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Journal of Sea Research 54 (2005) 176–184

JOURNAL OF  
**SEA** RESEARCH

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# Surface activity of *Corophium volutator*: A role for parasites?

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Received 22 September 2004; received in revised form 5 April 2005; accepted 5 April 2005

Available online 8 June 2005

## Abstract

In soft-bottom intertidal habitats, the normally infaunal amphipod *Corophium volutator* is often found active on the sediment surface during low tide, exposed to desiccation and shorebird predation. Here we examine whether such risky behaviour is related to parasite infections. Surface-active and buried *C. volutator* were collected during a low tide period in the Danish Wadden Sea, and the infection patterns of the two groups were described in relation to sex and size. Surface-active males and females were more heavily infested by microphallid trematodes (four species) than buried specimens of the same sex and size class. Although the density of surfaced amphipods decreased as a function of exposure time, the mean parasite load of those that remained on the surface increased. A narrow size-specific parasite intensity threshold above which the amphipods were always surface active did not exist: heavily infected individuals were also found buried in the substrate. Although likely to be beneficial to the parasites, this suggests that the behavioural alteration is a side-effect of the infections rather than a consequence of direct parasitic manipulation. Besides the presumed mortality associated with the parasite-related surface activity in a range of size-classes, the intensity-size frequency distribution indicated that larger and hence heavily infected hosts are removed from the population. Together it demonstrates that microphallid trematodes impact the population dynamics of *C. volutator*.

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**Keywords:** *Corophium volutator*; Field observations; Microphallidae; Surface behaviour; Trematodes

## 1. Introduction

Biota on intertidal mudflats is typically exposed to considerable fluctuations in environmental conditions during the tidal cycle. Burrowing and tidal migration are strategies used by animals to avoid unfavourable

conditions, but some individuals seem to exhibit risky behaviour by remaining on the sediment surface under such conditions. So, specimens of the infaunal amphipod *Corophium volutator* are frequently found crawling on the sediment surface of tidal flats at low tide (Watkin, 1941; Meadows and Reid, 1966; Fish and Mills, 1979), exposed to desiccation and an increased risk of predation by shorebirds (Hicklin and Smith, 1984; Peer et al., 1986; Boates and Smith, 1989; Matthews et al., 1992). The amphipods' reproductive

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behaviour could be one explanation for this, because males typically crawl on the surface searching for burrows inhabited by receptive females (Watkin, 1941; Meadows and Reid, 1966; Fish and Mills, 1979). Alternatively, surfacing specimens could be controlled by parasites that thereby enhance the probability of infecting their shorebird final host through trophic transmission (McCurdy et al., 1999a). Similarly, surfacing behaviour of bivalves has often been explained by the presence of parasites interfering with their ability to burrow (Lauckner, 1983; Bowers et al., 1996; Thomas and Poulin, 1998; Jensen et al., 1999; Mouritsen, 2002).

In the present study, we assess the role of digenetic trematodes in causing surface activity of *C. volutator*. These parasites represent a ubiquitous element of littoral faunas and are widespread and abundant in populations of *C. volutator* (Lauckner, 1987a). In the Danish Wadden Sea, the mud snail *Hydrobia ulvae* serves as first intermediate host for a wide range of microphallid trematodes, and *C. volutator* is used as second intermediate host in which the parasite larvae encyst as metacercariae. Various shorebirds serve as final hosts reached by trophic transmission. The shorebirds occurring in the Danish Wadden Sea are mostly spring and autumn migrants (Meltofte et al., 1994), which limits the temporal overlap between parasites and their final hosts. Such circumstances may favour the development of parasitic manipulation of host behaviour, such as increased surface activity, which enhances the probability of parasites being transmitted (Dobson, 1988; Poulin, 1994). Indeed, several parasites with complex life cycles are known to control intermediate host behaviour to facilitate consumption by potential final hosts (see reviews by Bush et al., 2001 and Moore, 2002). In accordance, studies by McCurdy et al. (1999b, 2000) indicate that male and female *C. volutator* harbouring infective stages of the trematode *Gynaecotyla adunca* spend more time crawling on the surface than uninfected individuals, and Mouritsen and Jensen (1997) have shown a similar pattern in *C. volutator* exposed to microphallid trematodes in the laboratory.

