



ORIGINAL ARTICLE

The effect of *Sacculina carcini* infections on the fouling, burying behaviour and condition of the shore crab, *Carcinus maenas*

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Abstract

Crabs infected by rhizocephalans usually do not moult. Because moulting is the ultimate defence against fouling epibionts, infected as opposed to uninfected crabs can be expected to harbour a diversity of hard-bottom organisms on their cuticula. Here we provide unequivocal evidence that this is the case in the *Carcinus maenas*–*Sacculina carcini* association. In a Danish sample of shore crabs, 75% of sacculinized individuals harboured macroscopic epibionts, whereas only 29% of the uninfected crabs were colonized. The mean numbers of fouling barnacles and serpulid tubeworms per individual were 7.7 and 47.3 for uninfected and infected crabs, respectively, corresponding to coverage of the cuticula by 0.7 and 5.4%. Infected crabs were 12% lower in tissue dry weight than uninfected individuals, which may be a factor causing the moult of sacculinized crabs to be postponed. Finally, a laboratory experiment suggested that infected crabs are less likely to bury than uninfected specimens. Because burying is an important fouling defence, such a parasite-induced behavioural change will favour the colonization by epibionts. It is argued that rhizocephalans infecting crabs from soft-bottom communities may indirectly affect the structure of the free-living benthic community by adding hard-bottom species that otherwise would be absent.

Key words: Barnacles, community structure, epibionts, parasitism, rhizocephalans, serpulids

Introduction

Rhizocephalans are morphologically modified crustacean parasites infecting, among other crustaceans, the often ecologically important brachyurans. The main body of the parasite is a root-like system of branches that extends into most of the host's tissue, whereas the gonads of the parasites emerge externally under the abdomen of the crab (e.g. Høeg & Lützen 1995). Two important consequences of infection are that the host is castrated and (if a male) feminized behaviourally and morphologically, and that externally infected crabs in most cases cease moulting (Høeg & Lützen 1995; Werner 2001). The latter means that the cuticula of infected crabs can serve as a more permanent substrate for epibionts, which in turn should lead to a considerably higher abundance of fouling organisms on infected than on uninfected animals. If true, and considering the generally high abundance of crabs in

coastal areas, and that the prevalence of rhizocephalans is often substantial (10–50%; e.g. Alvarez & Calderón 1996; Mathieson et al. 1998; Mouritsen & Poulin 2002), this can be envisaged to impact the structure of the benthic community as a whole (see Poulin 1999; Thomas et al. 1999). However, the evidence that Rhizocephala-infected crabs in fact do harbour a better-developed community of epibionts than uninfected individuals is weak and largely circumstantial, particularly regarding the green shore crab *Carcinus maenas* (see Giard 1874; Phillips & Cannon 1978; Shields 1992; Thomas et al. 1999; Isaeva et al. 2001; Gaddes & Sumpton 2004).

Using the *Carcinus maenas*–*Sacculina carcini* association as the model system, we here provide unequivocal evidence that *Sacculina*-infected crabs are more heavily fouled by certain unspecialized epibionts than uninfected individuals. In addition, we present data on the burying behaviour and

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general condition of infected versus uninfected specimens, which may partly explain the mechanism by which the difference in fouling between the two groups of crabs is established. The potential indirect community impact of the host–parasite association is discussed.

Material and methods

Study site, animal collection and standard protocol

The study was carried out at Rønbjerg Harbour in the central part of the Limfjord, Denmark (56°53'N 9°10'E) during August 1997, 1999 and 2000. Shore crabs, *Carcinus maenas*, were caught by eel traps at a water depth of approximately 1–3 m, and the catch was divided into two groups according to whether or not they were infected by *Sacculina carcini*. This was determined by the presence or absence of the parasite's external gonads (externae) on the abdomen of the host. Using this criterion of infection means that the group of 'uninfected' crabs may include individuals that were only internally infected, which ensures a conservative analysis. The animals were kept in large storage tanks supplied with running sea water until processed 1 or 2 days after capture.

