Competitive ability influences habitat choice in marine invertebrates

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Patterns of distribution and abundance of sessile marine epibenthic invertebrates are controlled by three factors: (1) the presence and abundance of larvae which are competent to settle, (2) the choice of settling sites by recruiting larvae, and (3) the biotic and physical events occurring during and after settlement. Although there is much information on the distribution of larvae and seasons of recruitment, substratum selection, and post-settlement events, very little is known of the ecological and evolutionary relationships between these factors.

Natural selection acts on entire life cycles, thus information about these relationships is essential for understanding patterns of recruitment and survival. For example, sessile organisms can modify the course of post-recruitment events by selective settlement and directional growth. Here, we present evidence that the larvae of several taxa of marine invertebrates avoid substrata where there is a high probability of death caused by a superior spatial competitor.

I found, as did Grave, that in the Eel Pond at Woods Hole, Massachusetts (USA), the two compound ascidians Botryllus schlosseri (Pallas) Savigny and Botryllodes leachii (Savigny) cover, by area, over 50%, and sometimes 100%, of hard substrata during the spring and summer. This period includes the season of recruitment for most other colonizers. Thus, settling larvae are likely to contact a Botryllus ascidian at some point during their lives. A common result of contacts between colonists is overgrowth of one organism by another. In this way, overgrowth is a consequence of competition for space (and perhaps other resources), and therefore can be an important factor in the distribution and abundance of encrusting species.

Botryllus schlosseri is the most successful overgrower (along with B. leachii) in the Eel Pond (Table 1) and is rarely overgrown by other species. As it is such an important member of the Eel Pond epibenthic assemblage (considering the post-settlement events of overgrowth and coverage), I investigated the effects of its density on the recruitment of other taxa.

Botryllus schlosseri collected from the Eel Pond were placed in finger-boats where they released larvae which were then transferred to 10 ml polycarbonate dishes. Two hours after settlement on the sides of the dishes, the juveniles were teased off and reattached to 5 x 5 cm glass plates. I set up three densities of juvenile Botryllus with three replicates of each: (1) 15 regularly spaced Botryllus juveniles, with all subsequent botryllid settlement removed daily; (2) 5 regularly spaced Botryllus juveniles with all subsequent botryllid recruits removed daily; and (3) no Botryllus juveniles with daily removal of all botryllid recruits. Three additional glass plates which initially carried no juveniles, but on which all recruits were allowed to remain, served as controls.

Experimental and control plates were positioned horizontally in a Latin square arrangement below a floating dock at 1 m depth. The experiment was started on 20 July, 24 h after the larvae had been transplanted. The lower side of each plate (which carried the juvenile Botryllus) was censused non-destructively until 28 July on a daily basis—this allowed me to distinguish between failure to settle and all but the earliest post-settlement mortality.

Figure 1 shows the numbers of each species that settled on the glass plates. To determine if there were any differences between each of the three density treatments and the controls, the data for each species were analysed using the null hypothesis that
settlement was uniform in each case. $\chi^2$ tests unambiguously
placed the species in two groups: (1) selective species or those
for which settlement was not uniform between treatments
(Fig. 1a, all $P < 0.005$) and (2) non-selective species or those for
which there were no significant differences in settlement
between density treatments (all $P > 0.2$). When settlement on
the plates carrying five B. schlosseri was compared with that on
plates where all botrylids had been removed, settlement was
uniform for all species ($P > 0.5$). On control plates, where
cumulative B. schlosseri settlement reached 15 per plate on the
third day of the experiment, settlement of selective species was
intermediate between that on plates carrying 15 B. schlosseri
and those carrying none or five juveniles. This implies that the
threshold for detection of B. schlosseri by selective species lies
somewhere between 5 and 15 resident Botryllus juveniles.

There is a clear relationship between patterns of recruitment
and a species' susceptibility to overgrowth. The species which
did not settle on plates where Botryllus number was 15 (selective
species) were also overgrown by Botryllus in 1,008 of 1,048
contacts (96.2%). These species are the first nine of Table 1. In
contrast, those species which settled uniformly, regardless of
B. schlosseri density (non-selective species), were rarely over-
grown by Botryllus (171 of 961 contacts or 17.1%). These
species include the remaining 10 of Table 1.

