

Parasites as prey: the effect of cercarial density and alternative prey on consumption of cercariae by four non-host species

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SUMMARY

In parasites with complex life cycles the transmission of free-living infective stages can be influenced by ambient community diversity, in particular via predation. Here, we experimentally investigated whether parasite density and the presence of alternative prey can alter predation rates on free-living cercarial stages of a marine trematode by several non-host predators. All four predator species consumed increasing numbers of cercariae with an increase in cercarial density, indicating that the removal of cercariae by predators is effective over a range of natural densities as well as in the presence of alternative prey for a number of predators typical of marine ecosystems. However, the relative removal rates and the effects of cercarial density and alternative prey differed among predator species. In barnacles and shrimps, significant interactive effects of cercarial density and alternative prey on cercarial predation occurred while in oysters and crabs cercarial removal rates were unaffected by both factors. As changes in cercarial densities directly translate into changes in infection levels in down-stream hosts in this parasite–host system, the observed predator-specific responses suggest that cercarial predation effects on disease risks will depend on the specific species composition of ambient communities and not on non-host biodiversity *per se*.

Key words: Transmission, trematodes, cercariae, predation.

INTRODUCTION

Across the globe biodiversity is being lost at a high rate. In general, decreased biodiversity is believed to reduce ecosystem functioning and service provision (Hooper *et al.* 2005; Worm *et al.* 2006; Keesing *et al.* 2010). An important and increasingly studied additional consequence of biodiversity loss is the potential increase in the transmission of infectious diseases. The relationship between biodiversity and reduced disease transmission has been shown across a variety of ecosystems involving various pathogens, hosts and transmission pathways (Keesing *et al.* 2006; Johnson *et al.* 2015). This apparent mediation of disease risk and reduction of infection levels by ecological community diversity is explained by the so called ‘dilution effect’. The term has been widely applied as a concept in terrestrial disease ecology, notably in studies on Lyme’s disease and other vector-borne diseases (Keesing *et al.* 2006). Here, an increase in species diversity is said to reduce disease risk by altering the abundance of competent disease reservoirs relative to non-competent reservoir species. This in turn reduces the encounter rate

between disease vectors and competent hosts, thereby reducing the number of vectors and their infection prevalence in the system (Ostfeld and Keesing, 2000; Schmidt and Ostfeld, 2001; Keesing *et al.* 2006). However, whether this effect is universal or whether the actual amplification or dilution of disease risk in a system depends on the specific species composition of reservoir hosts and vectors of that system and not on biodiversity *per se* is hotly debated (Randolph and Dobson, 2012; Salkeld *et al.* 2013; Lafferty and Wood, 2013; Wood and Lafferty, 2013; Johnson *et al.* 2015).

A similar ‘dilution effect’ as that observed in vector-borne diseases occurs in parasites with complex life cycles where the transmission of free-living infective parasite stages can be strongly influenced by changes in ambient community diversity and composition (Thieltges *et al.* 2008a; 2008b; Johnson and Thieltges, 2010). Changes in species richness can interfere with the transmission of infectious stages to their suitable hosts through a wider variety of mechanisms than simply changing the relative abundance of competent to non-competent hosts (Orlofske *et al.* 2012). These include predation and hyperparasitism, physical disturbances or barriers, chemical disruption in the form of toxic exudates and interference by decoy and alternative host organisms (Thieltges *et al.* 2008a; 2008b

