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1 **Consumer and host body size effects on the removal of trematode cercariae by ambient**
2 **communities**

3

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10

11 Running title: Body size effects on trematode removal

12 **SUMMARY**

13 Parasite transmission can be altered via the removal of parasites by the ambient communities
14 in which parasite-host interactions take place. However, the mechanisms driving parasite
15 removal remain poorly understood. Using marine trematode cercariae as a model system we
16 investigated the effects of consumer and host body size on parasite removal rates. Lab
17 experiments revealed that consumer or host body size significantly affected cercarial removal
18 rates in crabs, oysters and cockles but not in shrimps. In general, cercarial removal rates
19 increased with consumer (crabs and oysters) and host (cockles) body size. For the filter
20 feeding oysters and cockles, the effects probably relate to their feeding activity which is
21 known to correlate with bivalve size. Low infection levels found in cockle hosts suggest that
22 parasite removal by hosts also leads to significant mortality of infective stages. The size
23 effects of crab and shrimp predators on cercarial removal rates were more complex and did
24 not show an expected size match-mismatch between predators and their cercarial prey,
25 suggesting that parasite removal rates in predators is species-specific. We conclude that, to
26 have a comprehensive understanding of parasite removal by ambient communities, more
27 research into the various mechanisms of cercarial removal is required.

28

29 **KEYWORDS**

30 Transmission interference, trematode, parasite-host interactions, predator-prey relations,
31 predator size.

32

33 **KEY FINDINGS**

- 34 • Experiments showed that cercarial removal rates by ambient communities can be
35 affected by host body size
- 36 • Cercarial removal rates of consumers (crabs and oysters) increased with body size
- 37 • Removal rates also increased with body size of hosts (cockles)
- 38 • Low infections of cockle hosts suggest significant mortality of infective transmission
39 stages in hosts
- 40 • Parasite prevalence and intensity was low in cockle hosts showing that host organisms
41 also remove a large proportion of parasites from the system.

42

43 **INTRODUCTION**

44 Parasite transmission between hosts can be significantly altered by the ambient communities
45 in which parasite-host interactions take place. The associated change in disease risk for hosts
46 in a given environment can result from indirect mechanisms, e.g. via competitors or predators
47 affecting host densities (Keesing *et al.* 2006; Johnson and Thieltges, 2010), but can also stem
48 from direct mechanisms in form of the removal of free-living infectious stages by other
49 organisms (Thieltges *et al.* 2008a; Johnson and Thieltges, 2010). In the latter case,
50 consumption of parasites by non-hosts living in the vicinity of target hosts has been identified
51 to lead to significant reduction in infectious stages which subsequently leads to lower
52 infection levels and disease risk for hosts (Johnson *et al.* 2010). For example, consumption of
53 cercarial stages of trematodes by various aquatic invertebrates and juvenile fish has repeatedly
54 shown to reduce cercarial density and lower infection levels in target hosts (e.g. Thieltges *et*
55 *al.* 2008b; Kaplan *et al.* 2009; Orlofske *et al.* 2012; Welsh *et al.* 2014). The removal of
56 cercariae and other infective stages of parasites is not limited to specific feeding types but
57 occurs in pursuit and ambush predators as well as in filter and deposit feeders (Thieltges *et al.*

58 2008a; Johnson *et al.* 2010). Similarly, parasite removal can also be caused by hosts, either in
59 form of conspecifics or by susceptible alternative host species. In both cases, additional hosts
60 can become infected by infectious stages and thereby remove infective stages from the local
61 infection pool and reduce average infection intensity of individual target hosts (Thieltges and
62 Reise, 2007; Orlofske *et al.* 2012; Magalhães *et al.* 2017). It is likely that both forms of
63 removal of infectious stages are very common in natural systems and thus understanding the
64 mechanisms driving the magnitude of parasite removal are important for our understanding of
65 the multiple effects of ambient communities on disease risk.

