Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore

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ABSTRACT: The mussel *Semimytilus algosus* (Gould) often dominates the space on exposed rocky shores of subtropical South America. Dynamics of space occupancy was investigated in a rocky inter-tidal habitat in central Peru. A series of colonization experiments and quantitative sampling of mussel-associated faunas were conducted to clarify interspecific relationships among resident organisms. Spatial gaps created within the *S. algosus* zone were colonised successively by the barnacles *Jehlius cirratus* (Darwin) and *Notochthamalus scabrosus* (Darwin), a gallery-building polychaete, *Phragmato-poma moerchi* Kinberg, and a mussel, *S. algosus*. The rate of colonisation/recruitment was highest for barnacles, intermediate for *P. moerchi* and lowest for *S. algosus*. There was no evidence that barnacles either facilitate or inhibit colonisation by later colonists *P. moerchi* and *S. algosus*. Three filter-feeding taxa showed a clear competitive hierarchy. *P. moerchi* was competitively superior to barnacles and *S. algosus* was competitively superior to both barnacles and *P. moerchi*. Therefore, there are trade-offs between colonisation ability and competitive ability among these taxa. In addition to recruitment of young larvae on free rock surfaces, *S. algosus* individuals demonstrate continuous lateral migration at the edge of their aggregation, constantly expanding the boundaries. Gaps can be closed in this manner, with an average rate of edge advance of 1.2 cm mo^{-1}, which is comparable to the values estimated for *Mytilus californianus* on North American rocky shores. The *S. algosus* bed constitutes an important habitat to a range of organisms, many of them (particularly polychaetes) being restricted to this habitat on exposed rocky shores. Comparisons were made between faunas on free rock surfaces and in the mussel bed. Proportions of taxa restricted to the mussel bed were high among all invertebrates found there, in the range of 67 to 78 % in terms of number of taxa and 80 to 94 % in terms of number of individuals. Furthermore, juveniles of many organisms find refuge in the *S. algosus* bed, and barnacles which are competitively inferior to *S. algosus* can nevertheless exist epizoically on their shells. Thus, monopolisation of space by *S. algosus* generally leads to an increase in total species richness.

KEY WORDS: Gap dynamics · Space occupancy · Mussels Competition · Rocky shores · Mussel-associated fauna

INTRODUCTION

How organisms use space is one of the central questions in population and community ecology. It has been recognised that many communities are characterised by a small number of dominant taxa that tend to define the physical structures of a habitat, such as forest trees, sea grass meadows and coral reefs. In the case of intertidal rocky shores, mytilid bivalves are known to dominate the space and form an extensive bed in different parts of the world (cf. Seed 1976,

Suchanek 1985, Seed & Suchanek 1992). Apart from North American sites, however, the dynamics of space use and habitat colonisation in mussel-dominated communities have not been studied intensively. A geographically biased basis of our knowledge makes a sharp contrast to the perceived importance and generality of some ecological paradigms derived from a number of studies on species interactions in the mussel beds of North American rocky shores. Investigation on similar systems from different geographical regions is necessary for an integrative understanding

of processes on different scales (cf. Underwood & Denley 1984).

One of the important issues concerning the maintenance of space-monopolising structures in ecosystems relates to the aspects of recruitment and habitat colonisation. In particular, the ways in which gaps in space are formed and subsequently filled by organisms determine the nature and dynamics of community organisation. In marine benthic systems, interspecific competition as well as facilitation and inhibition are considered as important mechanisms of colonisation and succession (Connell & Slatyer 1977). On intertidal rocky shores there is usually a range of sessile as well as mobile organisms which can colonise open space, though they do not necessarily exclude other species. Amongst these, mytilid bivalves have been described as competitive dominants capable of monopolising space which is otherwise available for colonisation by other taxa. Thus, it has widely been understood that space occupancy by mytilids could significantly reduce species diversity on a rocky shore, a situation which may in some cases be effectively hindered by starfish predation (Paine 1974). Less well understood beyond a circle of rocky shore ecologists is the fact that 3-dimensional structures created by mytilids may facilitate colonisation by certain organisms (Suchanek 1979, 1985, Tsuchiya & Nishihira 1985, 1986, Tokeshi et al. 1989, Tsuchiya & Bellan-Santini 1989), which would either decrease in density or altogether disappear if mytilids do not exist on the rocky substratum.

