Mutualism Among Sessile Invertebrates:  
A Mediator of Competition and Predation

Abstract. Hydroids of the genus Zanclea are epizoic on encrusting bryozoans. The bryozoans protect these hydroids with skeletal material. Zanclea polyps on the bryo- 
ozan Celleporaria brunnea sting small predators and adjacent competitors, helping Celleporaria to survive and to grow over competing species. This mutualism enables the two species to cover a larger area than they could individually.

Space is an important limiting resource for many organisms. In marine benthic communities this is most evident for sessile invertebrates and algae inhabiting rocky substrates. For these organisms the habitat exists as discrete patches of limited area. Individuals (or colonies) are restricted to the particular substrate onto which their larvae settle and attach. Population size, survival, and reproductive output are all influenced by the amount of space that is occupied. Competition is often intense and involves the shading, undercutting, or overgrowth of one individual by another (1-4). Single species can dominate and sometimes monopolize a patch of substrate. This competitive dominance by one or a few species can be reduced by predators and through the physical disturbance of patches of habitat (2, 5).

Competition, predation, and physical disturbance are not the only phenomena that can regulate a species' use of spatial resources. Mutualism, in which two species positively affect one another's abundances, may be equally important (6, 7). Mutualistic associations between benthic species have been demonstrated (3, 7, 8), but infrequently. In studying the succession of marine invertebrate communities living on experimental panels (9), we found an example of mutualism between the bryozoan Celleporaria and the hydroid Zanclea. The bryozoan protects the hydroid by depositing CaCO₃ and the hydroid reduces the impact of competitors and predators on the bryo- 
ozan. This association improves the survival of both species and increases the amount of space that they can cover and hold. Zanclea grow as vinelike colonies in which polyps with capitate tentacles...
arise individually from a basal network of stolons. All known species are epizoic on other benthic species (10), usually on cheilostome bryozoans (11). These bryozoan colonies encrust the substrate as a calcareous sheet.

In communities of sessile invertebrates the competitive dominants usually include species of bryozoans. These dominant bryozoans are seldom overgrown by other species. They also prevent metamorphosing larvae from attaching to their exposed frontal surfaces. These surfaces thus represent abundant "secondary" substrate that remains relatively free of sediments, debris, and other species. Zanclea, however, can penetrate the bryozoan's antifouling defenses and colonize this, competitor-free substrate.

We found two species of Zanclea that are obligate epizoites on bryozoans. In Vineyard Sound, Massachusetts, Z. gemmosa (12) was found exclusively on the bryozoan Schizoporella errata (13). On experimental panels, Z. gemmosa larvae attached themselves only to Schizoporella colonies. The hydroid did not appear to interfere with the normal activities of its host. Its basal stolons grew over the bryozoan's surface, never extending beyond the colony's edge unless another Schizoporella colony adjoined. The stolons usually followed the shallow grooves between zooids of the bryozoan colony and never grew over the zooidal apertures from which the lophophores (tentacular feeding organs) protrude. Zanclea feeds on microcrustaceans (14) and bryozoans feed on phytoplankton (15), so these species do not compete for food.

Schizoporella responds to the presence of Zanclea by depositing CaCO₃ underneath and around the basal stolons of the hydroid (Fig. 1), ultimately forming a tube from which the Zanclea polyps protrude. This pattern of calcification was observed only in the presence of Zanclea (16); stolons of other hydroids that occasionally grew on the Schizoporella colonies never caused the reaction. Although we do not know what specific stimulus is responsible for this pattern of CaCO₃ deposition, it clearly isolates the hydroid tissues from the bryozoan, protects the hydroid against physical damage and predation, and incurs some energy cost to the bryozoan. The fact that Schizoporella deposits additional CaCO₃ only in the presence of Zanclea suggests that the association is not merely fortuitous.

Along the coast of southern California (17) we found a second, unidentified species of Zanclea that is an obligate epizoite on the bryozoan Celleporaria brunnea. The relationship between these species is similar to that described for Z. gemmosa and Schizoporella. However, there are three differences. The surface of Celleporaria is more rugose than that of Schizoporella. This is because Celleporaria, upon maturity, undergoes a secondary calcification that obscures the regular arrangement of zooids and gives it a nodular appearance; the basal stolons of colonizing Zanclea are covered by this secondary calcification. Second, Celleporaria is not an absolute dominant; it is commonly overgrown by a variety of other species. Third, Celleporaria has a specific predator, Hoploplana californica, a cryptically colored flatworm (18). We examined the effects of Zanclea’s presence on the ability of Celleporaria to compete with other sessile invertebrates and to escape predation by Hoploplana.

