

Trematode infections reduce clearance rates and condition in blue mussels *Mytilus edulis*

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ABSTRACT: Suspension feeders are important players in coastal food webs: by filtering particles suspended in the water column and depositing faeces and pseudofaeces in sediments, they mediate the coupling of pelagic primary and benthic secondary production. However, the potential interference of parasite infections on suspension feeding is not well investigated. We experimentally determined the effect of infections with metacercariae of the common trematode *Renicola roscovita* on clearance rates and condition of blue mussels *Mytilus edulis*. We also investigated whether there were differences in the effects of infections between different size classes of mussels. Using controlled infections under lab conditions, our experiment showed that infections significantly reduced the clearance rates of mussels. This effect was less pronounced in small (42% reduction) than in large mussels (71%). In addition, infections significantly reduced mussel body mass index in large (23% reduction) and small (17%) mussels compared to uninfected mussels. These reductions most likely resulted from a combined effect of an interference of the parasites with the mussel's feeding apparatus (with the palps being the preferred infection site of the parasite) and of the energetic demands of the parasites (with metacercariae growing in size after initial infection). These negative effects on mussel filter feeding capacity indicate that parasites can alter a crucially important functional trait of marine suspension feeders.

KEY WORDS: Parasitism · trematodes · bivalve feeding

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INTRODUCTION

Benthic suspension feeders play a key role in coastal food webs by coupling pelagic primary and benthic secondary production and thus mediating the energy transfer through coastal ecosystems (Gili & Coma 1998). Bivalves constitute a particularly abundant part of the benthic suspension feeders (Gili & Coma 1998, Newell 2004). Given the substantial volumes of water that each individual can filter, suspension feeding bivalves can significantly alter the abundance and composition of seston and plankton (Dame 1993), and potentially act as a natural eutrophication control which can significantly improve marine water quality (Officer et al. 1982, Wilkinson et al. 1996, Lindahl et al. 2005, Shumway 2011). Addi-

tionally, through the production of faeces and pseudofaeces, bivalves can increase the localized sedimentation rate of suspended matter (Dame 2011) and thus change the benthic community composition (van der Zee et al. 2012).

The mechanisms underlying bivalve suspension feeding are particularly well understood for mussels *Mytilus* spp. (reviewed by Gosling 2003). In mussels, the mechanical steps of processing of food are similar to those of other filter feeders: interception of particles, transport, selection, and ingestion volume control (Beninger et al. 1995). Water enters a mussel via the inhalant siphon and is filtered by the gills. The captured particles are then transported to the labial palps; these complex structures (Beninger et al. 1995) are important for ingestion volume control and parti-

cle selection (Beninger & St-Jean 1997). Two measures are commonly used to quantify mussel feeding activity: (1) the filtration rate, defined as the pumping or volume flow rate and, (2) the clearance rate, defined as the volume of water cleared of suspended particles per unit of time. Clearance rate is identical to the filtration rate when all particles are retained (Riisgård 2001). Both measures are influenced by various environmental factors such as water temperature, particle concentration, quality and quantity of available food, salinity and ambient water flow rate (Gosling 2003). In addition, mussel size and weight are well known intrinsic factors determining filtration rates in mussels, and the interplay of intrinsic and environmental factors has long been studied (Newell 1970, Bayne 1998, Gosling 2003).

However, little is known about how parasitism affects mussel filtration rates. Mussels serve as hosts to a variety of different parasite taxa, including shell boring polychaetes, intestinal copepods, and tissue-inhabiting trematodes (Lauckner 1983). In particular, the latter can occur in vast numbers of up to several thousand individuals per mussel (Lauckner 1983, Svärdt & Thulin 1985, Zens 1999). One of the dominant trematode species in mussels along northern European shores is *Renicola roscovita* (Lauckner 1983). Like all trematodes it has a complex life cycle including several sequential hosts. Periwinkles *Littorina littorea* serve as first intermediate hosts from which free-living infective stages (cercariae) emerge that infect the second intermediate host (mussels). Here, the infective stages encyst as metacercariae

