

Habitat and transmission – effect of tidal level and upstream host density on metacercarial load in an intertidal bivalve

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SUMMARY

Transmission of parasites may be mediated by their habitat, consisting of abiotic and biotic components. I investigated the effect of 2 important habitat components in intertidal ecosystems, tidal level (abiotic) and density of upstream hosts (biotic), on the transmission of trematode cercariae to cockle (*Cerastoderma edule*) hosts. A field survey showed no general trend in metacercarial loads of cockles regarding tidal level but species-dependent reactions. Parasites originating from *Littorina littorea* (*Himasthla elongata*, *Renicola roscovita*) showed highest infection levels in the low intertidal while parasites originating from *Hydrobia ulvae* (*H. continua*, *H. interrupta*) showed highest infection levels in the mid-intertidal. This reflected the density of upstream hosts at both tidal levels and positive relationships between the density of upstream hosts and metacercarial load in cockles suggested the biotic habitat component to be the dominant factor in transmission. This was confirmed by a field experiment, manipulating tidal level and the density of infected upstream snail hosts. While tidal level had no significant effect on the number of metacercariae of *H. elongata* acquired by cockles, the effect of upstream host density was strong. In conclusion, although tidal level usually is a very important abiotic habitat component in intertidal ecosystems leading to conspicuous zonation patterns in free-living organisms, it seems of minor importance for trematode transmission. In contrast, the biotic component upstream host density is suggested to be the dominant predictor for trematode transmission to second intermediate hosts. Assessing the relative importance of abiotic and biotic habitat components in transmission is vital for the understanding of transmission processes in the field.

Key words: parasitism, trematodes, *Cerastoderma edule*, cockle, habitat components, second intermediate host.

INTRODUCTION

The transmission of parasites is mediated by a variety of abiotic and biotic factors affecting their free-living stages. Particularly well studied are trematodes which have complex life-cycles mostly involving 2 intermediate and a final host. Here, abiotic factors like temperature, toxicants, salinity, pH and oxygen concentration of the transmission medium mediate the transmission of the infective miracidial and cercarial stages (Pietroock and Marcogliese, 2002). Biotic factors have been less studied but may also be important (Morley and Lewis, 2004). The different abiotic and biotic factors mediating transmission are spatially structured in the field and together constitute the habitat of hosts as well as of the free-living stages of their parasites. Hence, habitat should play a pronounced role in parasite transmission and has recently become a focus of parasitological research (Sousa and Grosholz, 1990; Ostfeld *et al.* 2005).

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In intertidal ecosystems, probably the most important abiotic component of habitats is caused by the tides. They structure tidal flats into different tidal levels, representing distinct habitats for marine organisms and often causing conspicuous zonation patterns (Bertness, 1999). Dominant parasites in intertidal ecosystems are trematodes (Mouritsen and Poulin, 2002). Although a potentially important factor, surprisingly little is known on the effect of tidal level on trematode transmission. There seems to be a general trend of second intermediate hosts to be more infected in higher parts of the intertidal zone compared to the lower parts (Lim and Green, 1991; Poulin *et al.* 2000; Mouritsen *et al.* 2003). However, the opposite effect could also be expected since a higher immersion time should result in higher encounter rates of parasites with their hosts. It is also possible that parasite responses to tidal level are species dependent, resulting in different tidal level preferences. The few published studies lack spatial replication and controlled experiments making it difficult to evaluate the actual role of tidal level compared to other potentially confounding habitat components.

Probably the most important biotic component of a habitat in intertidal ecosystems concerning parasite transmission is the density of upstream hosts,

producing the infective propagules for the next developmental stage in the complex trematode life-cycles. This is suggested by correlative data indicating the distribution and abundance of final hosts to correlate with infection levels in first intermediate trematode hosts (Hechinger and Lafferty, 2005; Fredensborg *et al.* 2006). Similarly, the density of gastropod first intermediate hosts is positively correlated with trematode infection levels in second intermediate hosts (Grosholz, 1994; Thieltges and Reise, 2006a) but experimental approaches to verify these correlations independent of potentially confounding factors are lacking.