In this study, surface-active and burrowed *C. volutator* on a Danish Wadden Sea mud flat were compared with respect to sex, size, prevalence and infection intensity of microphallid trematodes to test the hypothesis that individuals crawling on the sedi-

ment surface on ebbing tide are more heavily infected than burrowed individuals. The *C. volutator* population from our study site hosts at least four species of microphallid trematodes: *Microphallus claviformis* (Brandes, 1888), *Maritrema subdolum*, Microphallidae sp. no. 15 (Deblock, 1980) and an unknown *Levinseniella* species.

## 2. Materials and methods

The study was carried out on an intertidal *Corophium* bed (Mouritsen et al., 1997) in the Danish Wadden Sea near Ribe Kammersluse (55°21'N, 8°39'E) on 25 September 2000. The density of adult *Corophium volutator* (>4 mm) on the experimental plot was 13 000 individuals m<sup>-2</sup> in September (Fredensborg, 2001). Within a 20 × 20 m area located 100 m seaward from the high-water mark, the number of surface-active specimens of *C. volutator* were counted in ten 1-m<sup>2</sup> plots, and subsequently individually collected with tweezers, during four 40-min periods separated by 20 min and starting when the water had receded from the investigation area (i.e. 30–70, 90–130, 150–190 and 210–250 min after high tide). During each sampling event, it was ensured that counts and collections were carried out in previously undisturbed parts of the investigation area. To compare the infection characteristics of surface-active and buried amphipods, thirty 50-cm<sup>2</sup> core-samples were collected between 180–270 min after high tide, and sieved through a 500 µm screen. Adult individuals were picked at random from the benthic samples. To eliminate predator-interference, waders were actively kept out of the area during the entire sampling period by means of gestures and yells.

The collected animals were preserved in neutralised 4% formaldehyde and afterwards stored in 80% ethanol. In the laboratory, the length of each individual was measured from rostrum to telson, and the amphipods were sexed. All adults (>4 mm in body length) were subsequently dissected and examined for the presence of microphallid metacercariae using a microscope (100×). Maximum and minimum diameter of each encysted parasite was measured to the nearest 10 µm. The parasites were identified according to Deblock (1980) and Lauckner (1987b). Ovoid

Table 1  
Sample size, mean body length (mm) ( $\pm$  S.D.), prevalence and mean abundance ( $\pm$  S.E.) of *M. claviformis*, *M. subdolum* and Microphallidae sp. no. 15, pre-infective metacercariae, and an unknown *Levinseniella* species in male and female *Corophium volutator* sampled either on the sediment surface (210–250 min after high tide) or burrowed in the substrate