and await ingestion of their host by a definitive host (gulls and other birds feeding on mussels). In the bird, the adult parasites reproduce and shed eggs with the bird's faeces that infect new snails (Werdning 1969). In mussels, *R. roscovita* preferably settles in the palps (Fig. 1) but can also be found encysting in the gills, the digestive gland and other body tissues at higher infection levels (Lauckner 1983, Svärdh & Thulin 1985). Given the often high infection levels in mussels and, in particular, the preferred settling location within the mussel's palps, *R. roscovita* infections are very likely to affect mussel feeding. Indeed, infected mussels show slower growth than uninfected conspecifics in field experiments (Thieltges 2006). However, it is not known whether this is due to a reduction in particle processing ability, and if so, what the magnitude of such a reduction might be.

In this study, we experimentally determined the effects of infections with *R. roscovita* on mussel clearance rates and body condition by using controlled infections under laboratory conditions. We also investigated whether there were size-related differences in the effects of such infections.

MATERIALS AND METHODS

Parasite and host collection

Infected periwinkles *Littorina littorea* were used as cercariae donors to artificially create trematode infections. Several hundred snails were collected from

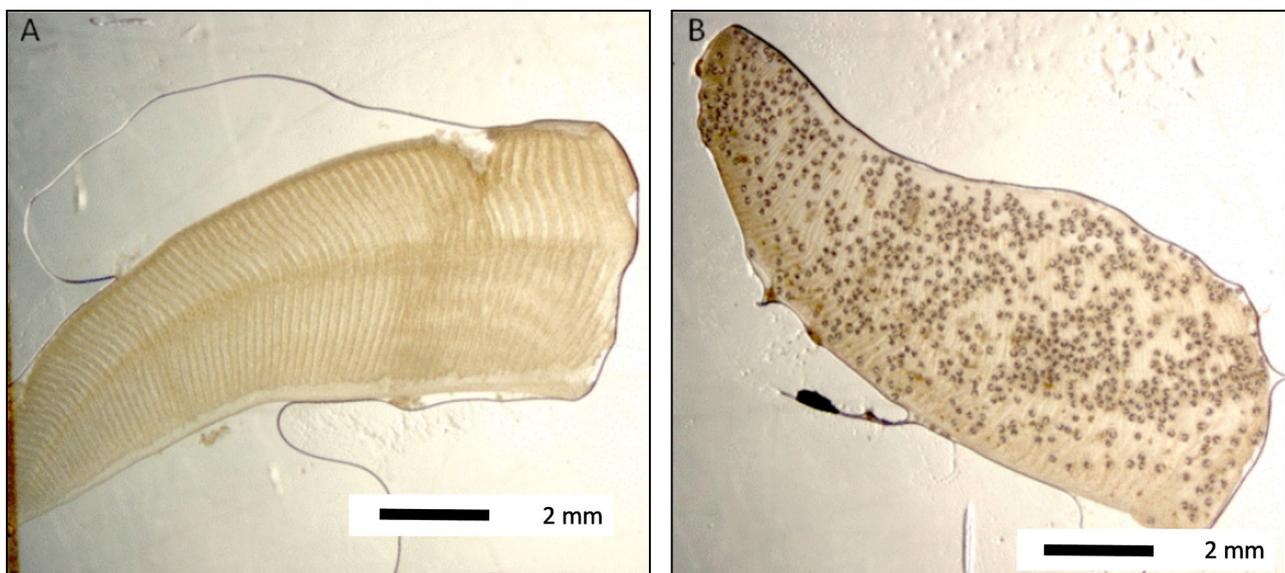


Fig. 1. (A) Uninfected palp of *Mytilus edulis* and, (B) palp heavily infected with metacercariae of the trematode *Renicola roscovita*

an intertidal mussel bed close to the island of Texel (Balgzand, Netherlands, 52.944° N, 4.903° E) in October 2010 and acclimated in aerated flow-through tanks (50 × 30 × 35 cm) with natural seawater. To reduce shedding of cercariae, snails were kept constantly in the dark at 15°C. After 2 d, snails were screened for infections by placing them in 6-well plates (filled with 10 to 15 ml of seawater) in an incubator at approx. 25°C for 3 to 5 h while exposing them to intense light to induce shedding of cercariae. Subsequently, the wells were checked for the presence of cercariae of *R. roscovita* under a dissection microscope. Infected and uninfected snails were kept separately in small aerated seawater tanks (13 × 21 × 13 cm) at a constant temperature of 15°C until the controlled infections of the mussels were performed. The water was exchanged daily and snails were fed ad lib with *Ulva lactuca*.