The present study deals with colonisation and space use of exposed rocky intertidal habitats in central Peru. Subtropical rocky shores on the Pacific coast of South America are often extensively colonised by 2 mussel species, *Semimytilus algosus* (Gould) and *Perumytilus purpuratus* (Lamarck) (Tokeshi et al. 1989). *S. algosus* appears to be restricted to low to middle latitudes of Pacific South America, while *P. purpuratus* is more common in cold temperate waters of Chile and southern Argentina. On the Pacific coast, the latter species increases in proportion towards higher latitudes and eventually forms a single mussel zone in central and southern Chile (Alveal et al. 1973, Castilla 1981). In the Peruvian intertidal where the 2 species coexist, they demonstrate distinct zonation with *S. algosus* forming a lower and often more extensive zone than an upper *P. purpuratus* zone (Paredes 1974, Tokeshi et al. 1989). The present study concentrates on the dynamics of the low/mid-intertidal *S. algosus* zone, which is temporally more variable and contains much higher species richness than the upper *P. purpuratus* zone. Besides *P. purpuratus*, the rock surfaces in the upper zone can be colonised only by a cirripede, *Notochthamalus scabrosus* (Darwin), a gastropod, *Littorina peruviana* (Lamarck) and a green alga, *Ahnfeltia* sp., due mainly

to a high risk of desiccation and heat (M. Tokeshi pers. obs.) (analogous to the *Septifer vergatus* (Wiegmann) zone above the *Mytilus edulis* L. zone on the Pacific northeastern Japanese coast; cf. Hoshiai 1964, Tsuchiya 1983). *S. algosus*, on the other hand, sometimes extends to the subtidal where it may attain large size (>7 cm); individuals in the intertidal rarely exceed 4 cm in length in the study site, though they build up huge populations (density-limited growth; cf. Okamura 1986a).

The specific objectives of the present study are, firstly, to clarify the patterns of colonisation on a primary rock surface in the *Semimytilus algosus* zone, with particular reference to the aspects of interspecific competition and facilitation/inhibition, and, secondly, to examine quantitatively the faunas associated with the mussel bed with a view to considering the possible role of *S. algosus* aggregation in either reducing or enhancing the overall species richness of a South American rocky intertidal system.

MATERIALS AND METHODS

The study was undertaken in the exposed promontory of the Ancón Bay in central Peru (11° 46' S, 77° 12' W). A series of colonisation experiments and regular sampling of mussel-associated faunas were carried out within the *Semimytilus algosus* zone between April 1986 and April 1987.

Colonisation experiments. *Expt A, patterns of succession:* Twenty circular areas of ca 20 cm in diameter were cleared of organisms and within each circle a 10 × 10 cm quadrat was established. At approximately fortnightly intervals colonisation was monitored using a 10 × 10 cm metal frame which was subdivided into 2 × 2 cm cells. On each occasion, the cumulative area of coverage by each organism was estimated by summing up coverage in individual cells; the results were expressed as the number of cells occupied. For some larger, less numerous organisms such as a gastropod *Tegula atra* (Lesson) individual counts were also made. In this experiment areas outside the 10 × 10 cm quadrat but within the 20 cm circle were kept cleared of organisms to eliminate any edge effect of the *Semimytilus algosus* bed, i.e. the influence of individuals existing at the edge of a mussel colony either facilitating or inhibiting colonisation processes within a quadrat.

Expt B, barnacle effects: This experiment tested the effects (facilitation/inhibition) of the first colonist, barnacles, on later colonists. Quadrats were prepared as in the first experiment, and after 8 wk to allow the establishment of barnacle colonies, 10 replicate quadrats were assigned to barnacle removal and 10 others to control. Barnacles were scraped off the rock

substrate with a knife at the start and throughout the experimental period of 5 mo. Coverage by *Phragmatopoma moerchi* Kinberg and *Semimytilus algosus* was estimated as in Expt A.