66

67 One of the factors likely to affect parasite removal rates is the body size of both consumers
68 and hosts of infective stages. The importance of consumer size for resource consumption is
69 well known from predator-prey interactions where it is strongly linked to both prey and
70 predator population dynamics (Caswell, 1989; Fryxell and Lunberg, 1998; Beaugrand *et al.*
71 2003). Predators usually target prey of specific sizes with larger predators generally
72 consuming larger prey and smaller predators consuming smaller prey (Brose *et al.* 2006;
73 Costa, 2009). The preference for specific prey size classes can result in a match-mismatch
74 between a predator and its prey if prey items are either too small or too large (e.g. Neill, 1975;
75 Nilsson and Bronmark, 2000; Strasser, 2002). Such a match-mismatch can also be expected to
76 occur in the case of predation upon infective stages of parasites. Indeed, a negative
77 relationship between predator body size and parasite removal has been observed in
78 invertebrate predators (damselfly nymphs and dragonfly larvae) and vertebrate (juvenile
79 versus adult mosquitofish) of trematode cercarial stages in freshwater systems (Orlofske *et al.*
80 2015; Catania *et al.* 2016). Further studies, also from different ecosystems, would be helpful
81 to evaluate the generality of the effects of predator body size on parasite removal. Secondary
82 to the size match-mismatch phenomenon, consumer size may also determine the per capita

83 removal rates of parasites, with larger consumers removing more infective stage than smaller
84 ones. This may be particularly true for some known parasite consumers such as filter feeders.
85 Filter feeder filtration rate, which is a factor of gill area and shell length, changes as filter
86 feeders grow (Møhlenberg and Riisgård 1978; Jones *et al.* 1992; Gosling, 2003).
87 Consequently, the number of parasites of a given size range removed (the clearance rate) can
88 potentially increase with an increase in the size of the filter feeder. Finally, similar to
89 consumers, the size of alternative hosts is likely to affect parasite removal rates as host body
90 size is generally positively correlated with parasite infection levels (Poulin, 2011). Hence,
91 larger hosts may remove more infective stages than smaller hosts. To date, neither the effects
92 of filter feeders or alternative hosts on parasite removal rates have been investigated.

93

94 In this study, we investigated the effects of consumer and host body size on parasite removal
95 using cercariae of a marine trematode as a model system. The echinostome trematode
96 *Himasthla elongata* (body length: 605–665 μm ; tail length: 535–605 μm ; Werding, 1969) is
97 found in marine intertidal systems around Europe and has a complex life cycle with birds
98 serving as definitive hosts and periwinkles (*Littorina littorea*) as first intermediate hosts (de
99 Montaudouin *et al.* 2009). The cercarial stages released from the periwinkles infect bivalves
100 such as the common cockle *Cerastoderma edule* as second intermediate host (Thieltges and
101 Reise, 2007; de Montaudouin *et al.* 2009). Several intertidal non-host organisms (organisms
102 which are not infected by *H. elongata*) have been shown to remove the cercariae of *H.*
103 *elongata* and subsequently reduce infection levels in bivalve target hosts (Thieltges *et al.*
104 2008b; Welsh *et al.* 2014). Among those are predatory brown shrimps *Crangon crangon* and
105 shore crabs *Carcinus maenas* and filter feeding Pacific oysters *Magallana gigas* (which do
106 not become infected by the parasite). We used mesocosm experiments to investigate the
107 removal rates of these consumers (crabs, shrimps, oysters) and hosts (cockles) depending on

108 their body size to identify potential size match-mismatches and to quantify whether larger
109 individuals remove more cercariae than smaller individuals. With this experimental approach
110 investigating several different parasite removal mechanisms we aim to advance our
111 understanding of the phenomenon of parasite removal and its effects on disease risk.

