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Tube-building in two epifaunal amphipod species, *Corophium insidiosum* and *Jassa falcata*

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ABSTRACT: *Jassa falcata* and *Corophium insidiosum* are epifaunal tube-building marine amphipods, whose niches overlap in habitat and food requirements. Laboratory experiments were conducted to study the influence of the quality of different available particulate substrates on settlement and tube-building behaviour of these two amphipod species. Our experiments suggest that *C. insidiosum* is less specialized in this respect than *J. falcata*. *C. insidiosum* is able to use organic materials for tube-building such as artificial (*Ulva* spec. powder) or mixed natural detritus as well as inorganic material (coarse sand); whereas *J. falcata* utilizes organic materials, but sand only to a very limited extent.

INTRODUCTION

In general, rocky shores show a much higher species diversity when compared to soft bottom communities and hence, should require a higher degree of ecological specialization in their fauna. One of the specific difficulties of hard-bottom dwellers concerns fixing themselves to the ground, so that they cannot be washed away by strong water movements. Tube-building is a common adaptation to this particular habitat requirement.

Amphipods belong to the most numerous and taxonomically diverse components of epifaunal marine invertebrate communities (Jacobi, 1987). Most of them live hemisessile in tubes whose walls consist of body secretions and exogenous materials. Their settlement behaviour is influenced by environmental factors such as currents, the substrate surface, and the availability of tube-building materials. In the present investigation, the influence of the type of building materials on settlement and tube-building behaviour was compared in two very common, coexisting and potentially competing amphipod species, *Jassa falcata* and *Corophium insidiosum*.

MATERIALS AND METHODS

Amphipods (*Jassa falcata* and *Corophium insidiosum*) were obtained by scratching epifauna from harbour jetties at the island of Helgoland (North Sea) and sorting them in the laboratory. Green macroalgae (*Ulva* spec.) were collected at the northern shore of Helgoland during low tide, and sand particles were removed by washing them in seawater. The algae were dried in an oven for 12 h at 90 °C and subsequently ground to obtain an artificial, relatively coarse detritus. A finer, mixed natural detritus was obtained from the laboratory seawater filter system and stored until use at 12 °C. Sand was taken from the southern beach of Helgoland and fractionated by passing it through sieves with 300 and 500 µm mesh widths.

Amphipods were put into plastic aquaria (17.7×11.4 cm bottom area) which received seawater from a flow-through system (ca. 0.3 l/min) and had drainage holes 5 cm above the bottom to guarantee a constant water level. With each species, experiments with 3 substrate types (*Ulva* spec. powder, mixed natural detritus, coarse sand; 3 replicate aquaria, with 30 individuals each) were carried out over observation periods of 19 days. Approximately equal amounts (by volume) of the following building materials were initially added to the aquaria: 0.4 g *Ulva* spec. powder; 10 ml natural detritus; 10 ml coarse sand (300–500 µm grain size fraction).

The aquaria bottoms were externally marked dividing their area into rectangles of 2.85×2.95 cm. Data sheets with identical patterns were prepared, and each day the total number and location of complete tubes were recorded on a new sheet. Tube-building was considered completed when the amphipods could fully retract into them after being mechanically disturbed.

RESULTS

Artificial detritus (*Ulva* spec. powder)

Figure 1 shows the tube-building activity of *Corophium insidiosum* and *Jassa falcata* during a 19-day observation period with exclusively *Ulva* spec. powder supplied as a substrate. A marked difference in tube-building behaviour was observed between the two amphipod species. After only one day, on an average 70 % of the *C. insidiosum* had constructed tubes. During the later course of the experiment, the average percentage of individuals that had built tubes ranged between 70–85, showing no marked increase with time. In contrast, only 10 % of *J. falcata* constructed tubes within the first day of the experiment, but the number of tubes increased continually during the course of the experiment to a final average of about 60 % (Fig. 1). With *Ulva* spec. detritus, *C. insidiosum* built significantly more tubes than *J. falcata* (days 1–5: $p < 0.0001$; days 8–12: $p < 0.001$; days 15–19: $p < 0.05$; one-way ANOVA).

Mixed natural detritus

When natural detritus was given as a building material, 51 % of the *Corophium insidiosum* built a tube during the first day of observation, showing a gradual increase during the course of the experiment, and eventually reached a maximum of 86 % (Fig. 2). In *Jassa falcata*, the percentage of individuals that built a tube increased over the first 9 days to maximum levels between 50–73 %. According to a one-way ANOVA, during the first 12 days significantly more tubes were built by *C. insidiosum* than by *J. falcata*. Later, however, the difference was no longer statistically significant (days 1–5: $p < 0.0001$; days 8–12: $p < 0.05$; days 15–19: $p > 0.05$).