Expt C, succession and competition: Following the course of events in Expts A and B, 3 separate experiments were conducted to establish the competitive relationships among colonising organisms which demonstrated successive replacement during austral spring- summer. These comprised 3 different filter-feeding taxa, the barnacles *Jehlius cirratus* Darwin and less commonly *Notochthamalus scabrosus*, a polychaete *Phragmatopoma moerchi* and *Semimytilus algosus*. In the first set of experiments, survival of barnacles was investigated. Thirty 10 × 10 cm quadrat areas were cleared of organisms and left for colonisation. After 8 wk to encourage initial settlement, these quadrats were assigned to 1 of 3 treatments (10 replicates each): (1) both *P. moerchi* and *S. algosus* removed; (2) *P. moerchi* removed, *S. algosus* left untouched; (3) both *P. moerchi* and *S. algosus* left untouched. In each treatment individuals of *S. algosus/P. moerchi* within a quadrat were carefully removed (including byssal threads and *P. moerchi* tube fragments) from the rock surface with a knife from Week 0 (start of experimental treatment) to Week 7 at weekly intervals. Abundance or spatial coverage of barnacles was assessed on Weeks 4 and 8 using the frame divided into 2 × 2 cm quadrat cells. The second set of experiments dealt with the survival of *P. moerchi* with and without *S. algosus*. Twenty 10 × 10 cm quadrats were established as above and 10 of these were assigned to *S. algosus* removal and the rest to control. The abundance of *P. moerchi* was assessed on Weeks 4 and 8. The third set of experiments tested the survival of *S. algosus* with or without *P. moerchi* with 10 replicates each and followed the same procedures as above.

Expt D, gap filling and lateral migration: Ten circular areas of ca 35 cm diameter were cleared of mussels and other organisms, and lateral colonisation by the expanding edge of the *Semimytilus algosus* bed was monitored by measuring the gap size defined as an average of 2 measurements, i.e. the longest diameter and the longest length perpendicular to the first measurement. Monitoring was conducted at fortnightly intervals until the gaps were completely closed.

Faunal sampling. In parallel with these colonisation experiments, the fauna associated with the *Semimytilus algosus* bed was sampled quantitatively at bimonthly intervals. The mussel bed (ca 9 m^2 in area) was mapped and grids were established to facilitate random sampling. Fifteen replicate sampling units (10 × 10 cm quadrats) were taken on each occasion. Mussels and associated organisms within a quadrat were quickly and thoroughly removed from the rock surface and transferred to a plastic bag with 10% formaldehyde. When surf intervened during the act of sampling, that sample was discarded and a new one taken; this precaution was taken in order to avoid biased sampling or loss of certain organisms such as free-ranging polychaetes. In the laboratory, samples were washed through a sieve of 0.25 mm mesh and individuals of different taxa were counted. Thus, the present study dealt with macrofaunal invertebrates, the majority of which reached a body size (length) of 10 mm or larger. Observations were also made on organisms which occurred on bare rock surfaces unassociated with the *S. algosus* bed. Rock surfaces within 8 m of shore at the study site were searched and organisms were noted for their presence. This observation covered the whole year.
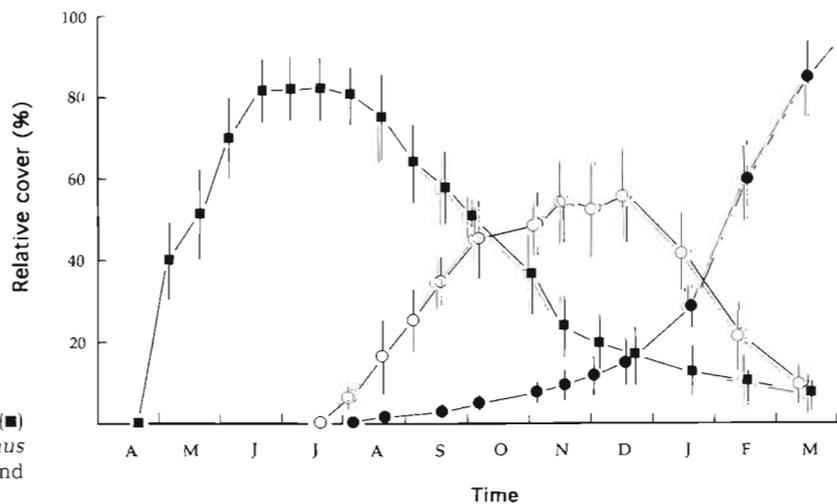