Mussel hosts *Mytilus edulis* were collected from beach groin constructions at the west coast of the island of Texel (Netherlands, 53.023° N, 4.707° E) in November 2010. Mussels from this locality were assumed to be free of *R. roscovita* infections because the first intermediate host, *L. littorea*, is not present due to high wave energy exposure (confirmed by screening 50 mussels for the presence of metacercariae). For the experiment, a total of 24 mussels were used, 12 from each of 2 shell length categories: small (19–22 mm) and large (46–49 mm). After carefully removing (a few) barnacles from their shells, all mussels were acclimated in an aerated flow-through seawater tank (50 × 30 × 35 cm), filled with natural seawater and kept in a climate chamber at a constant temperature of 15°C. During this time a diet of *Isochrysis galbana* was provided by adding 500 to 1000 ml of algal suspension (approx. 10⁶ cells ml⁻¹) once every day.

Experimental infections

To infect mussels with *R. roscovita*, the 24 experimental mussels were distributed equally in 6 small aerated plastic aquaria (13 × 21 × 13 cm). Each aquarium contained 2 small and 2 large mussels which were numbered individually with nail polish. Half of the aquaria also contained 15 snails (in each aquarium) infected with *R. roscovita* while the other half contained 15 uninfected snails. All 6 aquaria were placed in a climate chamber with a constant temperature of 20°C and constant light to initiate shedding of cercariae (Thieltges & Rick 2006). 100 ml (ca. 10⁶ cells ml⁻¹) of *I. galbana* were added to each aquarium daily.

After a total of 4 d, all periwinkles were removed and all mussels were kept together in the same flow-through tank (50 × 30 × 35 cm) in a climate chamber at a constant temperature of 15°C for 2 d to ensure encystation of metacercariae and acclimation to the same conditions as in the experiment. During this time mussels were fed with *I. galbana* by adding 500 to 1000 ml of algae (approx. 10⁶ cells ml⁻¹) once per day.

Clearance rate measurements and experimental design

We used the indirect clearance method to measure the clearance rate, the volume of water cleared of suspended particles per unit of time (Riisgård 2001). We determined the algae concentrations (*I. galbana*) of samples taken after certain time intervals by counting algal cells with a CASY Cell Counter and Analyser System (Schärfe System GmbH). The clearance rate could then be determined from the exponential decrease in algal concentration as a function of time (see 'Materials and methods: Data analysis'). In general, the proper measuring of filtration and clearance rates in mussels is known to be difficult (Riisgård 2001), since the rates strongly depend on many biotic and abiotic factors (reviewed by Gosling 2003). No laboratory method can be directly generalized to field conditions (Beninger 2009). The indirect clearance method we used is generally considered valid (Riisgård 2001), however, a notable shortcoming of this technique is the confounding influence of decreasing algal cell concentrations during the experiment. We mitigated this possible source of bias by replenishing the algal concentration (Riisgård 2001) during the incubation period.

