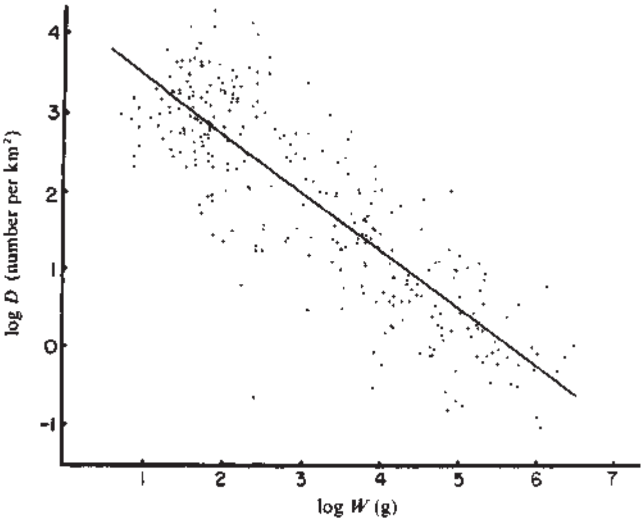

Fig. 1 Population density (D) compared with the mean adult body mass (W) for 307 mammal primary consumers; each point represents one species. Density values for each species are the mean of the means from each locality from which data were reported for the particular species. (Data are from the literature for the years 1950–79, derived from 115 journals and numerous books, ~650 references in all.) The line represents the least-squares regression line, $\log D = -0.75 (\log W) + 4.23$; $r = -0.86$, standard error of the slope = 0.026.

quantitative measure of a qualitative relationship that has been known for some time but only sporadically appreciated[14]. Species of small mammals are able to produce, on average, the same amount of biomass over time as do species of large mammals, whereas at a given moment their standing-crop biomass is considerably less, because the population turnover rates and individual growth rates per unit weight of small species are much greater[15-17].

The widespread occurrence of an approximately reciprocal relationship between population density and individual metabolic requirements among mammalian herbivores suggests that a general principle is involved. The independence of species energy control and body size revealed by this reciprocal relationship implies that random environmental fluctuations and interspecific competition act over evolutionary time to keep energy control of all species within similar bounds. It is unlikely that the occurrence of competition among species of different body sizes is restricted to herbivorous mammals. Along with the ubiquity of allometric scaling of metabolic rate with body size[4], this suggests that a reciprocal relationship, and particularly a value of ~ -0.75, characterizes a broader range of taxa and trophic levels. These points will be discussed more fully elsewhere.

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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 [1-3], substratum selection [4-6] and post-settlement events [7-15], very little is known of the ecological and evolutionary relationships between these factors[5,16-18]. 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[19]. Here, I 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[20], that in the Eel Pond at Woods Hole, Massachusetts (USA), the two compound ascidians *Botryllus schlosseri* (Pallas) Savigny and *Botrylloides 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 botryllid ascidian at some time during their lives. A common result of contacts between colonists is overgrowth of one organism by another[21-29]. In this way, overgrowth is a consequence of competition for space (and perhaps other resources[30]), and therefore can be an important factor in the distribution and abundance of encrusting species.

B. 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.

B. schlosseri collected from the Eel Pond were placed in finger-bowls 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 re-attached to 5×5 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[31] 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

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settlement was uniform in each case. χ^2 tests unambiguously placed the species in two groups: (1) selective species or those for which settlement was not uniform between treatments (Fig. 1*a*, 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 botryllids 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 overgrown 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[22,32,33] 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[34,35], 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 substrata 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