Fig. 1. Variation in relative cover (±1 SE) of (■) barnacles *Jehlius cirratus* and *Notochthalamus scabrosus*, (O) *Phragmatopoma moerchi* and (●) *Semimytilus algosus*
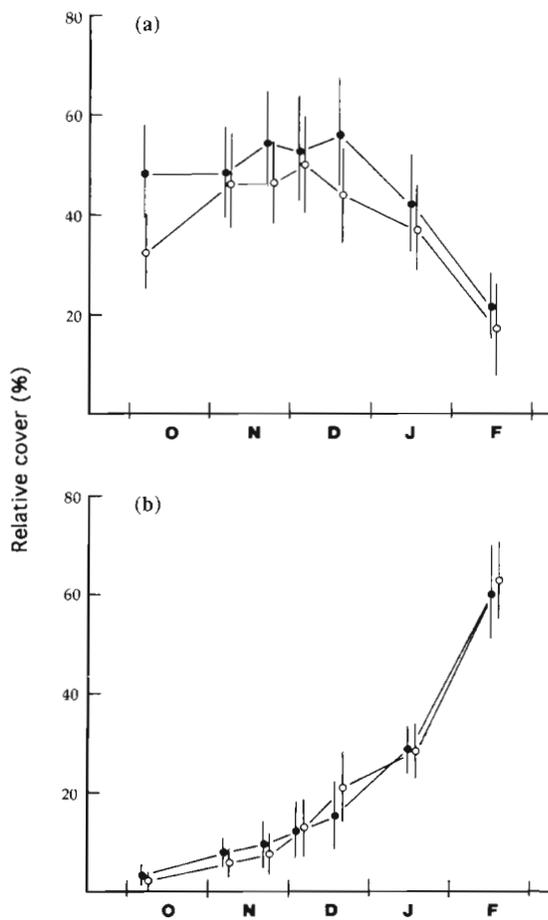
Fig. 2. Variation in relative cover (±1 SE) of (a) *Phragmato-poma moerchi* and (b) *Semimytilus algosus*, in quadrats with (●) and without (○) barnacles

RESULTS

Colonisation experiments

Expt A. Temporal patterns of colonisation on denuded rock surfaces within the *Semimytilus algosus* bed are shown in Fig. 1; taxa which occurred sporadically, such as *Phymactis clematis* (Drayton), *Tegula atra* and *Lottia ceciliana* (Orbigny), are excluded here. Barnacles, mainly *Jehlius cirratus*, rapidly colonised the open space and within 2 mo occupied ca 80% of cells (i.e. 20 out of 25). Three months after starting the experiment, a gallery-building polychaete, *Phrag-matopoma moerchi*, started to appear and reached 60% of occupancy in 5 mo, while the abundance of barnacles steadily declined from austral winter (July–August) onwards. *P. moerchi* abundance in turn followed a declining trend from December onwards and, together with barnacles, virtually disappeared from the rock surface towards the end of March. *S.*
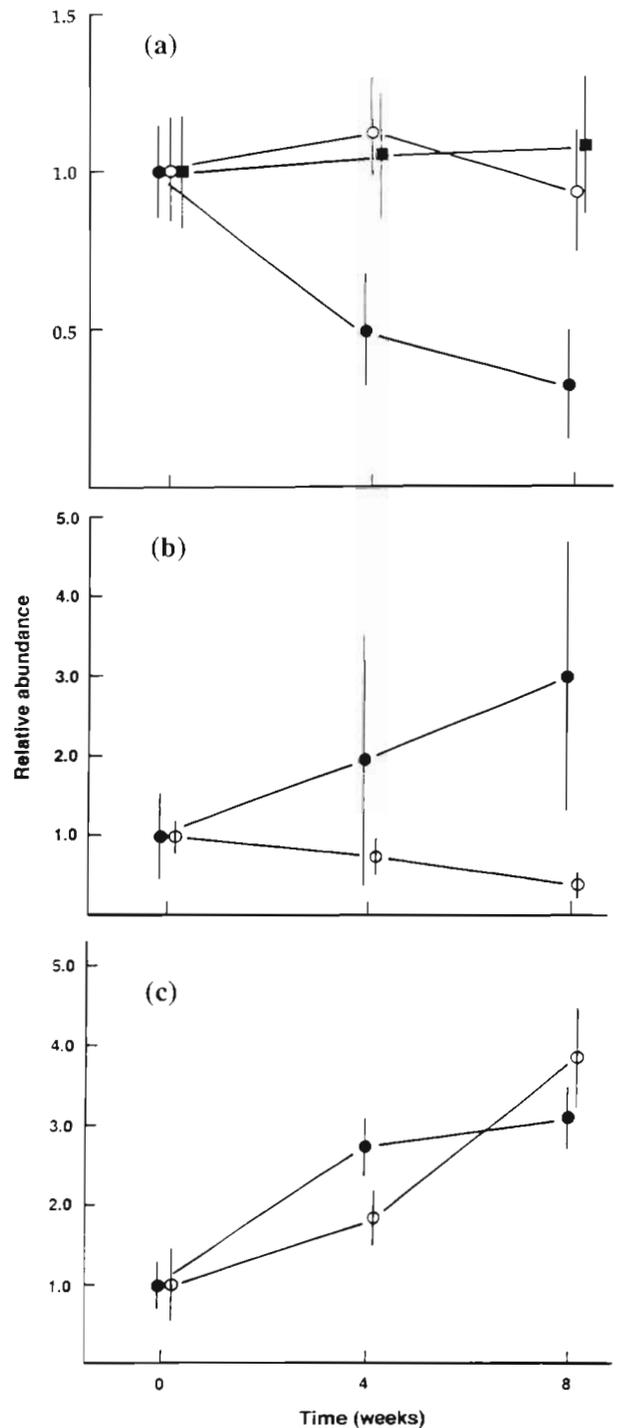