Infection and epibiota

In 1997, the carapace width of 938 uninfected and 196 sacculinized crabs was measured with callipers. During measurements, the presence or absence of macroscopic epibionts on each animal was recorded. Because the size distribution of the infected and uninfected crabs differed significantly (see Results), an additional sample of 12 uninfected and 12 infected individuals, chosen at random (no visual contact) but matched according to carapace width (<1 mm deviation), were killed and their legs removed. The number of macroscopic epibionts present on both the dorsal and ventral side of the cuticula of each crab was recorded, and the proportion of the surface area occupied by these organisms was then estimated from photographs taken of both sides: transparent graph paper was placed on each photograph and areas covered by fouling organisms marked, added, and then related to the entire projected surface area of the crab.

Infection and burying behaviour

Burying by crabs can influence the process of fouling (e.g. Becker & Wahl 1996; Wahl et al. 1998), and in order to investigate whether *Sacculina* infection affects the burying behaviour of the host, a laboratory experiment was carried out in 2000. Sixty-two

crabs, half uninfected and half sacculinized, but pairwise matched according to both carapace width and gender (i.e. equal size distribution and sex ratio), were individually transferred to 44 l experimental aquaria with a ca. 0.15 m² bottom covered by 5 cm of fine sand. The animals were left undisturbed for 2 min, after which time it was recorded whether or not the animals had buried into the substrate.

Infection and condition

Parasites subsist on nutrition provided by their host, and infected crabs may therefore be in poorer condition than uninfected individuals. Because crabs in poor condition may have a slower growth rate and hence fewer moults per unit time, epibionts might be allowed to accumulate for a longer period of time. This could be an additional explanation for a more developed fouling community on sacculinized crabs than on uninfected crabs. Hence, to test the condition of infected versus uninfected crabs, 30 pairs of crabs, matched according to infection status and carapace width (size range 25.9–58.9 mm) were collected in 1999. Although males predominated, both sexes were represented in the two groups of animals. The crabs were killed, cleaned for macroscopic epibionts, dried at 100°C for 36 h and subsequently weighed. The *Sacculina* externae present on infected crabs were removed prior to drying in order to approximate host tissue dry weight only. The internal part of the parasite could not easily be removed and therefore the dry weight of the infected host also included some parasite tissue. This means that any quantitative difference in dry weight between uninfected and infected crabs is a conservative estimate.

Results

Apart from a few records of attached macroalgae and mussels (*Mytilus edulis*), the majority of un-specialized epibionts found on the shore crabs were species of barnacles and the serpulid tube-worm *Pomatoceros triqueter* (Figure 1). Based on the 1997 sample of 1134 crabs, sacculinized hosts were significantly more likely (almost three-fold) to be fouled than uninfected individuals (Fisher's exact test, $P < 0.0005$) (Figure 2). However, the mean carapace width of infected crabs (48.1 ± 0.83) was significantly larger than that of uninfected crabs (44.5 ± 0.86 ; Student's *t*-test, $t_{1132} = 5.61$, $P < 0.0005$). This could suggest that the group of infected animals was on average slightly older than uninfected ones, and because the frequency of moulting decreases with age this might have



Figure 1. A sacculinized shore crab, *Carcinus maenas* (1997 sample), fouled by tubeworms, *Pomatoceros triqueter*. Note the slightly protruding abdomen caused by the presence of *Sacculina carcini* externae beneath the abdomen. Apart from the tubeworms, a few barnacles were also attached ventrally.

contributed to the higher proportion of fouled individuals among infected than uninfected crabs. However, the quantitatively small difference in mean size (<8%) can barely justify the very large difference in fouling, and the sample of infected and uninfected crabs matched according to size also demonstrated heavier fouling of infected than uninfected animals both regarding the number of epibionts (on average *ca.* six-fold more) and the area of the cuticula covered (*ca.* eight-fold more) (Table I).

The behaviour of sacculinized shore crabs differed from uninfected crabs. The former were significantly less likely to bury into the substrate (Fisher's exact

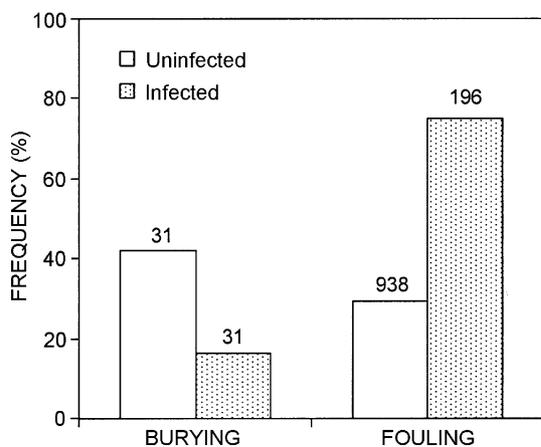


Figure 2. The proportion of uninfected (white columns) and sacculinized (shaded columns) shore crabs, *Carcinus maenas*, burying into the substrate under laboratory conditions (Burying) and found to be fouled by epibionts (mainly barnacles and tubeworms) in a large field sample (Fouling). The sample size is given above the columns. Note that the “uninfected” group may also include some internally infected crabs.