In this study, the effect of an abiotic (tidal level) and a biotic (density of upstream hosts) component of the habitat of an intertidal host, the cockle *Cerastoderma edule*, on the transmission of trematode cercariae infecting it as second intermediate host was investigated. The cockle is a common and abundant bivalve on European coasts and is often heavily infected by trematodes (de Montaudouin *et al.* 2000; Thieltges and Reise, 2006b). In the northern Wadden Sea (North Sea), 4 trematode species are dominant: *Himasthla elongata*, *H. continua*, *H. interrupta*, *Renicola roscovita* (Thieltges and Reise, 2006b). First intermediate hosts for these species are the gastropods *Littorina littorea* (*Himasthla elongata*, *Renicola roscovita*) and *Hydrobia ulvae* (*H. continua*, *H. interrupta*), final hosts are birds (Thieltges and Reise, 2006b). In a field survey, metacercarial loads of cockles between 2 tidal levels were compared at 5 sites, and the effect of tidal level and density of upstream hosts on infection levels in the second intermediate cockle host was investigated experimentally.

MATERIALS AND METHODS

Study area

Sampling and experiments took place on tidal flats around the island of Sylt in the northern Wadden Sea (North Sea) (Fig. 1). Mean (semidiurnal) tidal range is 2 m and salinity remains close to 30. Mean water temperature is 15 °C in summer and 4 °C in winter. The intertidal zone comprises approximately 1/3 of the area and sandy flats prevail over muddy sand and mud. Dominant biota in the intertidal zone are sandflats characterized by mounts of the polychaete *Arenicola marina*, *Zostera* spp. seagrass meadows and mixed beds of the epibenthic bivalves *Mytilus edulis* and *Crassostrea gigas*. In the intertidal zone, *Cerastoderma edule* is the dominant bivalve; dominant gastropods are *Hydrobia ulvae* and *Littorina littorea*. For further information on the area see Reise *et al.* (1989).

Field survey

Samples of cockles were taken at 5 sites in the intertidal zone that were considered to be representative

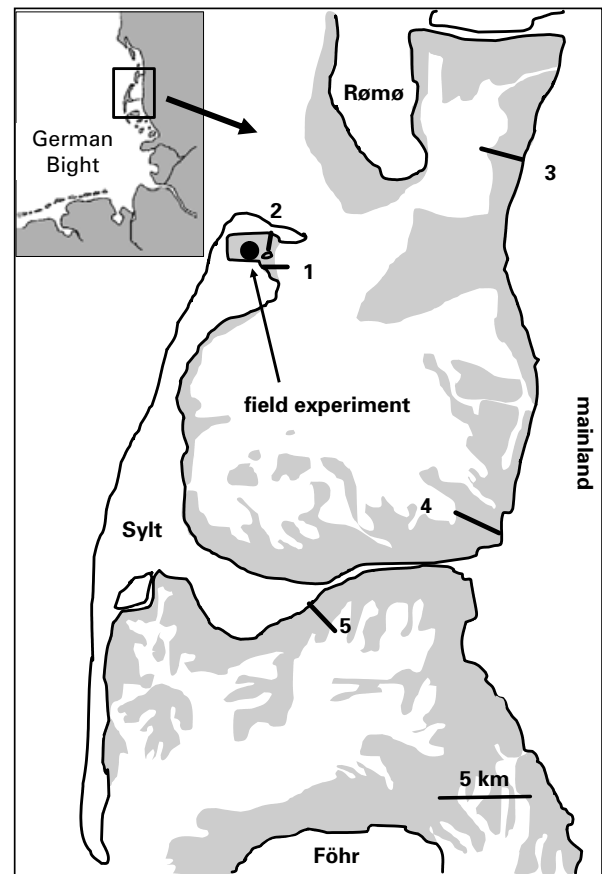


Fig. 1. Sampling sites (1–5) and experimental site (black dot) around Sylt island in the northern Wadden Sea (North Sea). Shaded areas indicate the intertidal zone.

for the study area (Fig. 1). At each site, 1 sample was taken in the mid-intertidal (+1.0 m mean low water level) and 1 in the low intertidal (+0.1 m) along transects rectangular to the coast line. The content of 4 randomly thrown 1 m²-frames (within 10 × 10 m; sieved with a 5 mm mesh) was taken to the lab where a random subsample of cockles with 2 winter rings from the same cohort (30–50 cockles, depending on availability of cockles with 2 winter rings) was taken for further analysis. The length of each cockle was measured with a calliper to the nearest 1/10 mm. The tissue of each cockle was removed, pressed between 2 glass slides and the number of metacercariae determined with a dissection microscope. Following this procedure, the tissue was carefully removed from the slides, dried at 75 °C for 3 days and flesh dry weight determined.