Coarse sand

Successful colonization of the aquarium bottom by *Corophium insidiosum* could also

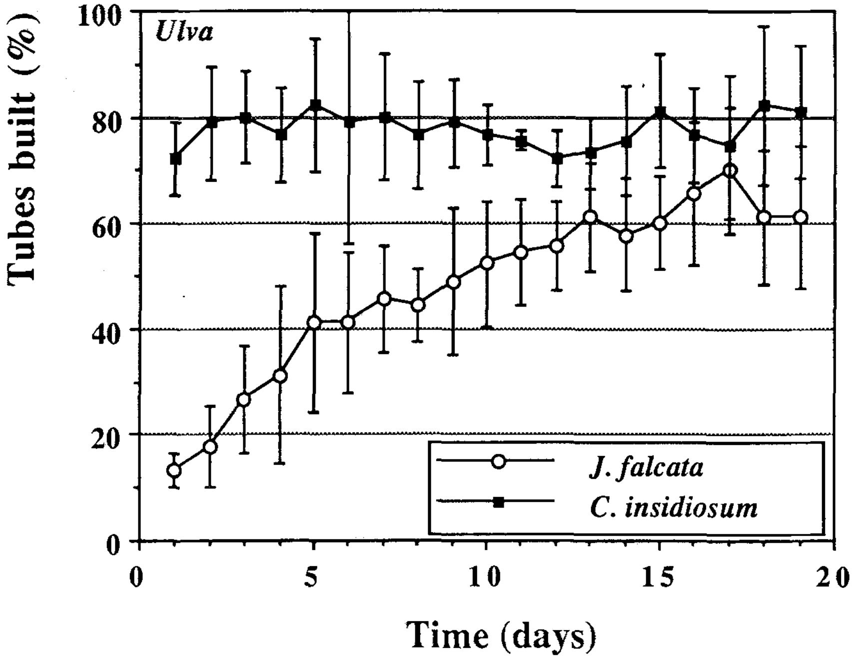

Fig. 1. Tube-building in *Jassa falcata* and *Corophium insidiosum* given artificial detritus (*Ulva* spec. powder) as a substrate. Percentage of animals building a tube during the 19-day observation period (n = 30 individuals in each replicate); error bars = arithmetic mean ± 1 standard deviation (n = 3 replicate experiments)

be observed when coarse sand was offered as a substrate (Fig. 3). During the first day of observation, 42 % of the individuals built a tube with this material. During the course of the experiment, this increased to about 80–91 %. *Jassa falcata*, in contrast, was hardly able to use sand as a building material. During the 19-day observation period, never more than an average of about 8 % (i.e. 2 individuals) lived in tubes. The difference between the two amphipod species compared here was statistically significant during the entire course of the experiment (consistently $p < 0.05$).

DISCUSSION

Investigations concerning tube building behaviour of epi- and infaunal amphipods have been carried out since the beginning of this century (e.g. Holmes, 1901; Hunt, 1925; Skutch, 1926; Schellenberg, 1929; Hart, 1930). Goodhart (1939) examined the acceptance of various building materials by *Leptocheirus pilosus*, and distinguished 4 major categories of amphipod tubes: (1) tubes burrowed into sand (e.g. *Ampelisca* spec.); (2) tubes burrowed into mud (e.g. *Corophium volutator*); (3) tubes built from various organic and inorganic materials on the surface of hard substrata (e.g. *Leptocheirus pilosus*); and (4) "nests" of algal fragments (e.g. *Amphitöe rubricata*). *Corophium insidiosum* can utilize both organic and inorganic particles for tube construction. Thus, it may be placed

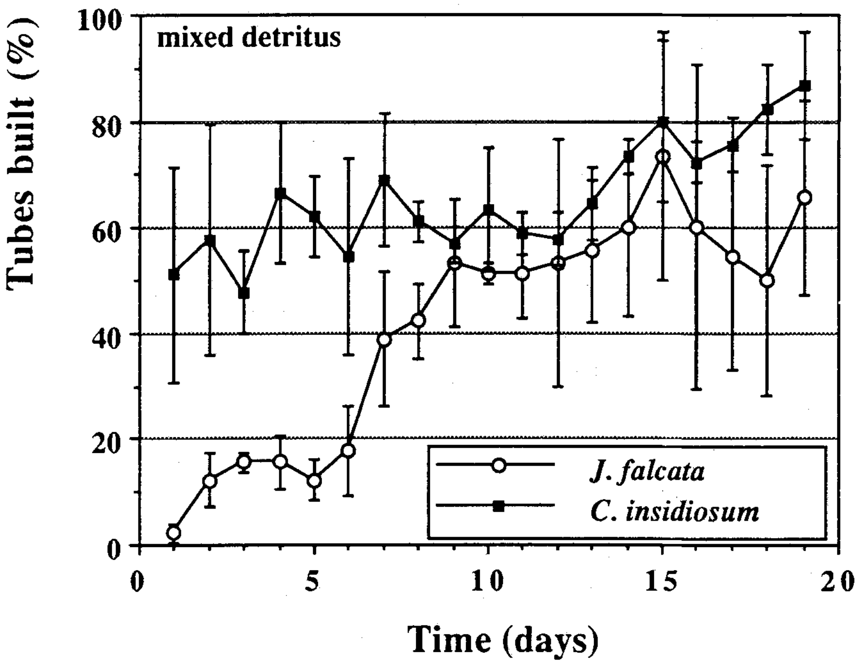

Fig. 2. Tube-building in *Jassa falcata* and *Corophium insidiosum* given mixed natural detritus as a substrate. Percentage of animals building a tube during the 19-day observation period (n = 30 individuals in each replicate); error bars = arithmetic mean ± 1 standard deviation (n = 3 replicate experiments)

in the same category of tube-builders as *L. pilosus* (Goodhart, 1939), whereas *J. falcata*, which utilized almost exclusively organic material, may not fit into any group within this scheme.