n	Size	Sum of all metacercaria		<i>M. claviformis</i>		<i>M. subdolum</i> and Microphallidae sp. no. 15		Pre-infective metacercariae		Unknown <i>Levinseniella</i> species	
		Prevalence	Abundance	Prevalence	Abundance	Prevalence	Abundance	Prevalence	Abundance	Prevalence	Abundance
<b>Surface</b>											
Males	24	57.9 $\pm$ 3.53	100	12.5 $\pm$ 1.53	6.71 $\pm$ 1.02	66	1.58 $\pm$ 0.35	79	3.33 $\pm$ 0.63	45	0.83 $\pm$ 0.25
Females	52	78.4 $\pm$ 5.92	100	22.2 $\pm$ 2.52	15.8 $\pm$ 2.32	96	3.19 $\pm$ 0.33	81	1.83 $\pm$ 0.27	67	1.44 $\pm$ 0.20
Total	76	72.0 $\pm$ 10.9	100	19.1 $\pm$ 1.86	12.9 $\pm$ 1.69	87	2.68 $\pm$ 0.27	80	2.30 $\pm$ 0.28	60	1.25 $\pm$ 0.16
<b>Sediment</b>											
Males	36	59.8 $\pm$ 5.06	91	3.47 $\pm$ 0.65	1.92 $\pm$ 0.38	41	0.50 $\pm$ 0.11	44	0.86 $\pm$ 0.29	11	0.19 $\pm$ 0.10
Females	66	78.2 $\pm$ 7.71	100	16.8 $\pm$ 1.58	12.2 $\pm$ 1.51	82	2.11 $\pm$ 0.21	64	1.38 $\pm$ 0.20	62	1.09 $\pm$ 0.13
Total	102	71.7 $\pm$ 11.9	97	12.1 $\pm$ 1.22	8.56 $\pm$ 1.10	68	1.54 $\pm$ 0.16	57	1.20 $\pm$ 0.17	43	0.77 $\pm$ 0.10

cysts with a diameter between 160 and 210  $\mu$ m were considered metacercariae of *Microphallus claviformis*. Spherical cysts with a diameter between 160 and 210  $\mu$ m were considered metacercariae of *Martremia subdolum* or Microphallidae sp. no. 15. Cysts larger than 220  $\mu$ m in diameter were considered to be metacercariae of *Levinseniella* sp., and cysts with a maximum diameter of 150  $\mu$ m and no or a thin outer layer were, in addition to unencysted mesocercariae, classified as pre-infective metacercariae.

Following Margolis et al. (1982), we calculated parasite prevalence (proportion of infected individuals) and mean parasite abundance (mean parasite load of infected plus uninfected individuals) for each of the five samples of amphipods.

Both parametric and non-parametric tests were used to analyse the data. All tests were two-tailed using the 5% level of significance. All analyses were conducted using the statistical package SPSS for Windows (release 10.0).

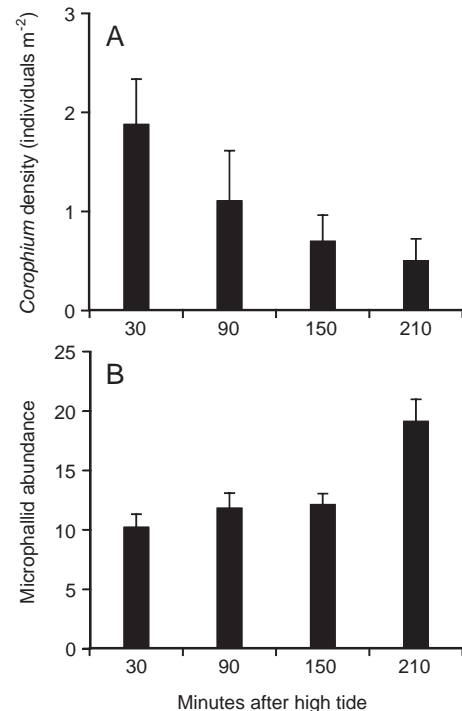


Fig. 1. (A) Mean density (ind m<sup>-2</sup>) ( $\pm$  S.E.) of *Corophium volutator* and (B) mean abundance ( $\pm$  S.E.) of microphallid infections in *C. volutator* collected 30–70, 90–130, 150–180 and 210–250 min after high tide.