At each sampling station, the density of first intermediate gastropod hosts was estimated as follows. (i) *H. ulvae*: at each site 5 sediment cores (5 cm diameter) were randomly taken, sieved with a 500 µm mesh and the density of *H. ulvae* estimated in the lab under a dissection microscope (0: no snails present, 1: low density (1–10 individuals), 2: medium density (>10 and <50), 3: high density (>50)). (ii) *L. littorea*: density was estimated in the field within 6 randomly

Table 1. Results of two-factorial crossed ANOVA designs on the effect of tidal level and site on metacercarial load in cockles (no. of metacercariae/g cockle flesh dry weight) in the field survey (Significant results are in bold. $n = 30\text{--}50$ cockles.)

<i>H. elongata</i>					<i>R. roscovita</i>				
	df	MS	F	p		df	MS	F	p
tidal level	1	138.79	6719.82	<0.001	tidal level	1	0.36	1.98	0.16
site	4	9.83	476.15	<0.001	site	4	140.93	768.08	<0.001
tidal level \times site	4	7.93	383.81	<0.001	tidal level \times site	4	9.95	54.21	<0.001
error	462	0.02			error	462	0.18		
<i>H. continua</i>					<i>H. interrupta</i>				
	df	MS	F	p		df	MS	F	p
tidal level	1	104.07	460.13	<0.001	tidal level	1	56.49	449.24	<0.001
site	4	70.59	312.12	<0.001	site	4	44.67	355.16	<0.001
tidal level \times site	4	17.73	78.39	<0.001	tidal level \times site	4	19.11	151.98	<0.001
error	462	0.23			error	462	0.13		

tossed 1 m²-frames over an area of approx. 100 m² around the sampling site (0: no snails present, 1: low density (single individuals), 2: medium density (>1 and <10 individuals), 3: high density (>10)).

Field experiment

The field experiment was conducted on a tidal flat in the northern part of Sylt island (Fig. 1). Cages of polypropylene with a mesh size of 10 mm and 12 cm diameter and 10 cm height (above surface) were placed 20 cm into the sand in a completely randomized block design. One row of 4 blocks (50 m apart) was placed at mid-intertidal level (+1.10 m mean low water) and another row of four blocks at low intertidal level (+0.1 m). The daily difference in submergence between sites during a tidal cycle was 5–6 h. Blocks consisted of 3 cages arranged in a triangle with 10 m distance and included 1 of 3 treatments: (i) no infected snails, (ii) 2 infected snails and (iii) 5 infected snails. Infected snails were obtained by collecting *Littorina littorea* in the vicinity of the institute, placing them in bowls under light in the laboratory and subsequently screening the water for cercariae of *Himasthla elongata*. Infected snails were then separated and kept in large aerated aquaria until the start of the experiment. Each cage contained 5 cockles of 15–17 mm shell length, taken from a virtually non-infected population (prevalence <5%, mean intensity <2), and placed into the cages after removing all macrofauna. The experiment was conducted in August and terminated after 12 days when all cockles were investigated for *H. elongata* metacercariae as described above. In addition, shell length of each cockle was measured with a calliper to the nearest 1/10 mm.

Statistical analysis

To account for potential effects of cockle flesh weight on infection levels in the field survey, the numbers of metacercariae were divided by cockle dry flesh weight (g). Differences in metacercarial load of cockles in the field survey were compared using a two-factorial crossed ANOVA design with tidal level and site as fixed factors. Site was considered as fixed factor since sites were not randomly selected but chosen to be representative for the study area. Prior to the analysis the numbers of metacercariae were log+1-transformed to meet the assumptions of parametric tests. Relationships between no. of metacercariae and density of first intermediate snail hosts were investigated using linear regressions.

The field experiment was analysed using a two-factorial crossed ANOVA block design with tidal level and density of infected snails as fixed factors and the additional block factor nested in tidal level. Prior to the analysis the numbers of *H. elongata* were log+1-transformed to meet the assumptions of parametric tests. Arithmetic means of each cage were used for the analysis, giving 4 replicates per treatment. Differences in final cockle shell length were compared using a *t*-test after log-transformation of the data.