The experimental setup consisted of 24 individual 2 l plastic containers filled with 1 l of seawater (UV-sterilized, 0.2 µm filtered) and provided with an airstone to maintain a constant air supply and uniform mixture of the water. In each container we placed 1 of the 24 experimental mussels at 15 min before measurements were started (pilot experiments had shown that mussels started with filtration at constant rates within this time). In addition to the 24 experimental containers, we set up 6 containers without mussels as controls to detect potential changes in algal concentration caused by factors other than the presence of mussels (e.g. intrinsic algal mortality). The experiment was performed at 15°C and under constant light. Prior to the experiment the cell concentration of our algal culture stock was measured to calculate the volume needed to produce a starting concentration (t_0) of

around 13 to 14×10^3 algal cells per ml in the tanks (following Riisgård & Randløv 1981). Immediately after adding the algae, a sample of 10 ml was taken out of each container and the algal concentration measured and set as the input concentration per respective tank. Subsequently, samples were taken every 15 min for 2 h. After each measurement, samples were cast back into the respective container to avoid a decrease of the water volume during the experiment. Algal cell counts of each sample were performed twice to minimize potential effects of measurement inaccuracy. If the counted cell number decreased below 1×10^3 cells ml^{-1} , or if it was expected to decrease below this value before the next measuring point, another dose of algal culture was added to bring the number back to the initial concentration (following Riisgård 2001). The experiment was conducted during 1 d in 3 sequential runs with 2 replicates of each treatment combination (and 2 control containers), resulting in a randomized (temporal) block design.

Dissection, condition index and palp size

Immediately after completing all the measurements, the mussels were frozen at -18°C until dissection. At this point, 7 d had passed since the induction of the infections (4 d infections, 2 d acclimation, 1 d experiment). To avoid any bias, identical procedures, particularly in tissue dry mass measurements, were used for both infected and uninfected mussels. Prior to dissection, mussel shell length (max. anterior-posterior dimension) was measured to the nearest 0.01 mm with a digital vernier calliper. Subsequently, the posterior adductor mussel was cut, the shell opened and the tissue (palps and gills carefully separated) placed between 2 thick glass slides (compressorium). Under a stereomicroscope, all metacercariae of *R. roscovita* were counted (or their absence verified in uninfected mussels) and their location noted (palps, gills, foot and rest of the body). Finally, the tissue was carefully transferred from the slides to crucibles and dried at 60°C for 3 d to determine dry mass and to calculate the condition index (CI) of each mussel ($\text{CI} = W/L^3$, whereby W = dry weight [mg], and L = length [mm] [Dare 1976]) following Riisgård (2001).

Data analysis

We used the mean of the 2 algal cell counts per sample for further analysis. Since the control containers showed no agglomeration or loss of algae during

the 2 h of measurements (see 'Results'), we did not correct cell counts for algae loss other than by filtration by the mussels. For each sampling interval, the clearance rate of each mussel was calculated from the algae counts in a container in between adding new algae. The decline in algal cells was estimated by calculating the slope of the regression line describing the ln-transformed cell numbers as a function of time. This offered a more reliable estimate than the formula applied by Riisgård (2001) because it allowed us to include more measurements than only the first and the last one. To determine the clearance rate in ml min^{-1} we multiplied the slope of each regression by -1000 (to account for the 1000 ml volume in which the mussels were kept). Depending on how often new algal culture was added, there were 1 to 4 clearance rate estimates per mussel achieved during the 2 h of measurements. If there was more than 1 measurement, the mean clearance rate was used for further analysis.

We tested for differences in mussel size (log-transformed) between infected and uninfected mussels within each size class using separate *t*-tests. To test for differences in clearance rates and condition between infected and uninfected and small and large mussels, we used a factorial ANOVA design with mussel size and infection status as fixed factors. In addition, we added a block factor to test for potential differences among the 3 separate runs. Clearance rates and condition indices were both log-transformed to meet the assumptions of parametric tests (confirmed by visual inspection of residual plots). Potential agglomeration or loss of algae during the 2 h of measurements in the control containers were tested for using linear regression (log algal concentration over time).

To compare relative infection levels between small and large mussels, we calculated palp surface area (P) as $P = 1.84 \times L^2$, whereby L = shell length, cm (Kiørboe & Møhlenberg 1981). The number of metacercariae mm^{-2} palp surface area was determined by dividing the total number of metacercariae found in a mussel by the calculated palp surface area. In addition, we calculated the number of metacercariae mm^{-2} mussel by dividing the total number of metacercariae found in a mussel by a measure for the surface area, its length (mm^{-2}).