112

113 **MATERIALS AND METHODS**

114 *Source of consumers and hosts*

115 Shore crabs (*Carcinus maenas*), brown shrimps (*Crangon crangon*), common cockles
116 (*Cerastoderma edule*) and Pacific oysters (*Magallana gigas*; also commonly known as
117 *Crassostrea gigas*) of various sizes were collected from the intertidal area along the eastern
118 coast of the island of Texel (Wadden Sea, The Netherlands). Cockles (known to serve as
119 intermediate hosts for *Himasthla elongata*) were collected from an intertidal sand flat north of
120 Texel where *H. elongata* infections are known to be low (confirmed by dissecting 50 cockles:
121 3 infected individuals with <2 metacercariae per host). The other three species do not serve as
122 hosts for *H. elongata* (Thieltges *et al.* 2006) and were therefore not dissected. After
123 collection, all epibionts, if present, were gently removed and all four species were kept in
124 tanks containing filtered and aerated seawater within a climate-controlled room (15°C) at the
125 NIOZ Royal Netherlands Institute for Sea Research (Texel, The Netherlands).

126

127 *Source of cercariae*

128 Periwinkles (*Littorina littorea*) collected from the intertidal area around the island of Texel
129 were screened for the presence of *H. elongata* infections by checking for the release of
130 cercariae under increased temperature treatments (for details see Welsh *et al.* 2014). Infected
131 periwinkles were stored in flow through aquaria at 15°C and regularly fed sea lettuce (*Ulva*
132 *lactuca*). To obtain cercariae for the experiments, 150-200 infected snails were incubated in

133 1800 mL of filtered seawater at 27°C under light for 3 hours to encourage the release of
134 cercariae. From this concentrated cercariae solution, 50 *H. elongata* cercariae (40 in the crab
135 experiment) were pipetted under a stereo microscope into small 100 mL plastic containers
136 within 1.5 hours and then added to the experimental units (thus a maximum age of cercariae
137 of 4.5 hours).

138

139 *Experimental set up*

140 The effect of consumer and host body size on removal rates of cercariae was investigated in
141 laboratory experiments by determining removal rates of five size categories of each species
142 (Table 1). In addition, a sixth treatment without consumers or hosts served as a control to
143 account for potential losses of cercariae due other factors (knowing the number of added
144 cercariae was 40 or 50) and to test for the general presence of a cercarial reduction effect
145 (control vs. species addition treatments). The experiments were conducted in four separate
146 runs, with each run testing removal rates of a single species (one individual per replicate, 6
147 replicates per treatment level, Table 1). Each replicate consisted of a 2 l aquarium filled with
148 1500 mL of filtered seawater and randomly placed in a single climate-controlled room
149 (18.5°C ± 0.2°C).

150

151 All consumers and hosts were starved and kept in the experimental aquaria for 24 hours prior
152 to the experiments to allow for acclimation. After this acclimation period, 40 or 50 (for crab
153 treatments and all other species, respectively) cercariae were added to each replicate aquaria
154 and left undisturbed for 3 hours. This time period ensured full swimming ability of cercariae
155 for the whole experimental period, which is known to slowly decrease after about 8 hours
156 (Thieltges and Rick, 2006; Studer and Poulin, 2013). At termination, the test organisms were
157 quickly removed from the aquaria using long forceps and the water from the aquaria was

158 sieved using a 25 μ m sieve. The retained cercariae were backwashed into individual 100 mL
159 pots which contained 10 mL of 99% ethanol for fixation and 0.5 mL Rose Bengal for staining.
160 Cercariae were later enumerated under a light stereomicroscope. In addition, 24 hours after
161 the experiment ended all cockles were dissected under a light microscope and metacercariae
162 counted to determine infection intensity. This allowed for the determination of actual cercarial
163 removal from cercarial loss due to infections.

164

165 *Analyses*

166 The effect of presence/absence and of the size of cercarial consumers and hosts was analysed
167 using three binomial Generalized Linear Models (GLM) with log-links. Including a log-link
168 assumed a linear pure death process, i.e. all predatory incidences were considered to be
169 independent events (see Liddell *et al.* 2017 for further details).