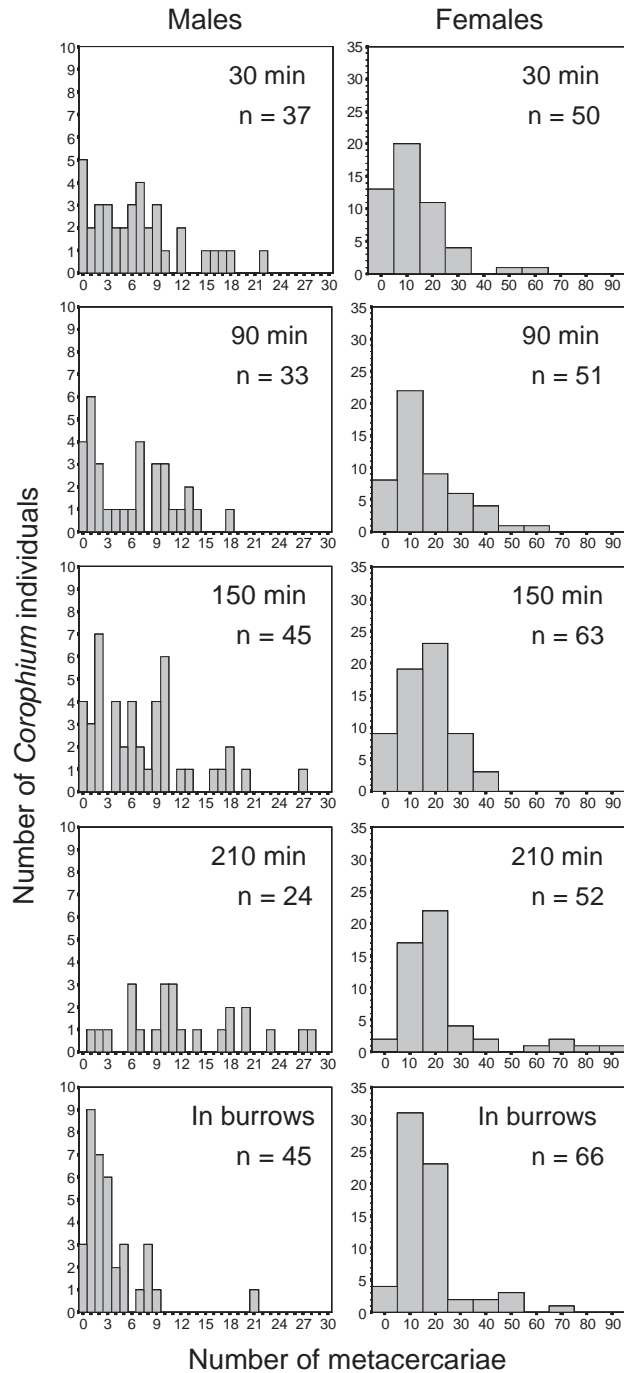


Fig. 2. Observed frequency distributions of the number of metacercariae in males (to the left) and females (to the right) *Corophium volutator* collected (1): four times after high tide (indicated by minutes after high tide) from the sediment surface and (2): once from burrows in the sediment (in burrows).

### 3. Results

*Microphallus claviformis* was the most abundant parasite in both surface-active and burrowed *Corophium volutator* specimens of either sex (Table 1). It was present in all surface-active individuals and in 90% of the burrowed ones. The other microphallids (*Maritrema subdolum* + Microphallidae sp. no. 15, unidentified pre-infective metacercariae and *Levinseniella* sp.) contributed with about one third of the total number of metacercariae and were generally found in more than half of the population.

The density of surface-active *C. volutator* was negatively correlated with time (Fig. 1A, Spearman's  $\rho = -0.40$ ,  $n = 40$ ,  $p < 0.05$ ), whereas the mean abundance of microphallid metacercariae in the surface-active specimens increased with time (Fig. 1B, Spearman's  $\rho = 0.27$ ,  $n = 355$ ,  $p < 0.05$ ). The frequency distributions of infections in males and females following high tide show that the number of individuals with fewer than 10 metacercariae per individual tends to decline with time (Fig. 2), which may explain the increasing parasite abundance among remaining surfaced individuals. The overall parasite prevalence was 96% and it did not differ significantly between the four samples of surfaced and the sample of burrowed amphipods (Pearson,  $\chi^2_4 = 6.17$ , ns). However, both surfaced male and female *C. volutator* were more heavily infected than burrowed specimens of either sex (Mann-Whitney test: males  $z = -5.018$ ,  $p < 0.001$ ; females  $z = -2.138$ ,  $p < 0.05$ ; Fig. 2). This is