RESULTS

The final dissections showed that all controlled infections were successful, with small and large

Table 1. Number of *Renicola roscovita* metacercariae (mean \pm SD) in different body tissues of infected small and large *Mytilus edulis*. Autopsies indicated that none of the uninfected mussels carried metacercariae

Mussel size	Labial palps	Gills	Foot	Other tissue	Total
Small	362 \pm 95	397 \pm 56	110 \pm 71	627 \pm 276	1559 \pm 242
Large	1247 \pm 470	647 \pm 341	218 \pm 89	920 \pm 526	3032 \pm 1247

Table 2. Shell length, palp surface area, number of metacercariae mm⁻² mussel length and number of metacercariae mm⁻² palp surface area (mean \pm SD) of small and large, infected and uninfected *Mytilus edulis*

	Shell length (mm)	Palp size (mm ²)	Metacercariae	
			(no. mm ⁻² mussel)	(no. mm ⁻² palp)
Small mussels				
Infected	21.28 \pm 1.19	8.35 \pm 0.92	3.53 \pm 0.63	44.44 \pm 9.99
Uninfected	21.03 \pm 0.55	8.14 \pm 0.43	–	–
Large mussels				
Infected	47.52 \pm 0.89	41.56 \pm 1.54	1.38 \pm 0.64	30.51 \pm 12.76
Uninfected	47.12 \pm 0.88	40.87 \pm 1.63	–	–

mussels acquiring, on average, approx. 1500 and 3000 metacercariae, respectively (Table 1). No other macroparasites were noticed in the experimental mussels. In small mussels, 48% of the metacercariae were encysted in the palps and gills; in large mussels this proportion was higher (62%, Table 1). Although larger mussels carried a higher total load of metacercariae, their relative parasite burden per mussel length was about 2.5 times lower than in small mussels (Table 2). The difference between parasite load per palp surface between large and small mussels was less pronounced, with small mussels carrying about 1.5 times higher numbers of metacercariae (Table 2).

While none of the small mussels needed a new addition of algae during the experiment, some of the uninfected large mussels needed up to 4 new additions of algal culture. In contrast, several of the infected large mussels did not need an extra dose. However all individual declines in algal concentration for each period were still linear when new algae were added, and algal concentrations were comparable in all trials. Furthermore, in trial experiments we conducted, *M. edulis* did not show differences in filtration rates when exposed to algal concentrations between 2 and 12 $\times 10^3$ *I. galbana* cells ml⁻¹. Hence, we consider our clearance rate experimental design to be robust. The control containers showed no agglomeration or loss of algae during the 2 h of measurements (no statistical effect of time on algal concentration in linear regressions, $p = 0.98$ [$<5\%$ difference between start and end value]). In general, there was no statistical difference in mussel size between infected and

non-infected mussels within each size class (t -tests; small mussels: $F_{1,10} = 0.17$, $p = 0.688$; large mussels: $F_{1,10} = 0.6$, $p = 0.469$) (Table 2), indicating that mussel size was not confounding the measurements.

The experiment revealed statistically significant effects of mussel size and infection status on mussel clearance rate and condition and a marginally significant interaction term (Table 3). There was no significant effect of the (temporal) block factor for clearance rates but the block factor was statistically significant when looking at mussel condition (Table 3). Mean clearance rates of infected mussels were only 58% (small mussels) and 29% (large mussels) of those observed in uninfected mussels (Fig. 2).