170

171 The first model (1) included all factor levels for each consumer or host body size class, the
172 second model (2) included only two levels, the control versus consumer or host presence, and
173 the third model (3) only included a constant, thus assuming that the control and all size class
174 treatments show the same removal rate. Comparing model 1 and 2 allowed to test whether
175 consumer or host body size had a significant effect on the removal of cercariae. Comparing
176 models 2 and 3 allowed to test whether there was an overall effect of consumer or host
177 presence. Model comparisons were done using analysis of deviance. The difference in
178 deviance between two models (Δ Dev) was divided by the dispersion factor (ϕ) from the most
179 complete model and then compared to the delta degree of freedom χ^2 at 0.05. Calculations of
180 ϕ were derived by dividing the residual deviance for the most complex model by the degrees
181 of freedom. When two models significantly differed, this indicated that the most complex
182 model had the better fit. From the best fitting models, the clearance rate ($L h^{-1}$) of each

183 consumer or host was calculated by dividing the instantaneous cercarial removal rates
184 retrieved from the model outputs by the volume of the experimental units (2 L). This was
185 done in an effort to allow for comparisons with literature data on clearance rates.

186

187 All analyses were carried out using R (R Development Core Team, 2013) version 3.0.2 in R
188 Studio (version 0.98.1103; R Studio Team, 2014).

189

190 **RESULTS**

191 Consumer or host body size significantly affected cercarial removal in crabs, oysters and
192 cockles, but it did not affect removal by shrimps (Figure 1; Table 2). Similarly, while these
193 three species lead to a significant removal compared to the control, the presence of shrimps
194 had no significant effect on the number of remaining cercariae (Table 2). The removal of
195 cercariae by crabs showed an overall increase with an increase in crab size, i.e. the number of
196 cercariae remaining decreased with an increase in crab size class (Figure 1). As such, the
197 clearance rate of crabs increased with crab size (Table 3). A similar pattern was seen in the
198 filter feeding oysters and cockles (the latter also serving as host for the parasite). In both cases
199 the number of cercariae remaining decreased with an increase in shell length (Figure 1, Table
200 2), hence the clearance rates increased with an increase in oyster and cockle size (Table 3).

201

202 Although cockles are known to serve as intermediate host for *Himasthla elongata*, overall
203 infection levels were unexpectedly low. Prevalence varied between 16.7 and 66.7% among
204 the cockle size classes but infected cockles harboured, on average, only between 1 and 2.7
205 metacercarial stages (Table 4), suggesting that the observed cercarial loss in the experimental
206 units only marginally resulted from cercariae infecting the cockles. There was no observed
207 correlation between infection intensity or prevalence and cockle size.

208

209 **DISCUSSION**

210 Our series of experiments revealed that consumer and host body size significantly affected
211 cercarial removal in crabs, oysters and cockles but not in shrimps. In general, cercarial
212 removal rates increased with consumer or host body size.

213

214 Infection intensity observed within the cockle host species was extremely low across all sizes,
215 with no correlation occurring between size and infection intensity. This contradicts previous
216 findings which suggested that older, and thus larger, filter feeding hosts accumulate more
217 trematode metacercariae than younger and smaller individuals via their increased filtration
218 rate (Wegeberg et al. 1999). In cockle sizes of 0.6-1.4cm a 60% *H. elongate* infection
219 success was observed, which was significantly higher than the 16% success observed in
220 cockles <0.6cm (Wegeberg et al. 1999). In this study infection success was considerably
221 lower with a maximum of 5.4% success in the smallest size class (1.6cm). However, as the
222 size range did not cover cockles smaller than 1.6cm we are not able to directly compare
223 infection intensities. As the number of cercariae recovered at the end of the experiment
224 combined with the low number of recovered metacercariae from within cockle tissue did not
225 equate to the total number of cercariae added, we can assume that the cockle host removed
226 cercariae via filter feeding, just as observed in the non-host oysters. The cercarial loss from
227 the system caused by hosts may have consequences for energy flow (Thieltges et al. 2008).