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Johnson and Thieltges, 2010). Of these mechanisms, predation on free-living stages has been particularly well studied, indicating that predators often interfere with parasite transmission by removing substantial numbers of parasitic free-living infectious stages from their environment, thereby reducing encounters between hosts and parasites and ultimately lowering infection levels in down-stream hosts (Thieltges *et al.* 2008a; Johnson *et al.* 2010; Orlofske *et al.* 2012). However, these removal rates are typically obtained from experiments using specific densities of parasites (i.e. number of infectious stages) and not for a range of different densities. Given that there tends to be a relationship between the consumption rate of a predator and the abundance of its prey (functional response, Oaten and Murdoch, 1975) it may be that the strength of the observed transmission interference differs across a range of parasite densities. Hence, it remains to be determined whether organisms removing parasites reach a saturation point thereby impairing the transmission interference. If predators were to reach saturation at high parasite densities or even reduce their consumption rate due, for example, to swarming effects [i.e. where a high abundance of prey diminish consumption rate through a variety of mechanisms, such as clogging of filters (Jeschke *et al.* 2004)] this would have important implications for the generality of observed effects of transmission interference. In addition, the consumption rate of predators is also known to be affected by the presence of alternative prey (Oaten and Murdoch, 1975; van Baalen *et al.* 2001). Under natural conditions predators have access to a range of prey species, while experimental setups typically involve a simple one predator – one prey design. The recorded consumption rate of predators may therefore merely be a phenomenon observed in the lab in the absence of any alternatives. Unfortunately, to date, studies on the density of infective stages and the presence/absence of alternative prey mediating the rate of parasite removal by predators are limited to a single system, cercarial stages of the trematode *Ribeiroia ondatrae* infecting freshwater amphibians (Schotthoefer *et al.* 2007; Orlofske *et al.* 2012, 2015). This clearly hinders our understanding of the generality and magnitude of the effect of predator interference with parasite transmission.

In this study, we experimentally investigated the effect of parasite density and alternative prey on the consumption of free-living cercarial stages of a marine trematode (*Himasthla elongata*) by several non-host predators. Previous work had shown that cercariae of this species are frequently consumed by a variety of predators (Welsh *et al.* 2014). The trematode species uses the gastropod *Littorina littorea* as first intermediate and some bivalves (mainly mussels and cockles) as second intermediate hosts and bivalve-eating birds as definitive hosts (Thieltges

et al. 2006). By exposing shrimps (*Crangon crangon*), crabs (*Hemigrapsus takanoi*), oysters (*Crassostrea gigas*) and barnacles (*Semibalanus balanoides*), which either actively prey upon motile, free-living cercarial stages or passively filter them out of the water column, to several ecologically relevant densities of cercariae (based on calculations from literature data) in presence or absence of alternative prey we aimed to quantify the effect of both factors on parasite removal rates by predators. As cercarial densities directly translate into metacercarial infection levels in down-stream hosts in this system (Liddell *et al.* 2017), any changes in cercarial densities due to cercarial predation can be expected to ultimately affect disease risk in down-stream hosts. Hence, our experiments contribute to our still limited understanding of the presence and magnitude of the effects of ambient community diversity on parasite transmission interference.

MATERIALS AND METHODS

Experimental organisms and alternative prey

Cercariae of *H. elongata* were used for the experiments. After emergence from the hosts, the relatively large cercariae (body length: 605–665 μm ; tail length: 535–605 μm ; Werdning, 1969), which are visible to the naked eye, swarm actively through the water column. For the experiments, cercariae were obtained from common periwinkles (*L. littorea*) collected in the vicinity of the NIOZ Royal Netherlands Institute for Sea Research on Texel (Wadden Sea, The Netherlands). Snails known to be infected from shedding trials were kept in the dark in aerated flow-through aquaria and fed regularly with sea lettuce (*Ulva lactuca*) until cercariae were required for experiments. Shedding of cercariae by snails was then induced by incubating around 30 snails in 2.7 L of seawater at 27 °C under light for 3 h. Subsequently the necessary numbers of cercariae were pipetted within 1 h (thus the maximum age of cercariae was 4 h) into pots to be administered to the appropriate containers of the experiment.

Four species with different feeding mechanisms or hunting strategies and which do not serve as hosts for the trematode species were used in this study: shrimps and crabs as motile active predators and oysters and barnacles as sessile filter feeders. Shrimps (*C. crangon*; mean \pm S.D.: 34.4 \pm 1.9 mm length), crabs (*H. takanoi*; 18.8 \pm 1.5 mm carapax width), barnacles (*S. balanoides*, attached to empty mussel shells; 34.5 \pm 8.2 barnacles of 2–3 mm diameter per shell) and oysters (*C. gigas*; 48.6 \pm 4.1 mm diameter) were collected in the vicinity of the NIOZ in the south east of Texel (The Netherlands). Collected organisms were housed in aerated containers or flow through aquaria in the

same climate chamber at 15 °C and fed regularly. Crabs were fed on a diet of oysters, mussels, fish (herring) and shrimp. Shrimps were fed fish (herring) and consumed conspecifics. Oysters were fed algal bivalve feed (*Isochrysis galbana*). Barnacles were collected shortly before the experiment and thus did not require feeding.