Fig. 3. (a) Relative abundances of barnacles *Jehlius cirratus* and *Notochthalamus scabrosus* in different treatments: (■) both *Phragmatopoma moerchi* and *Semimytilus algosus* removed; (○) *P. moerchi* removed, *S. algosus* untouched; (●) both *P. moerchi* and *S. algosus* untouched. (b) Relative abundances of *P. moerchi* when *S. algosus* was manipulated: (●) *S. algosus* removed; (○) *S. algosus* untouched. (c) Relative abundances of *S. algosus* when *P. moerchi* was manipulated. (●) *P. moerchi* removed; (○) *P. moerchi* untouched. All values are mean ±1 SD

algosus first appeared in August but their increase in abundance was slow until December. Thereafter, *S. algosus* rapidly increased and virtually monopolised the space by April, although it was not completely filled until an additional 2 mo had elapsed. Thus, the 3 taxa demonstrated a clear pattern of colonisation and the open space reverted to its original state of *S. algosus* dominance within a year. It is also notable that the rate of colonisation/recruitment for the first 2 to 3 mo of settlement was highest for barnacles (2.3 ± 0.7 cells wk^{-1}, mean ± 1 SD), intermediate for *P. moerchi* (1.1 ± 0.1 cells wk^{-1}), and lowest for *S. algosus* (0.19 ± 0.07 cells wk^{-1}).

Expt B. The results of the second experiment demonstrate that there is no statistically significant difference in the densities of either *Phragmatopoma moerchi* (Fig. 2a) or *Semimytilus algosus* (Fig. 2b) colonising substrates with and without barnacles. Therefore, barnacles neither facilitated nor inhibited later colonists. The effects of *P. moerchi* and *S. algosus* on one another are unlikely to alter this conclusion (see results of Expts C and D below), as each of these taxa colonised quadrats with and without barnacles in similar abundances (ANOVA for differences in density, p > 0.05).