test, $P=0.049$, Figure 2). Moreover, the dry weight of infected crabs was generally lower (approximately 12%, based on back-transformed grand means) than that of uninfected crabs (Figure 3). A full model ANCOVA indicated homogeneity of error variance across groups (Levene's test, $F_{1,58}=2.25$, $P=0.14$) and the absence of a significant interaction between the two weight–size relationships (Figure 3) ($F_{1,56}=0.19$, $P=0.66$). The reduced model demonstrated a highly significant effect of infection status ($F_{1,57}=18.64$, $P<0.0005$).

Discussion

The present results demonstrate that *Sacculina carcini*-infected shore crabs are more likely to harbour epibionts than uninfected individuals, and that the average abundance of obligate hard-bottom species such as barnacles and the tubeworm *Pomatoceros triqueter* is several fold higher on infected crabs. This difference between uninfected and sacculinized crabs may have been more pronounced had internally infected individuals been excluded from the group of “uninfected” animals.

Arrested moulting of hosts with mature infections is probably the main reason for the observed differences in fouling between the two groups of crabs, creating a more permanent substrate on which fouling organisms can settle and develop. The mechanism by which the moulting cycle is interrupted in sacculinized crabs is poorly understood, but it has been emphasized that mechanical obstruction rather than physiological processes is involved (Reinhard 1956). However, suppressed ecdysis is not observed in all crab–Rhizocephala associations (Reinhard 1956; Høeg & Lützen 1995; Alvarez et al. 1995) and other factors may also be influential. One such factor could be the reduced general condition of sacculinized crabs (Figure 3), which may postpone moulting significantly, if not arresting it entirely. Sexual dimorphism in shore crabs is weak and largely confined to a relatively broader abdomen and smaller master chela in females (Shen 1935; Elnor 1980). Because *Sacculina* tend to feminize male hosts morphologically, the average lower dry weight of infected individuals (Figure 3) might reflect such changes rather than reduced condition. However, the changed morphology of sacculinized males is believed to involve mainly broadening of the abdomen (J. Lützen, pers. commun.), which should increase rather than decrease the weight of infected crabs, and the gender-specific difference in master chela size is in any case insignificant in the presently studied size classes of crabs (see Elnor 1980). Hence, the observed lower dry weight of infected crabs

Table I. Mean \pm standard error of crab size, number of attached barnacles and tubeworms (*Pomatoceros triqueter*), and proportion of projected surface area occupied by the epifauna for uninfected and *Sacculina*-infected shore crabs, *Carcinus maenas*. Regarding the latter two parameters, median and maximum values are also given in parentheses. Z and P values are summary statistics for Wilcoxon signed ranks tests ($n=12$ for all values).

Parameter	Uninfected	Infected	Z	P
Carapace width (mm)	51.0 \pm 2.8	50.9 \pm 2.7	0.89	0.93
Epifaunal organisms				
Number	7.7 \pm 4.1 (0, 40)	47.3 \pm 22.4 (27, 261)	2.30	0.022
Coverage (%)	0.7 \pm 0.4 (0, 3.7)	5.4 \pm 2.8 (1.2, 27.4)	2.80	0.005

probably reflects the negative effect of parasitism on host condition.

Yet another factor may lead to the increased fouling of sacculinized crabs. It appears that behavioural mechanisms, such as burying into the substrate or hiding in rock crevices and under stones, significantly reduce epibiont colonization (e.g. Becker & Wahl 1996; Wahl et al. 1998), and as *Sacculina*-infected shore crabs seem less likely to bury into sediments (Figure 2), as also observed in rhizocephalan-infected portunid crabs (Innocenti et al. 1998), they may experience a higher colonization rate for that reason alone. Thus, several rather different consequences of the infection work in concert to result in a much heavier fouling of sacculinized than healthy shore crabs.