The type of alternative prey items offered to predators was chosen based on knowledge on the natural diets of the predators used in the experiments. The alternative prey for the crabs and shrimps consisted of frozen fish (herring) which was defrosted the night before administration and cut into small portions (approx. 0.96 g per crab, 0.72 g per shrimp) at a size that predators could easily handle. The alternative prey for the oysters and barnacles consisted of highly concentrated *I. galbana* algal bivalve feed (Instant Algae by Reed Mariculture Inc. USA; 4.1 billion cells mL⁻¹), administered as 3–4 drops of algal feed per oyster and per unit of barnacles, resulting in algal concentration inducing feeding activity in oysters and barnacles based on observations in preliminary experiments. In all four predator experiments, the alternative prey items added were of a significantly larger volume or quantity than the potential cercarial prey to ensure that predators were offered attractive alternative choices to cercariae at all cercarial densities.

Experimental set-up

Plastic containers (25 × 11 × 9.5 cm³) were filled with 500 mL of seawater, constantly aerated and placed on a bench in a completely randomized block design with two temporal blocks. The room temperature was maintained at 18 °C (the average summer water temperature in the study area; van Aken, 2008). In the case of crabs, shrimps and oysters, a single individual was placed in each container and the assigned treatment administered. Barnacles were added attached to a single mussel valve (34.5 ± 8.2 barnacles per container). The four species were tested in four separate experiments, each using the same two-factorial block design, with cercarial density (20, 60, 100 or 300 cercariae) and alternative prey (present or absent) as main factors and two temporal blocks (days 1 and 2). Each treatment combination was replicated four times in each block, i.e. eight replicates for each treatment combination in total.

Cercarial density selection was based on literature data on cercarial shedding rates of *H. elongata* from their first intermediate host, the common periwinkle *L. littorea*, and on literature data on the average abundance of periwinkles (for details see Liddell *et al.* 2017). These calculations suggested a realistic maximum shedding of about 300 cercariae in the vicinity of an infected snail per tide and we thus

used this as the maximum cercarial density administered. As this maximum cercarial concentration is likely to be diluted in the field in the water column and by intra-specific dilution in form of up-take by down-stream hosts such as mussels and cockles (Mouritsen *et al.* 2003; Thielges and Reise, 2006; Magalhães *et al.* 2016) we used several lower cercarial densities (100, 60 and 20 cercariae) to mimic various levels of cercarial dilution.

Crabs, shrimps, oysters and barnacles were placed in their containers a day before the experiment to acclimatize. Treatments were then administered and the experiments run for 3 h. After that the organisms were removed and the contents of the containers sieved through a 20 µm mesh and dyed using Rose Bengal stain (test runs had proven this method to retrieve 100% of cercariae). The number of parasites remaining in the sieved contents was recorded using a light microscope.

Statistics

The relationship between parasite density (20, 60, 100 or 300 cercariae), the presence of alternative prey (absent *vs* present), and a block factor on the number of remaining parasites was analysed using a binomial Generalized Linear Model (GLM) with a log-link. Assuming a so-called *linear pure death process*, which means that all removals are independent events, the number of free-living cercarial stages remaining at the end of the experiment follows a binomial distribution. The parameters of the distribution are given by the initial number of parasites and by the probability that a parasite is still free-living at the end of the experiment. This probability equals

$$p = e^{-\theta}$$

where θ is the removal rate per unit of experimental time. It is further assumed that this removal rate is a function of parasite density, the presence of alternative prey, their interaction, and a block effect. So

$$\theta = \mu + \alpha_i + \beta_j + \gamma_{ij} + \delta_k$$

where μ is the intercept, α is the effect of cercarial density, β of the presence of alternative prey, γ their interaction, and δ is the block effect. The model used the absolute number of remaining parasites after the 3 h experimental time period.