Expt C. The decline of the barnacles from August onwards was accompanied by increases in *Phragmatopoma moerchi* and *Semimytilus algosus* (Fig. 1), suggesting that either both or one of these species negatively affected the barnacle population. Fig. 3a shows the results of an experiment in which either *P. moerchi* or *S. algosus* was removed during this period of barnacle decline. The abundances of barnacles were standardised as values relative to those on Week 0 (start of experimental treatment) in order to clarify the trends. Relative abundances of barnacles did not vary significantly when both *P. moerchi* and *S. algosus* were removed; no new recruitment of larvae seemed to have occurred during the experimental period. The same pattern of no significant variation in relative abundance was observed in the treatment where only *P. moerchi* was removed; relatively low abundance of *S. algosus* during this period seemed to have caused no significant negative effect. However, the treatment in which both *P. moerchi* and *S. algosus* were left untouched demonstrated a significant decline in barnacle abundance on Weeks 4 and 8 (ANOVA, p < 0.01), as was observed in Expt A. Thus, it is reasonable to conclude that *P. moerchi* directly outcompeted barnacles during the initial phase of barnacle decline (i.e. August to December).
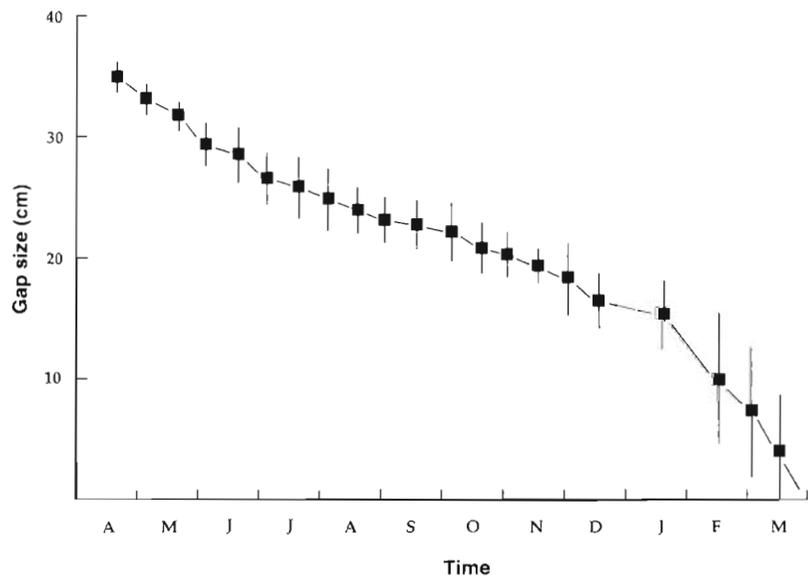

Fig. 4. Change in gap size (mean ±1 SD) in the *Semimytilus algosus* bed

A decline in the *Phragmatopoma moerchi* population from December onwards as revealed in the first colonisation experiment was further investigated in an experiment in which *Semimytilus algosus* was manipulated (Fig. 3b). Relative abundances of *P. moerchi* showed contrasting trends in the 2 treatments, increasing in the absence of *S. algosus* and decreasing in its presence from Weeks 4 to 8, though differences became statistically significant only in Week 8 (ANOVA, p < 0.05). Thus, *P. moerchi* was negatively affected by *S. algosus* in austral summer.

Another set of experiments tested whether the initial colonisation by *Semimytilus algosus* was hindered by existing individuals of *Phragmatopoma moerchi*. The relative abundances of *S. algosus* showed a similar pattern of increase with and without *P. moerchi* (Fig. 3c), indicating that there was no significant (p > 0.05) negative effect of the latter species on the former.

Expt D. Open gaps were steadily colonised by *Semimytilus algosus* individuals at the boundaries (Fig. 4), with the mussels constantly shifting positions and expanding the periphery of their colonies. In this process barnacles and *Phragmatopoma moerchi* individuals which colonised the gaps were gradually overshadowed by the advancing edges of mussel aggregations. As colonisation progressed, the circular shape of the initial gap was lost due to differential rates of colonisation at different points on the boundary, leading to a rapid closing of the gap in the final phase of colonisation, i.e. January to March. The rate of colonisation or expansion of the boundary for the first 9 mo was in the range of 0.8 to 2.0 cm mo^{-1}, with an average of 1.2 cm mo^{-1}. Gaps were completely closed at the end of 1 yr.