Parasitism is increasingly recognized as an important process influencing the structure and function of natural communities, mainly as a consequence

of the parasites' ability to inflict significant host mortality and to decrease the reproductive output of the host population (Freeland 1983; Price et al. 1986; Minchella & Scott 1991; Hudson & Greenman 1998; Combes 2001; Mouritsen & Poulin 2002). Hence, parasites occupy a role in the ecosystems similar to that of predators and herbivores by reducing the abundance of certain species relative to others not used as hosts. Interestingly, in addition to this functional role, parasites very often also change the phenotype of their host significantly (e.g. Moore & Gotelli 1990; Poulin 1995). For example, if a behaviourally modified host species is abundant or occupies an ecologically important role in the community, there will probably be ramifications to community structure and function. However, empirical evidence for this indirect role of parasitism in community ecology is just beginning to emerge, and, presently, theoretical considerations tend to dominate the contributions (Thomas et al. 1998, 1999; Poulin 1999; Combes 2001; Mouritsen & Poulin 2002, 2005). In this context, brachyuran crab–Rhizocephala associations have been emphasized as host–parasite systems with potential indirect impacts on benthic community structure (Poulin 1999; Thomas et al. 1999), and our analysis seems to support this. The Danish coastline is, apart from localized hard-bottom habitats in the form of harbours, stony reefs and cobble beaches, mostly sedimentary, and obligate hard-bottom organisms such as barnacles and tubeworms are principally restricted to these scattered hard-bottom areas. However, both barnacles and tubeworms possess a pelagic larval stage that disperses widely into the surrounding soft-bottom habitats. Here, the larvae will settle on any hard surface they encounter, and the cuticula of shore crabs infected by *Sacculina carcini* may be the only substrate available on which they are allowed to develop. Hence, the presence of sacculinized crabs will in effect elevate both species richness and diversity in the soft-bottom community of free-living species. The quantitative importance of this process may, however, be modified somewhat in aged

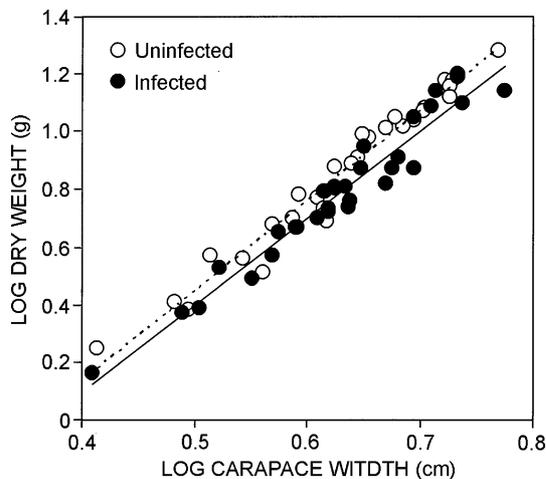


Figure 3. The log-transformed relationship between dry weight and carapace width for uninfected (○, broken line) and sacculinized (●, solid line) shore crabs, *Carcinus maenas*. Regression line, uninfected: $\log(\text{DW}) = 3.106 \cdot \log(\text{CW}) - 1.106$ ($r^2 = 0.96$, $n = 30$, $P < 0.0005$). Regression line, infected: $\log(\text{DW}) = 3.028 \cdot \log(\text{CW}) - 1.119$, ($r^2 = 0.94$, $n = 30$, $P < 0.0005$). Note that the “uninfected” group may also include some internally infected individuals, and that the dry weight of infected crabs also includes internal parasite tissue.

populations of crabs, because old/very large crabs having undergone terminal moult may harbour a well-developed community of epibionts as well (e.g. Styriehave et al. 2004; McGaw 2006). Moreover, rhizocephalans castrate their host and that may reduce the host population size. Because uninfected crabs also harbour epibionts, a parasitic regulation of the crab population might hence decrease rather than increase the abundance of hard-bottom organisms. However, because *Carcinus maenas* has a pelagic larval stage, such an effect may manifest itself solely at the largest spatial scale; not at the present small-scale focus (between and within habitats).

However, it remains to be shown statistically that benthic soft-bottom communities are in fact significantly affected by the presence of *Sacculina carcini* in local populations of shore crabs. Catches of sacculinized crabs, heavily fouled by barnacles and tube-worms, in a Limfjord habitat of mixed sand and eel-grass beds, kilometres away from the nearest significant hard bottom (K. N. Mouritsen, pers. observ.), suggest this to be merely a matter of effort.

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