A series of GLM models from the most complex to the least complex were fitted (see online Fig. S1). The most complex model included all explanatory variables (cercarial density, alternative prey, their interaction, and a block effect) whereas the simplest model (the null model) excluded all explanatory variables and only included the intercept. Testing for the best fitting model by

identifying significant differences between models of descending complexity was carried out using the Analysis of Deviance. For example, model 1 which included all terms was tested against model 2 in which the interaction was left out. The delta deviance (the difference in deviance between the two models) was subsequently divided by the dispersion factor (ϕ) from the most complete model ($\Delta \text{Dev}/\phi$) and compared to the delta degree of freedom χ^2 at 0.05. The dispersion factor was calculated by dividing the residual deviance for the most complex model by the degrees of freedom. A significant difference between two models reveals that the most complex model of the two is the better fit.

From the best fitting models, cercarial removal rates (per experimental runs) and cercarial survival (%) were calculated. Removal rates were calculated for the 3 h experimental period and based on the estimates of the intercept for each significant factor included in the best fitting model output. Cercarial survival was calculated from the estimates of the intercept for each significant factor included in the best fitting model output. From these cercarial survival data, the proportion cercariae removed (%) can be calculated (proportion cercariae removed = 100 – cercarial survival).

All analyses were carried out using R (R Development Core Team, 2013) version 3.0.2 in R Studio (version 0.98.1103; RStudio, 2015).

RESULTS

All four predators consumed more cercariae when higher densities of cercariae were offered, both when alternative prey was absent and present, i.e. the absolute removal in terms of numbers of cercariae generally consumed increased with cercarial density (Fig. 1). However, the relative cercarial removal rates (i.e. consumption per unit time) differed among the four predators depending on cercarial density and alternative prey (Table 1; see online Figures S2–S5; for raw data see Welsh et al. 2017). In barnacles, the best fitting model included the interaction between cercarial density and presence/absence of alternative prey (model 1; Table 1). This probably resulted from the fact that cercarial removal rates were higher at presence than at absence of alternative prey at intermediate cercarial densities while they were lower at high densities (Fig. 2). In addition, the best fitting model also included a temporal block effect, which resulted from overall higher removal rates during the second run of the experiment (Fig. 2; online Table S1). Overall, the survival of cercariae after removal by barnacles was between 5 and 35% (online Table S1). In contrast to barnacles, none of the factors tested affected cercarial removal rates by oysters (Table 1), i.e. oysters were removing cercariae at a constant rate, independent of the cercarial density or the presence/absence of alternative prey.

The cercarial removal rate of oysters was 1.01 and 36% of cercariae survived.

For crabs, the best fitting model only included the block effect (model 7; Table 1). Cercarial removal rates by crabs were slightly higher in the first (0.21) than in the second (0.14) experimental run. Accordingly, cercarial survival was slightly lower in the first compared with the second run (81% and 87% respectively). Finally, for shrimps the best fitting model included an interaction between cercarial density and the presence/absence of alternative prey (Table 1). This interaction was based on an almost 5-fold increase in searching rates of shrimps at the highest cercarial density when alternative prey was absent (Fig. 3). Here, cercarial survival was relatively low with 47%, while in all other cases cercarial survival ranged between 77 and 91% (online Table S2).

DISCUSSION

All four predator species consumed increasing numbers of cercariae with an increase in cercarial density, i.e. the absolute cercarial removal increased with cercarial density. However, the relative cercarial removal rates (i.e. per unit time) and the effect of cercarial density and alternative prey differed among predator species. In barnacles and shrimps, significant interactive effects of cercarial density and alternative prey on cercarial consumption were present, while in oysters and crabs neither cercarial density nor the presence/absence of alternative prey had a significant effect on cercarial removal rates by the predators.