RESULTS

Field survey

There were marked differences in the numbers of metacercariae of the 4 dominant trematodes accumulated in cockles both among sites and between tidal levels with significant interactions between the 2 factors (Table 1). However, there was no clear overall trend in cockles generally having a higher or lower

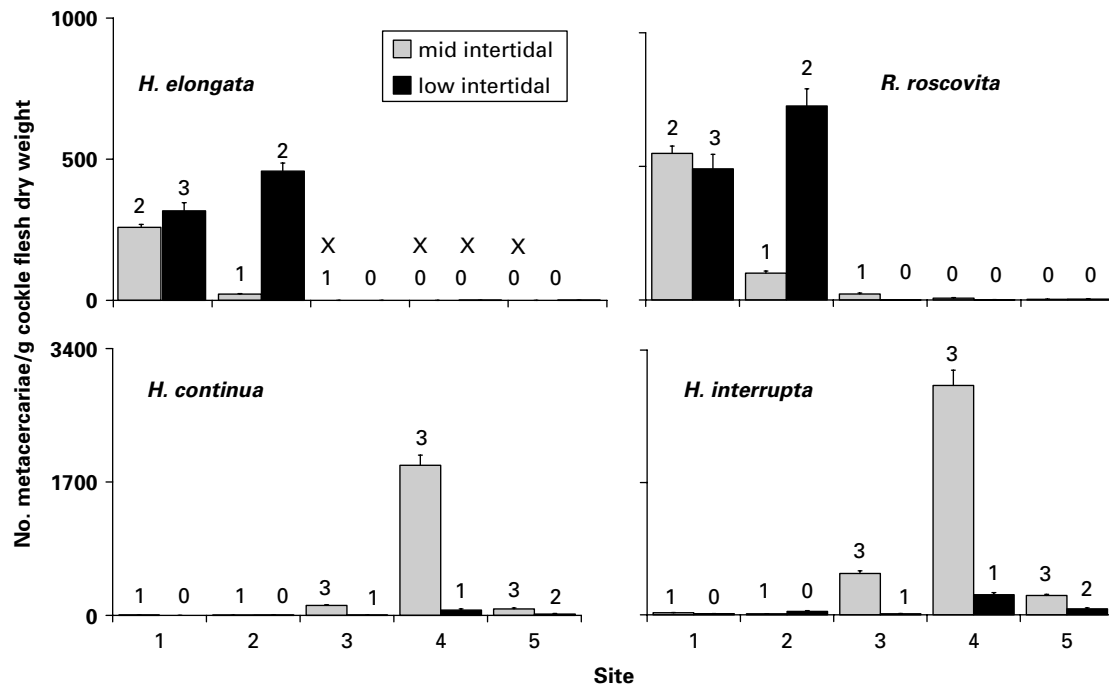


Fig. 2. Mean number of metacercariae/g cockle flesh dry weight (+s.e.) at the field survey sites (1–5) of the four dominant trematode species (*Himasthla elongata*, *H. continua*, *H. interrupta*, *Renicola roscovita*). Numbers above columns indicate density estimates for upstream hosts (see text). X denotes localities where a parasite species was absent. $n = 30\text{--}50$ cockles.

Table 2. Results of two-factorial crossed ANOVA design with an additional block factor on the effect of number of infected snails (first intermediate upstream hosts) and tidal level on metacercarial load of cockles (no. of metacercariae/cockle) in the field experiment

(Significant results are in bold. $n = 4$ replicates.)

	df	MS	F	p
infected snails	2	28.84	12.01	<0.01
tidal level	1	6.85	2.85	0.12
infected snails × tidal level	2	3.28	1.37	0.29
block (tidal level)	6	3.38	1.41	0.29
error	12	2.4		

metacercarial load at a certain tidal level (Fig. 2). Instead, there were species-dependent responses of parasites to tidal level. Parasites originating from *Littorina littorea* (*Himasthla elongata*, *Renicola roscovita*) showed highest infection levels in the low intertidal (especially at site 2) while parasites originating from *Hydrobia ulvae* (*H. continua*, *H. interrupta*) showed highest infection levels in the mid intertidal (especially at sites 3 and 4) (Fig. 2). This reflected the density of the upstream hosts with highest densities of *L. littorea* and *H. ulvae* in the low and mid intertidal, respectively (Fig. 2). Regression analyses over the total sample further indicated a positive correlation between the density of upstream hosts and metacercarial load in cockles (corrected

for cockle weight by dividing no. of metacercariae by cockle flesh dry weight in g): *Littorina littorea*: *H. elongata*: $r^2 = 0.73$, $n = 10$; *R. roscovita*: $r^2 = 0.76$, $n = 10$; *Hydrobia ulvae*: *H. continua*: $r^2 = 0.25$, $n = 10$; *H. interrupta*: $r^2 = 0.32$, $n = 10$; when an outlier (site 4) was removed in the last two relations they become stronger *H. continua*: $r^2 = 0.62$, $n = 9$; *H. interrupta*: $r^2 = 0.54$, $n = 9$.