Table 3. Results of factorial analysis of variance (ANOVA) testing for differences in clearance rate and condition (both log₁₀ transformed) between uninfected and infected *Mytilus edulis* of 2 size classes (small and large)

Effect	df	MS	F	p
Clearance				
Size	1	1.357	35.503	<0.001
Infection	1	0.903	23.618	<0.001
Size \times Infection	1	0.144	3.761	0.068
Block	2	0.084	2.192	0.141
Error	18	0.038		
Condition				
Size	1	0.60	92.071	<0.001
Infection	1	0.06	8.605	0.009
Size \times Infection	1	0.001	0.214	0.649
Block	2	0.027	4.099	0.034
Error	18	0.007		

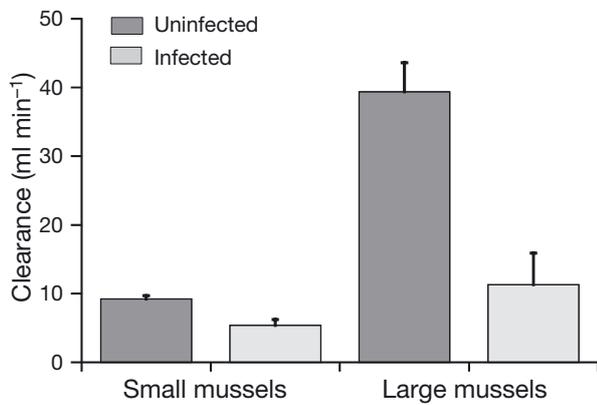


Fig. 2. Clearance rates (mean + SE) of small (19–22 mm) and large (46–49 mm) *Mytilus edulis* with and without metacercarial infections of *R. roscovita* in the laboratory filtration experiment (back-transformed from \log_{10}). $n = 6$ per treatment combination



Fig. 3. Condition index (mean + SE), calculated as dry weight \times shell length⁻³, of small (19–22 mm) and large (46–49 mm) *Mytilus edulis* with and without metacercarial infections of *R. roscovita* in the laboratory filtration experiment. $n = 6$ per treatment combination

In general, large mussels had higher clearance rates than small mussels (Fig. 2). Similarly, small mussels had a lower condition than large mussels (Fig. 3) and the condition index was lower in infected compared to uninfected mussels, both in small and in large mussels (77% and 83% of uninfected mussels, respectively; Fig. 3). Since mussel length was not statistically different between infected and uninfected mussels within the 2 size classes, the difference in condition resulted from higher body dry mass of uninfected mussels (small: 20.1 ± 3.3 mg; large: 430.2 ± 33.8 mg) acquired (or maintained) during the 7 d from starting the infections to the termination of the experiment (see above) compared to infected mussels (small: 14.5 ± 1.4 mg; large: 346.3 ± 25.9).

DISCUSSION

The experiment showed that infections with the trematode *Renicola roscovita* significantly reduced the clearance rates of mussels. This effect was less pronounced in small (42% reduction) than in large mussels (71%). In addition, during the short course of the experiment, infections also significantly reduced mussel condition in large (23% reduction) and small (17%) mussels.

These results corroborate our hypothesis that the preferred location of the parasites in the gills and palps interferes with the filtration in infected mussels. This interference most likely results from a mechanical disturbance through the encapsulated cysts in the gills and palps. However, infections in other tissues (e.g. digestive gland) may have added

to the reduced filtration activity by negatively affecting their hosts. Such negative effects may result from the fact that metacercariae of *R. roscovita* grow in size after the initial infection of their hosts (Lauckner 1983) and thus require increased energy resources from their hosts. However, the duration of our experiment may have been too short for such energy demands resulting from metacercarial growth to be relevant. An alternative source of parasite-induced energy drain may be the costs of host immune responses and tissue repair for the mussel hosts. The multiple penetrations of mussel tissue in the course of infection may lead to loss of hemolymph and increased production of hemocytes, which could be energetically costly. Should this actually be the main driver of parasite-induced mussel energy drain, the effect of infections may only be transitory and decreasing in the long run. However, data from a previous field experiment on the effects of *R. roscovita* infections on mussel growth during a longer observation time (10 wk) since initial infection (Thieltges 2006) suggest that negative effects of metacercarial infections also continue over longer time periods. More detailed experiments will be needed to disentangle the effect of (1) reduced food intake due to mechanical interference of the filtration process, (2) energy drain by energetic demands of metacercariae during their growth and, (3) potential energetic costs of immune responses and tissue repair on mussel filtration and condition.