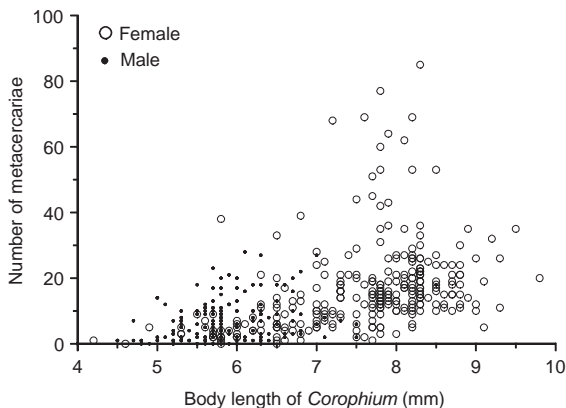


Fig. 3. Number of microphallid metacercariae in males (black dots) and females (white circles) of *Corophium volutator* as a function of body length. All samples combined.

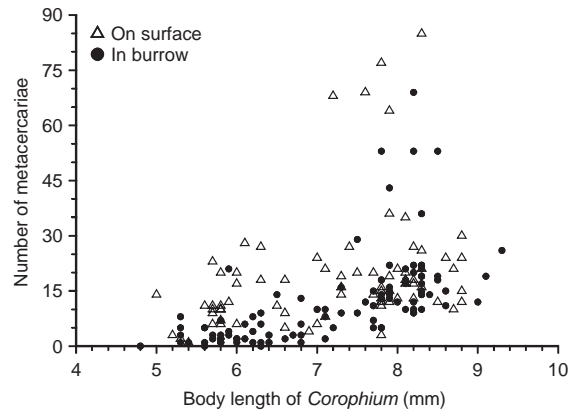


Fig. 4. Number of microphallid metacercariae in burrowed (black dots) and surfaced (white triangles) *Corophium volutator* as a function of body length. For surfaced amphipods, only specimens collected 210–250 min after high tide are included.

not due to size differences between specimens from the two sites. So, the average body lengths of males ( $5.8 \text{ mm} \pm 0.14$ ; mean  $\pm$  95% C.I.) and females ( $7.2 \text{ mm} \pm 0.25$ , mean  $\pm$  95% C.I.) from the surface (sampled 210–250 min after high tide) did not differ from the burrowed specimens (males:  $6.0 \text{ mm} \pm 0.17$ ; females:  $7.2 \text{ mm} \pm 0.22$ ; mean  $\pm$  95% C.I.) (t-test for both males and females:  $p > 5\%$ ).

The population of *C. volutator* was female-skewed (Table 1), but no significantly different sex ratio could be demonstrated among the four samples of surfaced and the sample of burrowed amphipods (Pearson,  $\chi^2_4 = 3.05$ , ns).

The parasite load was considerably higher in females than in males (Table 1, Fig. 2). Nearly 6% of the females harboured more than 40 metacercariae (maximum was 85), whereas all males had less than 30 metacercariae each. This pattern is most likely a result of the size difference between males and females: the number of metacercariae increases significantly with length in both male (Spearman's  $\rho = 0.334$ ,  $p < 0.001$ ,  $n = 175$ ) and female amphipods (Spearman's  $\rho = 0.541$ ,  $p < 0.001$ ,  $n = 282$ ), and females were generally larger than males (Fig. 3). Only 3.4% of the male population were longer than 7 mm, whereas 32.3% of the females exceeded this size. Furthermore, sex specific accumulation of metacercariae is an unlikely explanation for the observed pattern as there was no difference between sexes regarding mean infection intensity in individuals of less than 7 mm length (t-test,  $t_{232} = -0.684$ , ns).

