developmental stages stayed relatively constant over the year, suggesting that only mature infections were recorded throughout the study, the prepatent period of *E. patellae* infections can be assumed to be rather short as supposed by Rees (1934) and Crewe (1951). Thus, it seems plausible that infections acquired by the limpets in late July and August were mature in September already. To confirm this assumption and to better understand such patterns, laboratory and field-based experiments examining parameters that control transmission of *E. patellae* miracidia as well as possible interrelations between factors are needed in combination with data on seasonal presence and abundance of bird final hosts at the site.

The noticeable decline in the numbers of infected limpets following the peak in September might either be attributable to enhanced host mortality or loss of infections. The latter presumably plays a minor role, since once established trematode infections in long-lived gastropod species are rather perennial (Rothschild 1942; Robson and Williams 1970; Sousa 1983, 1993; Huxham *et al*. 1993). Moreover, it seems highly unlikely that self-cure or spontaneous loss of an intramolluscan trematode cumulate in one particular month. A more conclusive explanation for the observed reduction would be enhanced host mortality. Some limpets might not have survived the infection, especially considering the fact that rediae have a particularly destructive influence on the host due to their mechanisms of nutrition (Sousa 1983, Gorbushin 1997). Furthermore, parasitic invasion may lower the host's ability to adapt to changing environmental conditions (Lafferty and Kuris 1999). Comparatively high temperatures, exceeding 20°C, which are regularly reached on bare rocks at low tide during the summer months (personal observation) constituting additional environmental stress, may have led to a disproportionate increase in mortality rates of infected limpets as reported from other host-parasite systems (Jonsson and André 1992, Huxham *et al*. 1993, Thieltges 2006). Impaired host fitness through parasite invasion might also increase the susceptibility to predation and thus add indirectly to parasite-induced host mortality.

There was a clear positive correlation between monthly water temperature and the proportion of fully developed cercariae, suggesting this factor to be an important external driver impacting intramolluscan infection dynamics. Corresponding to our findings, previous studies noted the complete absence of mature *E. patellae* cercariae in the rediae (Copeland *et al*. 1987) and in the limpets' mantle blood vessels (Kollien 1996), respectively, during the winter months, confirming that cercarial maturation in *E. patellae* largely relies on ambient temperature. Seasonal fluctuation in intramolluscan development of infective stages under natural conditions has barely been studied so far. Similar to the present study, Køie (1975) and Fermer *et al*. (submitted) found a temporal pattern in cercarial development in the trematodes *Opechona bacillaris* (Molin, 1859) and *Meiogymnophallus minutus* Cobbold, 1859, respectively, indicating that in temperate regions maturation of cercariae is generally confined to the summer months. These observations are consistent with laboratory findings, showing that development of daughter sporocysts (Upatham 1973) as well as rediae (Ataev 1991) is temperature dependent, with higher temperatures accelerating the production of parthenitae.

Although we observed fully developed cercariae within the rediae from May to November, infective stages were only found to accumulate in the limpets' mantle blood vessels from June to September. The majority of infective stages are presumably liberated during this period of time, which thus can be seen as the main transmission window for *E. patellae* cercariae on the south coast of Ireland. The presence of mature cercariae in the mantle blood vessels coincided with the period of highest mean water temperatures (Fig. 2), suggesting that 14°C constitutes a threshold for enhanced cercarial release, as known from other host-parasite systems (Lo and Lee 1996, Fingerut *et al*. 2003, Thieltges and Rick 2006). Since infection

success of *E. patellae* in mussels is positively affected by temperature (Prinz *et al*. 2009a), cercarial liberation might be largely repressed until conditions are met which favour transmission to the next host.

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