228

229 In the two filter feeders, oysters and cockles, this increase in parasite removal rates with
230 oyster or cockle body size relates to the general feeding ecology of the species. Bivalves
231 constantly filter water via their gills and the filtration rate is a function of gill area which is
232 positively correlated with bivalve body size (Møhlenberg and Riisgård, 1978; Jones *et al.*

233 1992; Gosling, 2003). However, as the filter feeding mesh of the bivalves' gills is independent
234 of body size, prey size selection in bivalve filter feeders does not change as the organism
235 grows (Gosling, 2003). Hence, particles that are captured by the filter feeding mesh of the
236 gills will be filtered at an increasing rate with increasing body size. As cercarial stages of
237 trematodes fall within the size range of particles filtered by bivalves (Gosling, 2003), cercarial
238 removal can also be expected to increase with bivalve body size as observed in our
239 experiments. As the positive relationship between body size and filtration rates are universal
240 in bivalves and possibly also in other filter feeders, measures of filtration capacity such as
241 clearance rates can probably, as long as the size range of the particles captured overlaps with
242 the size of the respective infective stages of parasites, be used as a proxy for the parasite
243 removal capacity of any filter feeding organism. As filtration is often relatively unspecific
244 within the range of particles filtered, a large range of filter feeding organisms such as bivalves
245 may be able to remove infective stages of parasites and may thus play an important role in
246 altering parasite transmission in aquatic ecosystems (Burge *et al.* 2016).

247

248 Although both oysters and cockles significantly removed cercariae from the water, the
249 subsequent fate of the removed cercariae is likely to differ between oysters and cockles. In the
250 case of oysters, the uptake of cercariae of *Himasthla elongata* will not lead to infections as
251 Pacific oysters are not infected with metacercarial stages of the species (Krakau *et al.* 2006).
252 The cercarial removal capacity of oysters has previously been recognised and has been shown
253 to lead to reduced infection levels in the parasite's target hosts (Thieltges *et al.* 2008c).
254 However, when those studies were conducted the dependency of cercarial removal on oyster
255 body size was, and remained, unknown until now. In contrast to the oysters, common cockles
256 do serve as hosts to metacercarial stages of *H. elongata* (Thieltges *et al.* 2006; de
257 Montaudouin *et al.* 2009). Hence, in this case the uptake of cercarial stages by cockles via

258 their filtration can lead to infections. As filtration rates increase with body size, larger cockle
259 hosts will be exposed to larger numbers of infective stages and most likely have higher
260 infection levels. While there is some evidence for a positive relationship between cockle size
261 (or age) and metacercarial infection levels in the literature (de Montaudouin *et al.* 1998;
262 Jensen *et al.* 1999; Thieltges 2008), cercarial removal only lead to very low infections of
263 cockles in our experiment, with a mean intensity of 1-2.7 metacercariae and no relationship
264 with cockle size. This suggests that the uptake of cercariae by cockles does not necessarily
265 lead to infections but that a large number of cercariae may rather be lost in the course of the
266 filtration, possibly by immobilising cercariae on the cockles' gills and thereafter, being
267 potentially digested.

268

269 Like oysters and cockles, crabs also showed a positive relation between body size and
270 cercarial removal but this pattern differed from our expectation. We had assumed that a size
271 match–mismatch would occur in crabs, whereby the infective parasite stages would be too
272 large for smaller crabs and too small for larger crabs to remove. However, cercarial stages
273 were removed by all size classes of crab with larger crabs removing more cercariae than
274 smaller crabs. As the range in crab sizes used in our study not only covered the most common
275 sizes found in our study area but also included very small and very large crabs, it is not
276 expected that a size mismatch has been missed. The observed increase in cercarial removal
277 rates with crab size suggests that cercarial removal is possibly not a result of direct predation
278 by crabs (using their claws) but rather a different mechanism. Various crab species have been
279 shown to use their mouth parts to catch small particles, similar to filter feeding in bivalves
280 (Gerlach *et al.* 1976; Watts, 2014). In addition, small 10µm polystyrene microspheres have
281 been shown to be taken up by *C. maenas* crabs and retained by their gills which are normally
282 used only for oxygen uptake and not particle filtration (Watts, 2014). It is thus likely, that