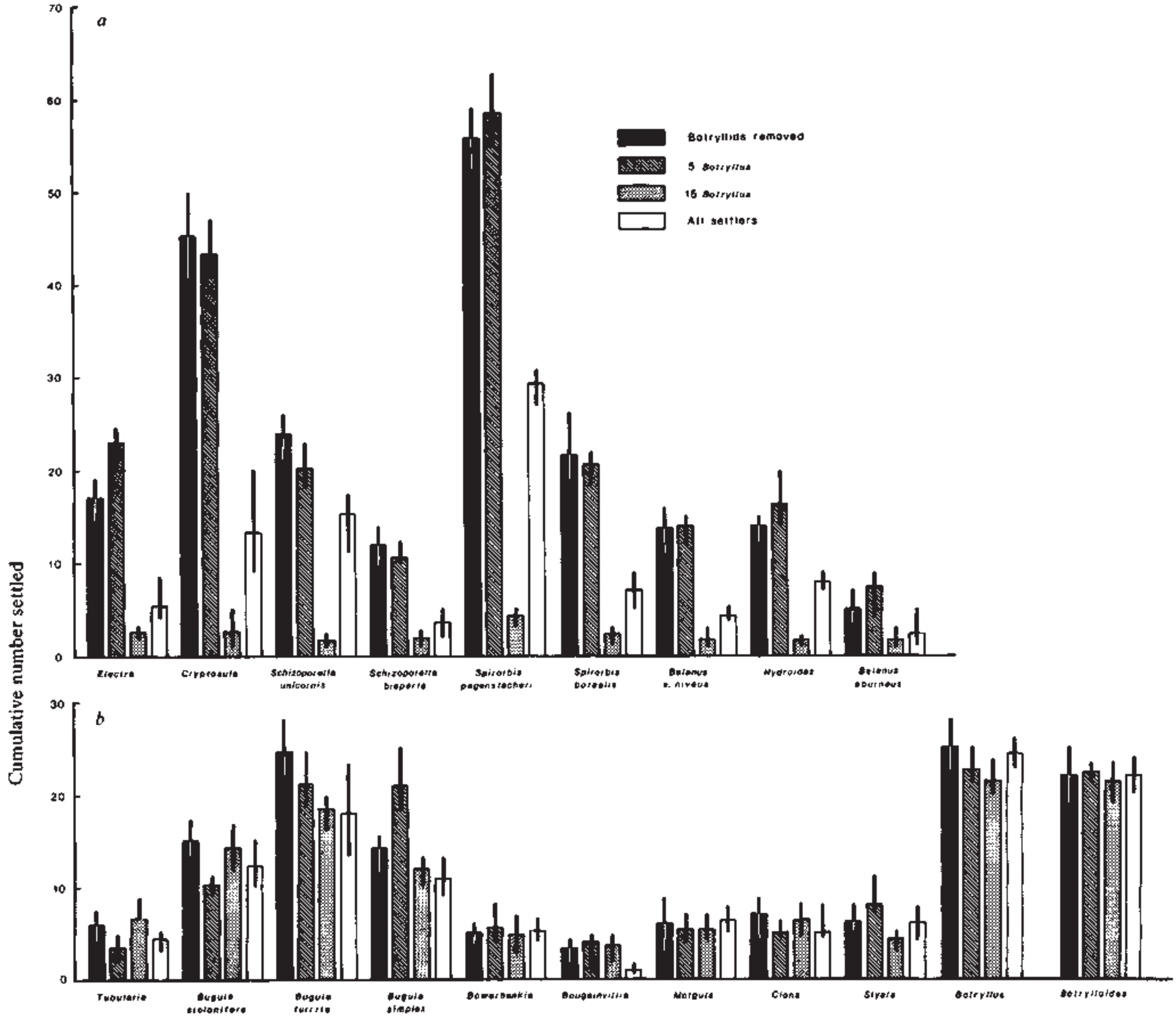

Fig. 1 The cumulative settlement for all species which settled during the experiment. Bars represent the mean settlement for the three replicates of each density treatment and the controls. Lines indicate the range of settlement values. The plates were arranged in a Latin square so that plate position effects could be detected: the χ^2 analyses indicated that 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 colonists 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 botryllid ascidians. With the exception of the botryllids, all members of this group have elevated feeding structures and therefore are generally resistant to the effects of overgrowth (see refs 23, 28).

Table 1 Results of contacts between *Botryllus schlosseri* and the adults of the species which recruited during the period 20–28 July 1979

Overgrown	Wins	Ties	Total	Wins/total (%)	Losses/total (%)
Electra crustulenta	76	0	78	76/78 (97.4%)	2/78 (2.6%)
Cryptosula pallasiana	159	0	159	159/159 (100%)	0/159 (0%)
Schizoporella biaperta	43	0	43	43/43 (100%)	0/43 (0%)
Schizoporella unicornis	58	0	63	58/63 (92.1%)	5/63 (7.9%)
Spirorbis pagenstecheri	382	0	382	382/382 (100%)	0/382 (0%)
Spirorbis borealis	118	13	131	118/131 (90.1%)	0/131 (0%)
Balanus amphitrite niveus	79	10	89	79/89 (88.8%)	0/89 (0%)
Balanus eburneus	47	5	52	47/52 (90.4%)	0/52 (0%)
Hydroides dianthus	46	5	51	46/51 (90.2%)	0/51 (0%)
Botrylloides diegensis	147	108	391	147/391 (37.6%)	136/391 (34.8%)
Tubularia larynx	3	87	84	3/87 (3.5%)	0/87 (0%)
Bougainvillia sp.	2	32	34	2/34 (5.9%)	0/34 (0%)
Bugula stolonifera	2	59	61	2/61 (3.3%)	0/61 (0%)
Bugula turrita	4	76	80	4/80 (5.0%)	0/80 (0%)
Bugula simplex	3	99	102	3/102 (2.9%)	0/102 (0%)
Bowerbankia gracilis	6	64	70	6/70 (8.6%)	0/70 (0%)
Molgula manhattensis	1	26	27	1/27 (3.7%)	0/27 (0%)
Ciona intestinalis	1	15	16	1/16 (6.3%)	0/16 (0%)
Styela clava	2	95	97	2/97 (2.1%)	0/97 (0%)

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 win is scored when *Botryllus* overtops and kills >50% of a colonial organism, or entirely kills a solitary organism. A tie is scored when growth of both participants ceases along a contact, or when *Botryllus* simply grows around another colonizer without perceptible harm to either. Although *Botryllus* infrequently overgrows certain taxa, it is rarely overgrown itself by any taxa. Nevertheless, the canopies 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[6,33,36]; (2) the preferential settlement of predators, commensals and parasites near their prey, partners and hosts, respectively[5]; (3) the selection by some bryozoans and polychaetes of particular algae (or positions on these algae) which correlates with patterns of survival of juveniles and adults[17,18,37]; and (4) the gregarious settlement of some arborescent bryozoans which enhances their interspecific competitive ability[38].

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 selection.

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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[1], and it has been shown to block polyspermy in echinoderm[2,3], echiuran[4] and frog[5] eggs, but no studies have been reported of electrical phenomena occurring when mammalian eggs are fertilized. We report here the fertilization potential of golden 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 a sperm induces 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[6] 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[7]. Removal of the zona allows sperm to reach the plasma membrane soon after insemination. Spermatozoa obtained from the cauda epididymis were activated with acrosome reaction by incubation in modified Tyrode solution containing 20% human serum[8] and 1% bovine adrenal gland extract[9] 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

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