Field experiment

Only the density of infected snails showed a significant effect on the number of metacercariae accumulated in the cockles during exposure while tidal level, block and interaction were not significant (Table 2). However, cockles from the mid-intertidal level harboured 2–3 times more metacercariae than the ones from the low intertidal (Fig. 3). The number of infected snails had a strong effect on metacercarial load in cockles with cockles in cages with 5 snails obtaining 4–6 times higher metacercarial loads than in cages with 2 snails. Cockles in cages without snails obtained a few metacercariae only in 3 cages at the low intertidal site (mean per cage 0.2–2.6 metacercariae/cockle). Only low growth occurred during the short duration of the experiment (12 days) resulting in a slightly higher mean cockle length at the low (16.7 ± 0.6 mm) compared to the mid (16.1 ± 0.6 mm) intertidal site. Due to the large number of replicates (120 ind. cockles) this difference was statistically significant (t -test, $P < 0.001$).

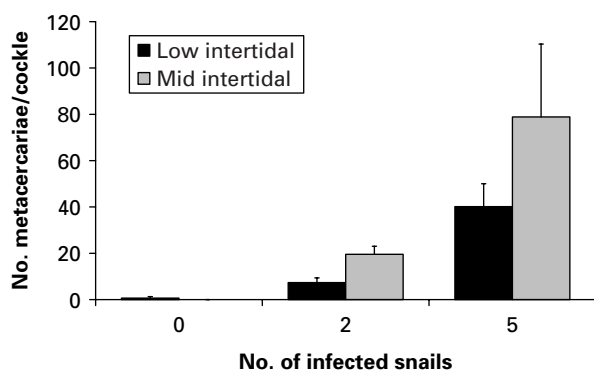


Fig. 3. Mean number of *Himasthla elongata* metacercariae/cockle (\pm S.E.) in the field experiment with number of infected snails (0, 2, 5) and tidal level (mid-intertidal, low intertidal) as fixed factors. $n=4$ replicates.

DISCUSSION

Both habitat components (tidal level and upstream host density) affected transmission and resulted in differential metacercarial loads in the cockle hosts. However, only the biotic component (upstream host density) showed significant effects and is suggested to be the dominant predictor for trematode transmission to second intermediate hosts.

In the field survey no general trend in differences in metacercarial loads of cockles between the 2 tidal levels were found for all 4 cockle species. Instead, responses to tidal level were species-dependent and statistically significant only in 3 species. Parasites originating from *Littorina littorea* (*Himasthla elongata*, *Renicola roscovita*) showed highest infection levels in the low intertidal while parasites originating from *Hydrobia ulvae* (*H. continua*, *H. interrupta*) showed highest infection levels in the mid-intertidal. This reflects the density of upstream hosts at the 2 tidal levels with *L. littorea* and *H. ulvae* occurring at higher densities at the low and mid-intertidal, respectively. The importance of upstream host density is further indicated by the positive relationships between upstream host density and metacercarial loads in cockles. Although the density of infected snails was not determined in the field survey, the total density of snails (infected and non-infected) may be used as a proxy for the pool of cercariae present from upstream hosts at a site as was done with bird final host densities in studies on parasites in first intermediate hosts (Hechinger and Lafferty, 2005; Fredensborg *et al.* 2006).

The difference in density of the 2 upstream hosts between tidal levels may indicate an indirect effect of tidal level on metacercarial loads in cockles by determining the distribution and abundance of upstream hosts. *H. ulvae* usually depends on sheltered areas on the local tidal flats and is hence rarely found in the lower intertidal where stronger currents prevail (Schanz *et al.* 2002). Hence, tidal level may

indirectly mediate infection levels in cockles in parasite species originating from *H. ulvae* via tidal level-dependent current strengths determining the abundance and distribution of the host. In contrast, *L. littorea* occurs at all tidal levels but it is most abundant on epibenthic structures such as shell debris fields and mussels beds where it finds attachment and grazing possibilities (Wilhelmsen and Reise, 1994). Suitable areas can occur over the whole tidal range and were only aggregated at the low intertidal in the field survey by chance. Hence, in parasites originating from *L. littorea* indirect effects of tidal levels on cockle infection levels should be negligible.