283 cercarial removal in shore crabs is based on mechanisms similar to filter feeding in bivalves
284 and indeed we have observed cercariae stained with fluorescent dye in the digestive tract and
285 on the gills of shore crabs (pers. obs.). Such alternative mechanisms of cercarial removal may
286 explain the different findings in other aquatic predators where a negative relationship between
287 predator body size and parasite removal due to prey size mismatches has been observed (e.g.
288 damselfly nymphs, dragonfly larvae, mosquitofish; Orlofkse *et al.* 2015; Catania *et al.* 2016).
289 Our findings thus suggest that predator effects on cercarial removal rates may be more diverse
290 than only relating to direct predation and may also include indirect mechanisms such removal
291 via mouth parts or gills similar to the filter feeding in bivalves and other filter feeders.

292

293 In contrast to shore crabs, the second predator investigated, the brown shrimp, did not
294 significantly remove cercariae. This contradicts with previous studies which have reported
295 cercarial removal by brown shrimps (Welsh *et al.* 2014; Thieltges *et al.* 2008b). However,
296 these differences in findings are probably related to differences in the experimental designs
297 used among the studies. Welsh *et al.* (2014) used 6 shrimps with a length of 3 cm per replicate
298 and found a significant reduction in the number of cercariae by 93%. In contrast, our study
299 only used a single shrimp per replicate and we observed about 20% fewer cercariae in a
300 comparable size class (3.2-3.5 cm). Although cercarial removal was not statistically
301 significant in this study, the results from Welsh *et al.* (2014) suggest that higher densities of
302 shrimps would have probably led to higher removal rates. In a different previous study, brown
303 shrimps of 1.5-2.5cm length lead to a reduction in infection levels of cockle hosts by 78%
304 (Thieltges *et al.* 2008b). However, this study used 10 shrimps per replicate and the observed
305 effect was most likely not only due to cercarial removal by shrimps but also due to
306 interactions of shrimps and cockles leading to disturbances in cockle filtration and
307 subsequently to lower infection levels (Thieltges *et al.* 2008b). These comparisons show that

308 brown shrimps have the ability to remove cercariae but only at higher shrimp densities. The
309 absence of an effect of shrimp body size shown in this study may further suggest that cercarial
310 removal may be independent of body size in shrimps in general, again differing from the
311 expectation that there should be a size dependent match-mismatch as observed in other
312 cercarial predators (Orlofkse *et al.* 2015; Catania *et al.* 2016). Hence, the effect of predators
313 on cercarial removal may be less predictable than in filter feeders and probably depends
314 strongly on the mechanisms of cercarial removal in a respective predator.

315

316 In conclusion, our study shows that consumer and host body size can significantly affect
317 cercarial removal rates and that removal rates generally increased with the body size of
318 consumers (crabs and oysters) and hosts (cockles). In the case of filter feeders (oysters and
319 cockles), the observed effects probably directly relate to the filter feeding activity and suggest
320 that general measures of filtration capacities, such as clearance rates, may be used as proxies
321 of cercarial removal capabilities. In contrast, size effects on cercarial removal rates by
322 predators were more complex and did not show a consistent size match-mismatch, suggesting
323 cercarial removal rates depend on species specific mechanisms. It is suggested that other host
324 and non-host organisms be tested for body size effects on cercariae removal in order to
325 calculate the net effects of different size classes on cercarial abundances. It is also
326 recommended to test the combined effects of non-host organisms sizes with varying cercariae
327 sizes (i.e. different cercarial species). Our results indicate that more research into the various
328 mechanisms of cercarial removal is needed to arrive at a comprehensive understanding of the
329 mechanisms underlying parasite removal in communities.

330

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333

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337

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