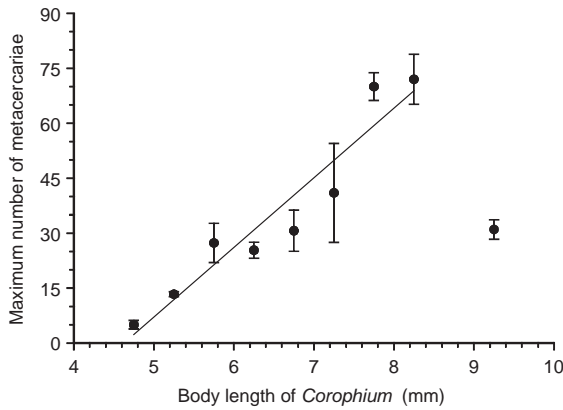


Fig. 5. Maximum number of microphallid metacercariae in *Corophium volutator* as a function of body length. For each length intervals of 0.5 mm, the mean number of metacercariae ( $\pm$  S.E.) for the three individuals with the highest parasite load is indicated. For individuals less than 8.5 mm in length, the relationship between maximum number of metacercariae and body length is linear (maximum number of metacercariae =  $-88.0 + 19.0 \times \text{length}$ ,  $r^2 = 0.79$ ,  $n = 24$ ).

Having demonstrated the absence of sex-specific accommodation of metacercariae between individuals from the surface and from the bottom, we can directly compare the intensity of metacercariae in the amphipods from the two sites as a function of their sizes (Fig. 4). For each interval of body length, the parasite load was significantly higher in surfaced than in burrowed amphipods (paired t-test:  $t_{55} = 4.0$ ,  $p < 0.001$ ) as an indication that the observed surface behaviour of *C. volutator* is related to the presence of large numbers of metacercariae.

Although the infection intensity generally increased with host size (Fig. 4), the maximum number of metacercariae harboured by the amphipods was substantially lower in the largest size group than predicted from the otherwise linear relationship between maximum parasite load and size in the smaller host individuals (Fig. 5).

#### 4. Discussion

The present results demonstrate that *Corophium volutator* specimens crawling on the sediment surface at low tide harbour more microphallid trematodes on average than tube-dwelling specimens, and that the proportion of heavily infected individuals increases with time. The latter is most likely due to the burrow-

ing of mainly lightly infected specimens as exposure-time increases, but surfacing of heavily infected individuals late in the low-tide period could be an additional factor (see Fig. 2). Hence, microphallids appear indeed to be one factor that may cause — directly or indirectly — surface activity of *C. volutator* as laboratory experiments have previously suggested (Mouritsen and Jensen, 1997).

The behavioural change of infected amphipods is intensity dependent, and the intensity required to induce surface activity is positively related to host size (Fig. 4). However, because of (1) the considerable and overlapping variation in infection intensity in surfaced and burrowed amphipods, irrespective size group, and (2) the presence of heavily infected burrowed individuals, a threshold parasite-load above which the behavioural change is induced does not exist. This weakens the possibility that the surface behaviour is induced directly by the parasites, e.g. by the release of certain neurotransmitters or by encystment in specific behaviour-controlling nerve tissues (see Helluy, 1984; Helluy and Holmes, 1989). The surface behaviour may rather be the indirect result of the infection causing food deficiency, increased oxygen demand and/or obstruction of the locomotory apparatus. For instance, the volume of microphallid cysts increase up to 40-fold during development, and the nourishment for this growth must come from the host (Benjamin and James, 1987; Galaktionov et al., 1996). Consequently, infected amphipods may have an increased food demand, and relocation (i.e. surface activity) could be a way of obtaining unexploited food sources. Regarding oxygen demands, Mouritsen and Jensen (1997) showed that microphallid infections could result in gill anaemia, which in turn might reduce the efficiency of oxygen uptake. At low tide, the water contained in the burrows tends to become deoxygenated (Teal, 1959; Petersen and Johansen, 1967), and heavily infected hosts may therefore leave their burrows to reach higher oxygen tensions at the surface. Furthermore, probably as a result of the mechanical obstruction of muscle tissues and various internal organs, heavily infected specimens of *C. volutator* are less capable of bending and flexing their body and appendages (Meißner and Schaarschmidt, 2000; Damsgaard, 2002). This can interfere with the amphipods' ability to construct and enter burrows, and