The mechanisms by which settlement is decreased for some
taxa, but not for others, are unclear. Allelopathy $^{2,32,33}$ cannot
account for these results, for when selective species do settle on
the plates (for example, at low Botryllus densities), they often
settle immediately adjacent to the competitive dominant. In
addition, because Botryllus cannot ingest particles as large as
most recruiting larvae $^{24,31}$, selective predation does not explain
the results. It is more likely that the settling larvae of some taxa
can recognise the density of resident Botryllus, and reject sub-
strata when that density exceeds a certain threshold.

Selective settlement has been observed in a number of taxa,
but it is not understood which factors make particular substrata

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Fig. 1 The cumulative settlement for all species which settled during the experiment. Bars represent the mean settlement for the three replicates
de each density treatment and the controls. Lines indicate the range of settlement values. The plates were arranged in a Latin square so that plate
position effects could be detected: the $\chi^2$ analyses indicated there were no significant differences between replicates, thus there were no plate
position effects. Of the 60 transplanted larvae, only one died during the experiment. Any settler not immediately identified was allowed to grow
after the term of the experiment until identification was possible. At the end of the experiment, none of the colorists covered $>2$ mm$^2$, thus
coverage was low. a, Data for species which showed a settlement effect at different B. schlosseri densities. These are termed selective
species—this group includes four encrusting bryozoans, three tube-building polychaetes and two barnacles. All these species have feeding
structures close to the substratum, thus easily obstructed by overgrowth. b, Data for those species which showed no significant differences in
settlement at different Botryllus densities. These are termed non-selective species—this group includes four arborescent bryozoans, two
stoloniferous hydroids, three solitary ascidians and two colonial botrylids ascidians. With the exception of the botrylids, all members of this group
have elevated feeding structures and therefore are generally resistant to the effects of overgrowth (see refs 23, 28).
These data were collected during the summer of 1979 from contacts between animals living on algae, floating docks, rocks and glass plates in the Eel Pond. All contacts were followed from their initiation until their resolution by overgrowth or mutual retreat. Total contacts equal wins + losses + ties. A contact is scored as a win, a loss or a tie based on the overgrowth rates of the two participants. A tie is scored when growth rates of both participants are equal or when B. schlosseri simply grows around another colonizer without perceptible harm to either. Although B. schlosseri infrequently overgrows certain taxa, it is rarely overgrown itself by any taxa. Nevertheless, the capacities of arborescent bryozoans and hydroids sometimes shade underlying compound ascidians.

(or habitats) better than others. Notable exceptions include: (1) the gregarious settlement of some barnacles which apparently ensures cross-fertilization and viability of eggs; (2) the preferential settlement of predators, commensals and parasites near their prey, parents and hosts, respectively; (3) the settlement by some bryozoans and polychaetes of particular algal (or positions on these algae) which correlates with patterns of survival of juveniles and adults; and (4) the gregarious settlement of some arborescent bryozoans which enhances their interspecific competitive ability.

The results from the Eel Pond indicate that some larvae can distinguish substrata where post-settlement events are likely to kill them. Apparently, these larvae avoid encounters with the competitive dominant, B. schlosseri, by settling away from dense stands of it. In comparison, the larvae that do settle where B. schlosseri is abundant are those most immune to overgrowth by it. Taken together, the data illustrate that competition during the post-settlement phase of an organism's life cycle can strongly influence the evolution of habitat selectivity.

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31.手短, 落人の Ecol. 32, 41-49 (1964).

Fertilization potential in golden hamster eggs consists of recurring hyperpolarizations

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The fertilization potential, or activation potential, has been demonstrated in the eggs of various species, and it has been shown to block polyspermy in echinoderm 13, echinuran and frog 14, but no studies have been reported of electrical phenomena occurring when mammalian eggs are fertilized. We report here the fertilization potential of frozen hamster eggs in vitro. To correlate the change of potential with the interaction between sperm and egg, only one sperm was attached to each egg. We found that 133 recurring hyperpolarizations, constituting a fertilization potential which differs from that in the eggs of other species.

Mature eggs were collected from the oviducts of superovulated females 15, and freed from the surrounding cumulus cells and zona pellucida by sequential treatment with 0.1% hyaluronidase (5 min at 23-26 °C) and 0.1% trypsin (4-5 min in medium used for rat eggs). Removal of the zona allows sperm to reach the plasma membrane soon after insemination. Spermatozoon obtained from the cauda epididymis were activated with acrosome reaction by incubation in modified Tyrode solution containing 20% human serum and 1% bovine adrenal gland extract at 37 °C for 4 h. All treatments and experiments were performed in a 0.4 ml drop of medium placed in a plastic Petri dish and covered with paraffin oil. A glass microelectrode was