The increase in the numbers of cercariae consumed by all four predator species with increasing cercarial density can be explained in terms of the mass action principle, which assumes that predators encounter their prey randomly and that the number of encounters a predator makes is proportional to the density of its prey (Arditi and Ginzburg, 1989). Interestingly, none of the predators reached saturation across the range of parasite densities tested in this experiment. As the parasite densities administered in this study were selected based on natural shedding rates of cercariae from their host snails and therefore represent abundances of infective stages that a predator is likely to encounter under natural conditions (see ‘Materials and Methods’ section), the experiments suggest that swarming effects, e.g. by clogging of filters, do not seem to occur at realistic parasite densities in the predators tested. However, while the absolute numbers of cercariae consumed generally increased with increasing cercarial density in all four predator species, the relative removal rates showed different responses to cercarial density and presence/absence of alternative prey in the four predator species. The fact that species sharing the same feeding mechanism (active

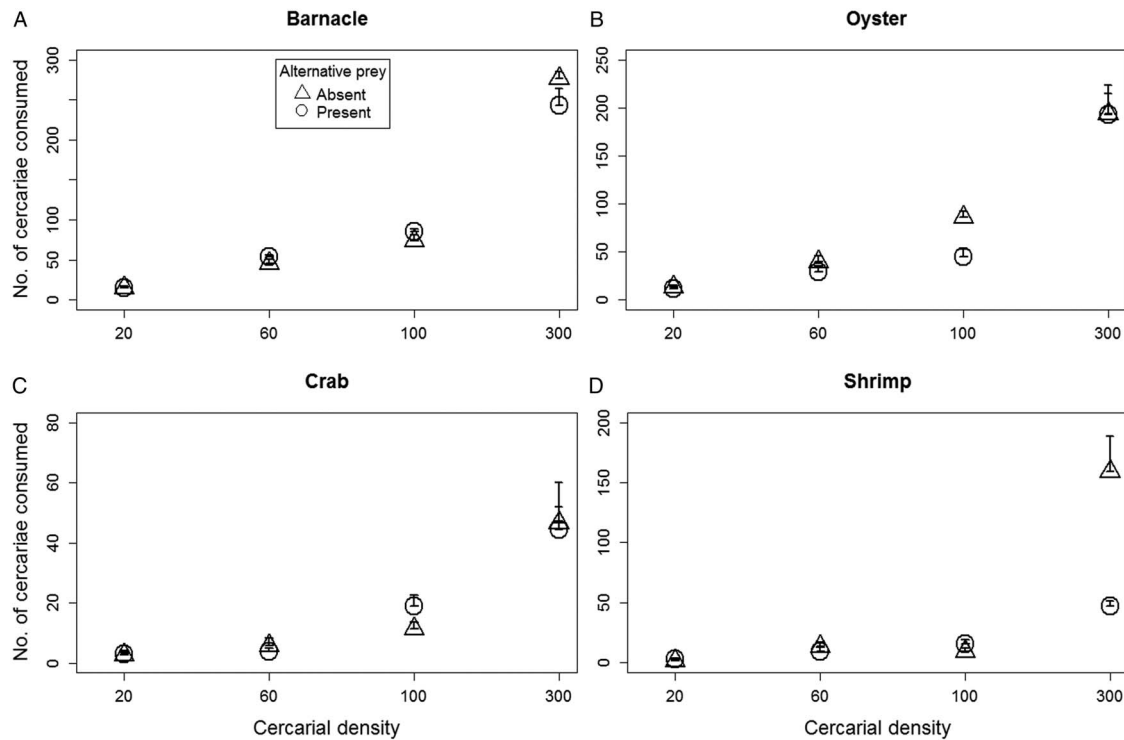


Fig. 1. Number of cercariae consumed by (A) barnacles; (B) oysters; (C) crabs; and (D) shrimps across a range of cercarial densities when an alternative food source was either absent or present. Note the different y-axes.

predation: crabs and shrimps *vs* passive filtration: barnacles and oysters) showed different patterns suggests that the responses are not universal or linked to specific feeding traits but rather species specific.