Corophium insidiosum and *Jassa falcata* differ not only in the use of building material, but also in the time needed for tube construction. *C. insidiosum* can construct tubes equally well using very different materials such as coarse sand, fine natural detritus, or coarse particles of ground macroalgae. However, the latter material seemed to be preferred, and colonies built with this material grew faster than those using other substrates. In general, colonization and tube-building by *C. insidiosum* occurred quite rapidly, and after only a few days most of the animals had constructed their own tube. *Jassa falcata*, in contrast, was almost completely restricted to the use of organic material, demonstrating difficulty in incorporating sand but showing no preference between coarse (*Ulva* spec.) or fine (mixed) detritus. Colonization by *J. falcata* was slower than *C. insidiosum*. After 10 days of observation, only ≤50 % of the animals had built a tube, regardless of the type of available material. In summary, *C. insidiosum* appears to be in this respect a much more flexible (or opportunistic) colonizer as opposed to *Jassa falcata*.

A possible cause for different capabilities to use sand as a building material might be a consistence differential of the specific secretion products used for tube construction. *C. insidiosum*, when offered no particles, built very stable tubes that consisted exclusively of secreted substances. These tubes could be removed undamaged from the

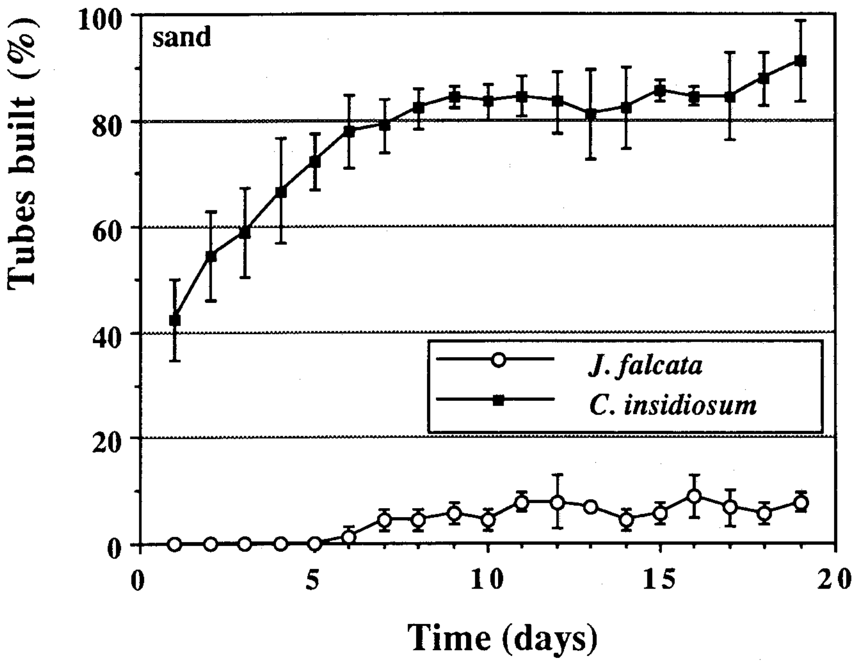

Fig. 3. Tube-building in *Jassa falcata* and *Corophium insidiosum* given coarse sand (300–500 μm grain size) as a substrate. Percentage of animals building a tube during the 19-day observation period (n = 30 individuals in each replicate); error bars = arithmetic mean ± 1 standard deviation (n = 3 replicate experiments)

aquaria walls using tweezers. In *J. falcata*, such solely secreted, particle-free tubes were unstable and were always destroyed when removed. This suggests that the secretion products of the latter species may not be cohesive enough to permanently glue coarse sand particles.

The different use by *Corophium insidiosum* and *Jassa falcata* of available building material provides an ecological advantage for the former in developing new colonies on bare hard bottoms with little sedimentation. However, both species are frequently found together in the same habitat and often in close vicinity to each other (Karez, 1991; Anger, 1979). This might be explained by a facilitation effect during early colonization: the opportunistic settler *C. insidiosum* can occupy free space which is unsuitable for *J. falcata* and, as a suspension feeder, may accumulate fine particles around its tubes. This may slowly change the character of the surrounding microhabitat (Mills, 1969), facilitating later settlement and tube-building by *J. falcata*. On the other hand, the more opportunistic species, *C. insidiosum*, should be able to easily colonize habitats that are already occupied by *J. falcata* populations. Mutual competition for tube-building material is restricted in these two species, as *C. insidiosum* can use any material, including that which is discarded by *J. falcata*.

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