heavily infected specimens may therefore remain at the surface. Because the impact of the above-mentioned not mutually exclusive mechanisms will depend on individual nutritional and competitive status and the exact position of the metacercarial cysts within the body-cavity of the host individual, a narrow threshold infection intensity for the induction of behavioural change is unlikely to occur, as indeed observed.

Although the surface behaviour of infected amphipods thus appears to be pathological side-effects of infection, it may nonetheless be beneficial to the parasites, and therefore not selected against during the course of evolution. Waders, including Dunlins (*Calidris alpina*) as the most abundant bird predator of *C. volutator* in the Wadden Sea and known final host to microphallids (Deblock, 1980; Laursen and Frikke, 1984), feed during daytime low-tides preferentially by visual means on surface-active prey organisms (Zwarts and Wanink, 1993; Mouritsen, 1994). Hence, by forcing the host (directly or indirectly) to the surface during low tide, the parasites' transmission success will be substantially increased in comparison to when the infected hosts remain in their burrows. This holds true also if a substantial proportion of the surfaced amphipods (and their parasites) should be lost to epibenthic non-host predators during high tide (see Mouritsen and Poulin, 2003a; Thompkins et al., 2004).

Female *C. volutator* were found to accommodate more microphallid cysts than males, but this can be explained by their size difference. Among amphipods larger than 7 mm, males account for less than 3%. The size-dependent infection intensity is explainable by the age-size relationship (parasites accumulate with time) and by the expected relationship between size and ventilation rate. A higher flow of water through burrows is also bound to result in a higher flux of infective parasite larvae swimming in the water column (Mouritsen and Jensen, 1997).

The observed female-biased sex ratios among adults are the rule within populations of *C. volutator*, usually explained by different ratios among newly hatched specimens (Schneider et al., 1994) or by differential mortality on adult males (e.g. Boates and Smith, 1989). The male dominance among specimens less than 7 mm in our case excludes the former possibility. Because males are more surface active

than females in their search for receptive tube-dwelling females, they are also more vulnerable to predators, and gradually the male population can be depleted.

A size-biased elimination of *C. volutator* specimens induced by parasites is also suggested by our data. The maximum cyst numbers increases linearly with body length and since the volume-length relationship in *C. volutator* is best described by a power-function, we would predict larger individuals to contain a disproportionately higher cyst number than smaller individuals. The opposite seems to be the case in particular for the largest *C. volutator* individuals (Fig. 5). This pattern suggests that selective mortality takes place on larger and more heavily infected specimens, and such selective mortality agents could easily be shorebirds at low tide and epibenthic predators (flatfish, crabs, shrimps) at high tide. Direct parasite intensity-dependent mortality could also be involved (Jensen and Mouritsen, 1992; Mouritsen and Jensen, 1997; Jensen et al., 1998; Meißner and Bick, 1999).

Our study shows that microphallid trematodes affect the behaviour of *C. volutator*, with possible implications not only for the parasites' life cycle but also the population dynamics of the amphipod. Many intra- and interspecific density-dependent processes may induce emigration from a site (Jensen, 1985; Flach, 1994), and migrants could indeed be specimens weakened by heavy parasite loads and hence inferior combatants in intra- and interspecific interactions. As parasites may be a cryptic factor determining the outcome of many biotic processes it is advisable to include parasites in population and community studies (see Mouritsen and Poulin, 2003b).

## Acknowledgements

The study was supported by a grant from the Carlsberg Foundation (K.N.M. and K.T.J.).

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