In barnacles and shrimps, the best fitting models included an interaction between cercarial density and presence/absence of alternative prey. This resulted from cercarial removal rates at low and intermediate cercarial densities being similar or higher at presence compared to absence of alternative prey, while at the highest cercarial density removal rates they were highest in absence of alternative prey. This was particularly the case for shrimps which showed an almost 5-fold increase in searching rate at the highest cercarial density when alternative prey was absent. In contrast, removal rates did not differ much between presence and absence of alternative prey at lower cercarial densities. This may indicate the phenomenon of prey switching (Murdock, 1969; Cornell, 1976) whereby a predator initially focuses on the most abundant or easily accessible prey type in its environment (in this case the alternative prey, i.e. the piece of fish or algae) and then switches to a new prey type as this becomes more abundant (in this case the parasites). However, whether such prey-switching really underlies the observed pattern in our experiments deserves further studies. Other work on trematodes from freshwater ecosystems also found more complex relationships between cercarial consumption and cercarial density, depending on both the identity of the predator (mosquitofish or

damsel nymphs) as well as of the parasite species (*Echinostoma trivolvis* or *R. ondatrae*; Orlofske *et al.* 2015). Together with our study, these results suggest that the effect of cercarial density on cercarial removal rates by predators actually depends on the particular parasite and predator species and may be further mediated by the presence or absence of alternative prey.

In the other two cercarial predators investigated in our experiment, oysters and crabs, neither cercarial density nor the presence/absence of alternative prey affected the rates with which they removed cercariae. Relative removal rates were similar over the range of cercarial densities administered within the two predator species and generally higher in oysters than in crabs (36 and 87% cercarial survival, respectively). Oysters have previously been reported as very effective predators of cercariae without serving as hosts to *H. elongata* (Thieltges *et al.* 2008a, 2009). They are very efficient filter feeders with high pumping rates (Ren *et al.* 2000; Ropert and Gouletquer, 2000) and bivalves, including oysters, have generally been shown to selectively consume particles of comparable size to cercariae of *H. elongata* from algae mixtures (Barillé *et al.* 1997; Cognie *et al.* 2003). Bivalves can generally show food density-dependent filtering activity (Gosling, 2003) but within the realistic food levels and parasite densities administered in our experiments this does not seem to occur as removal rates were not affected by cercarial density or presence/absence of alternative prey. Crabs in turn remove cercariae either by active predation or

Table 1. Results of model selection procedures. From the most complete (model code 1) to the least complete model (10) the degrees of freedom (D.F.) and model deviance are given for each model. Model 1 included the factors cercarial density (α), presence/absence of alternative prey (β), their interaction (γ), and a block effect (δ). Model deviances of the best fitting model for each species/experiment are shown in bold. The dispersion factor (ϕ) is given for the best fitting model only

Model code	Model	D.F.	Deviance			
			Barnacle	Oyster	Crab	Shrimp
1	$\alpha + \beta + \gamma + \delta$	55	864.9	1968.9	460.7	1067.8
2	$\alpha + \beta + \delta$	58	1049.1	2213.3	485.7	1627.0
3	$\alpha + \beta + \gamma$	56	1051.3	2019.6	500.3	1085.9
4	$\alpha + \beta$	59	1235.6	2267.4	523.0	1629.2
5	$\alpha + \delta$	59	1060.6	2325.3	485.9	1890.2
6	$\beta + \delta$	61	1111.2	2234.3	521.2	1768.9
7	δ	62	1125.8	2346.1	521.2	2289.8
8	α	60	1245.5	2378.4	523.1	1892.5
9	β	62	1299.6	2286.8	562.1	1779.3
10	1	63	1312.4	2396.2	562.9	2295.8
ϕ best fitting model			15.7	43.6	9.48	19.4

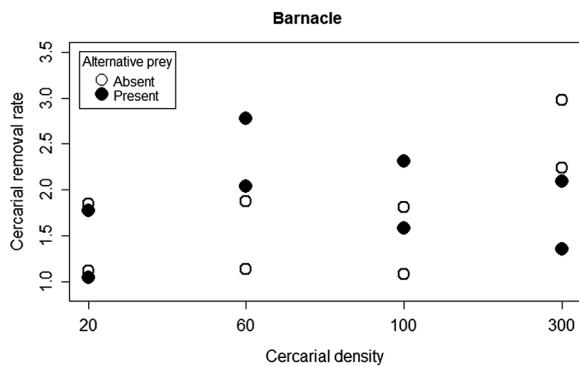


Fig. 2. Relative cercarial removal rates (per experimental run of 3 h) of barnacles across a range of cercarial densities and when an alternative food source was either absent or present. Plot based on model output and the factors contributing to the best fitting model (see Table 1).