Competition was measured as the frequency with which Celleporaria was able to overgrow other species on experimental panels (Table 1). Instantaneous measurements of overgrowth were taken at the line of contact between two colonies: the colony whose edge was covering zooids of the other colony was counted as having competed successfully. Long-term observations were also made by photographing the panels about every 6 weeks; the interaction between specific colonies was followed through time until one colony completely covered the other. Overgrowth of a large

Table 1. Ability of Celleporaria brunnea with or without attached Zanclea to overgrow competing species. Asterisks denote one (*) or two (**) interactions in which successful overgrowth by the competing species was arrested after Celleporaria was colonized by Zanclea.

<table>
<thead>
<tr>
<th>Competing species</th>
<th>Zanclea present</th>
<th>Zanclea not present</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Overgrowth at line of contact</td>
<td>Overgrowth of whole colony</td>
</tr>
<tr>
<td>Bryozoa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parmatina sp.</td>
<td>7/7</td>
<td>3/3</td>
</tr>
<tr>
<td>Rhynchozoa rostratum</td>
<td>2/3</td>
<td>2/2*</td>
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<td>Aleyonidium parvimicrum</td>
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<td>Smittoida prolifica</td>
<td>7/7</td>
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<tr>
<td>Costazia robertsoniae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaeta</td>
<td>1/1*</td>
<td>2/2**</td>
</tr>
<tr>
<td>Salmacina tribanchiata</td>
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<td>Purpura</td>
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</tr>
<tr>
<td>Leucosolenia eleanor</td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>10/11</td>
<td>14/14</td>
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Fig. 1. Scanning electron micrographs of the CaCO₃ skeleton of Schizoporella errata with or without Zanclea gemmosa. Specimens were prepared with a 10 percent solution of chlorine bleach to remove all organic material. (a) Normal calcification of Schizoporella without Zanclea. (b) Portion of a Schizoporella colony with Zanclea, showing the added calcification around the basal stolons of Zanclea. Note that the stolons generally occur between zooids and do not pass over the zooidal apertures.

(c) Opening in the calcification around the basal stolons through which a Zanclea polyp protrudes. (d) Area of a colony with only partial calcification around the stolons. The arrow on the left indicates the forming suture between skeletal material deposited by two adjacent Schizoporella zooids. The arrow on the right indicates a raised area where additional deposition of CaCO₃ underneath the hydroid stolon is evident.
Zanclea is 0.18 judged successful if it was continuing to grown. In several cases in which actions that were still incomplete at the end of the study, the colony on top was not overgrown, Celleporaria was quickly over its competitors. When Zanclea was advance over the other colony. The bryozoan by Zanclea resulted in the overgrown, subsequent colonization of the bryozoan. As shown in Table 1, when Zanclea was attached Zanclea the predatory flatworm perisarc, rendering them flexible and contractile (they may be held erect or much smaller than a bryozoan epizoite). Although Celleporaria colonized experimental panels at all localities, it was most abundant at those stations (3 of 20) where Zanclea was also present. At these three stations, the final mean abundance of Celleporaria on panels with Zanclea (30 ± 10 cm² per panel; N = 5) was significantly higher \( t(169) = 2.09 \) than its abundance on panels without Zanclea (2.5 ± 1.9 cm² per panel; N = 13). Similarly, the mean survival time of Celleporaria colonies with Zanclea (17 ± 4 months; N = 9) was significantly different \( t(98) = 7.7, P < .001 \) than that of colonies without Zanclea (8 ± 3 months, N = 9). The evidence seems overwhelming that the ability of these species to utilize space is strongly affected, if not determined, by mutualism.

**References and Notes**


10. Field panels (10 cm²) were suspended horizontally 0.5 to 2 m above the sea floor and non-destructively sampled every 4 to 6 weeks. Only the exterior of the panels was analyzed and photographed.


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