The general occurrence of *L. littorea* over a wide range of tidal levels may allow for direct effects of tidal level on infection levels in cockle hosts in the parasite species originating from this snail. However, the field survey data already indicate that this effect does not seem to be particularly strong since infection levels correlate well with upstream host density. The field experiment supports the suggestion of a weak direct effect of tidal level on cockle infection levels. Although there was a higher parasite load in cockles in the mid-intertidal compared to the low intertidal, this difference was not statistically significant. The higher metacercarial load of cockles at the mid intertidal site compared to the low intertidal site may result from (i) residual water at low tide being warmed up at sunny days thus facilitating the release and transmission success of cercariae, both correlated with temperature (Poulin, 2006) and/or (ii) infected snails heating up during low tide triggering the release of cercariae with the incoming tide. In contrast to tidal level, upstream host density had a clearly significant effect on metacercarial loads in cockles. This seems logical since the more snails present the more cercarial infective stages should be shed from the upstream hosts into the environment and thus the probability of the next (downstream) host to get infected should increase. Interestingly, this effect seems to occur on small spatial scales. Although the cages within a block were only 10 m apart, almost no infections occurred in the zero snail treatments indicating a very low dispersal range of cercariae (although the tailed *H. elongata* cercariae are active swimmers (de Montaudouin *et al.* 1998)) and/or high dilution effects. Hence, small-scale spatial heterogeneity (several meters) in the distribution of first intermediate hosts can already be expected to cause spatial heterogeneity in second intermediate hosts. On larger scales, other studies have also stressed the importance of upstream hosts in trematode transmission well in first (Hechinger and Lafferty, 2005; Fredensborg *et al.* 2006) as in second (Thieltges and Reise, 2006b) intermediate hosts, indicating this to be a universal phenomenon.

The strong effect of upstream host density on transmission may explain the inconsistency of the

experimental results with the field survey where *H. elongata* showed higher infection levels in the low than in the mid intertidal. In these cases, the density of the upstream host *L. littorea* was also higher at low compared to mid intertidal levels, indicating the importance of upstream hosts. Differences in upstream host densities among and within sampling sites are also likely to be responsible for the significant effects of site and the interaction terms in the ANOVA analysis.

Other studies on second intermediate hosts have uniformly reported a higher metacercarial load in bivalves at high compared to low intertidal sites (Lim and Green, 1991; Poulin *et al.* 2000; Mouritsen *et al.* 2003). However, due to a lack in spatial replication it remains unclear if this was a general phenomenon or just a local observation. The underlying mechanisms for the observed pattern in these studies were either unknown (Lim and Green, 1991; Poulin *et al.* 2000) or other factors like host density were overriding any potential effects of tidal level (Mouritsen *et al.* 2003). This study is, to my knowledge, the first to experimentally explore the importance of tidal level for trematode transmission in second intermediate hosts in the field. The results suggest only a weak direct effect of tidal level on transmission. Hence, although a very important habitat component of free-living intertidal organisms, tidal level seems to be of minor importance for the transmission of trematodes.

Tidal level and density of upstream hosts may of course not be the only habitat-constituting factors mediating trematode transmission on tidal flats. Other factors like host density (Mouritsen *et al.* 2003; Thieltges and Reise, 2006*a*) and host size (Poulin *et al.* 2000; Thieltges and Reise, 2006*b*) have been reported to affect transmission in second intermediate intertidal hosts. However, when compared to the effect of upstream hosts they also seem to be weaker in strength in the cockle-parasite system (Thieltges and Reise, 2006*a*). Infective propagules may also end up in alternative hosts or in dead end hosts that do not allow completion of the life-cycle (Krakau *et al.* 2006). Their effect in comparison to upstream hosts remains to be investigated but the positive relations between snail density and metacercarial load in cockles suggests that it may not be an overriding effect. There may of course also be indirect effects of habitat. The distribution and abundance of upstream as well as downstream hosts may be affected by various abiotic and biotic habitat components. In this case, tidal level may act indirectly as, for example, by determining the distribution of *H. ulvae* in this survey. Hence, trematode transmission in intertidal ecosystems should be mediated by habitat components in complex direct and indirect ways. This complex array of abiotic and biotic components of habitats, and their direct and indirect effects on transmission have to be

investigated when we want to arrive at an understanding of transmission processes in the field. The concept of habitat may help to integrate multiple abiotic and biotic components and to gain a more realistic picture of transmission processes compared to laboratory studies.

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