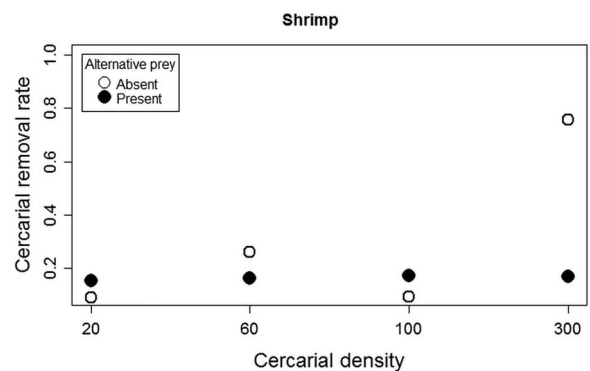


Fig. 3. Relative cercarial removal rates (per experimental run of 3 h) of shrimps in the presence of different cercarial densities and in the presence or absence of alternative prey. Plot based on model output and the factors contributing to the best fitting model (see Table 1).

by uptake via their gills (without becoming infected themselves; pers. observation). Given the lower removal rates in crabs, these mechanisms do not seem to be as effective as in oysters, leading to lower overall cercarial removal rates by crabs. However, in both cases removal rates did not differ in absence or presence of alternative prey, suggesting that parasite removal is often likely to be maintained even in complex communities with multiple prey species under more natural settings. Similar conclusions were made by two studies on predators of the cercariae of *R. ondatrae* in freshwater systems where dragonfly and damselfly larvae, cyclopoid copepods, hydroid polyps and mosquitofish continued to prey on cercariae when alternative prey was present (Schotthoefler *et al.* 2007; Orlofske *et al.* 2012). Our study expands on these findings with results from additional taxonomic groups (shrimps, crabs, barnacles, oysters) and mechanisms (e.g. filter feeding

bivalves) and suggests that many predator species will maintain their parasite removal capabilities under more realistic multiple prey situations.

In two of the predator species investigated in our experiments, crabs and barnacles, the best fitting model also included a (temporal) block effect. This resulted in significant differences in the cercarial removal rates of predators between the two runs of the experiments. While every effort was made to ensure that conditions remained constant in each experiment, conditions may still have been experienced differently by the predators. For instance, the batch of administered cercariae came from different groups of snails each day and may have been of different quality in terms of motility or life span. In addition, the behaviour of predators may have been affected by slight differences in ambient conditions between the different runs. However, the general patterns observed were consistent

between runs and by incorporating a temporal block factor into the statistical models we ensured that these temporal differences were taken into account when investigating the main effects.

In conclusion, the removal of cercariae by predators has been shown to be effective over a range of natural cercarial densities as well as in the presence of alternative prey for a number of predators typical of marine ecosystems. However, the response of removal rates of predators to different cercarial densities and presence/absence of alternative prey differed among the four predator species without an obvious link to specific predator traits. As changes in cercarial densities directly translate into changes in infection levels in down-stream hosts in this system (Liddell *et al.* 2017), the predator-specific responses observed suggest that cercarial predation effects on disease risks will depend more on the specific species composition of ambient communities than on biodiversity *per se*. These results mirror the recent discussion about the generality of dilution and related effects which suggest that the actual amplification or reduction of disease risk in a system may depend more on the specific species composition of ambient communities and not on biodiversity *per se* (Randolph and Dobson, 2012; Salkeld *et al.* 2013; Lafferty and Wood, 2013; Wood and Lafferty, 2013; Johnson *et al.* 2015). Our results suggest that predator specific responses to parasite density and presence/absence of alternative prey add a further layer of complexity to the general interference potential of predators on parasite transmission.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182017001056>.

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