Considering the time-frame of the infection period (7 d), the magnitude of the observed effects on mussel condition at first sight seemed unlikely. However, mussels are well known to increase in body mass

much faster than in shell length under laboratory conditions. For example, Riisgård et al. (2012) reported an increase in mussel dry weight from 22.9 to 72.0 mg within 17 d at a salinity of 30 and constant feeding, resulting in weight specific growth rate (μ) of 6.7% d⁻¹ ($\mu = \ln [W_t/W_o] t^{-1} \times 100$; with W_o and W_t being the initial and final body dry weight, respectively; Riisgård et al. [2012]). Unfortunately, we do not have initial body tissue dry weights for a similar calculation of μ . However, using the same formula, the difference in body weight between infected and uninfected mussels in our experiments amounts to a difference of 4.7% d⁻¹ in small and 3.1% d⁻¹ in large mussels; thus the observed changes in body condition within such a short time are well within the range reported in the literature. However, whether the difference in body weight resulted from a reduced growth of infected compared to uninfected mussels or from a loss of weight in infected versus uninfected mussels cannot be inferred from our experiment. The combined effect of interference with the mussel's feeding apparatus, and direct or indirect energetic demands imposed by the infections may also explain the observed reduction in shell growth of infected mussels reported from an earlier field experiment (Thieltges 2006); this indicates that *R. roscovita* infections translate into significant reductions of host filtration, condition and growth. Reduced condition of infected hosts has also been observed in other bivalve-trematode systems, e.g. in the brown mussel *Perna perna* infected with metacercariae of the genus *Proctoeces* (Calvo-Ugarteburu & McQuaid 1998). By contrast, Montaudouin et al. (2012) did not find an effect of infections with *Himastla interrupta* on cockle *Cerastoderma edule* condition. Thus, how universal such negative effects of metacercarial infections on bivalve condition are, and the underlying mechanisms, remain to be determined.

Since mussels are an important component of the suspension feeding guild in many coastal ecosystems, and considering their role in benthic-pelagic coupling (Gili & Coma 1998, Dame 2011), the observed effects of infection may ultimately influence energy transfer in coastal ecosystems. Such ecosystem-wide effects will depend on the actual infection levels in the field since the effects of metacercarial infections are considered to be density-dependent, i.e. the impact on the host increases with infection intensity (Fredensborg et al. 2004, Thieltges 2006). The laboratory infection rates with *R. roscovita* in our experiments are well within the range of infection levels observed in European coastal waters, where infection levels of up to 3000 to almost 6000 metacercariae per mussel (de-

pending on location) have been recorded (Svårdh & Thulin 1985, Zens 1999, Buck et al. 2005). However, the mean infection levels on many natural mussel beds are often lower and future studies will be needed to estimate the overall effect of infections on mussel filtration capacity and effects on energy flow in coastal ecosystems. Such calculations will also need to integrate the effects of other parasites on mussel filtration. For example, the parasitic copepod *Mytilicola intestinalis* also reduces the filtration capacity of mussels (Meyer & Mann 1950). However, in this case the underlying mechanism is not a direct interference with the filtration apparatus (the copepods inhabit the mussels' intestines) but most likely an indirect effect resulting from negative effects on mussel condition. Apart from effects on total filtration capacity, parasites may also interfere with the sorting capability of their hosts, in particular when they inhabit the palps, which are particle sorting organs (Beninger & St-Jean 1997). This limitation in sorting capacity will reduce quality and/or quantity of the ingested food, thus potentially affecting mussel condition, growth, and energy balance which, by extension, could possibly feed back into the system's dynamics.

In conclusion, our experiment showed that infections with the trematode *R. roscovita* significantly reduced the clearance rates of mussels, with subsequently negative consequences on individual condition. This suggests that parasites may also affect energy transfers in coastal systems via lowering molluscan secondary production. Our study shows that parasites can affect important traits in their hosts and suggest that further studies will be valuable to evaluate the overall direct and indirect effects of parasites in coastal ecosystems.

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Submitted: March 24, 2014; Accepted: February 23, 2015
Proofs received from author(s): May 21, 2015