Table 1. Invertebrate faunas observed on rock surfaces and in the *Semimytilus algosus* bed in the low-mid intertidal of Ancón, Peru

Taxa restricted to open rock surface (including crevices and the outer edge of a mussel bed)		
Phyllactis concinnata Dana	Anthozoa	Crevice occupant
Phymactis clematis (Drayton)	Anthozoa	Adult
Phragmatopoma moerchi Kinberg	Polychaeta	
Austromegabalanus psittacus (Molina)	Crustacea	
Prisogaster niger (Wood)	Gastropoda	
Fissurella spp.	Gastropoda	Adult, large ind.
Tegula atra (Lesson)	Gastropoda	Adult
Enoplochiton niger (Barnes)	Polyplacophora	Adult
Arbacia incisa (Blainville)	Echinoidea	Adult
Tetrapigus niger (Molina)	Echinoidea	Adult
Taxa occurring in both open rock surface and mussel beds		
Phymactis clematis (Drayton)	Anthozoa	Juvenile [a]
Enoplochiton niger (Barnes)	Gastropoda	Juvenile [a]
Tegula atra (Lesson)	Gastropoda	Juvenile [a]
Fissurella spp.	Gastropoda	Juvenile [a]
Lottia ceciliana (Orbigny)	Gastropoda	
Notochthamalus scabrosus (Darwin)	Crustacea	
Jehlius cirratus (Darwin)	Crustacea	
Balanus laevis Bruguiere	Crustacea	
Tetrapigus niger (Molina)	Echinoidea	Juvenile [a]
Taxa restricted to mussel beds		
Halosydna johnsoni (Darboux)	Polychaeta	
Pseudonereis gallapagensis Kinberg	Polychaeta	
Steggoa negra Hartmann-Schröder	Polychaeta	
Syllis gracilis Grube	Polychaeta	
Typosyllis spp.	Polychaeta	
Nereis callaona (Grube)	Polychaeta	
Lumbrineris annulata Hartmann-Schröder	Polychaeta	
Lumbrineris tetraura (Schmarda)	Polychaeta	
Scoloplos spp.	Polychaeta	
Mediomastus branchiferus Hartmann-Schröder	Polychaeta	
Ophiactis kröyeri Lütken	Ophiuroidea	
Unidentified Nemertini		
Unidentified isopods		

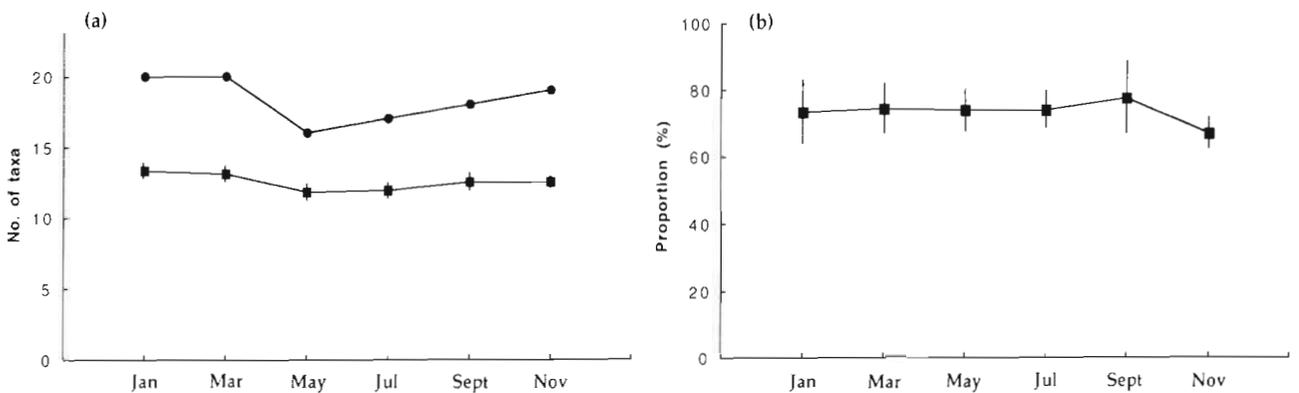[a] Juveniles commonly occur in mussel beds

Fig. 5. (a) Total number of invertebrate taxa (15 sampling units amalgamated) associated with the *Semimytilus algosus* bed (●) and mean number of taxa (±1 SD) per 100 cm² quadrat (■). (b) Variation (±1 SD) in the proportion of taxa which were restricted to the mussel bed among all taxa found
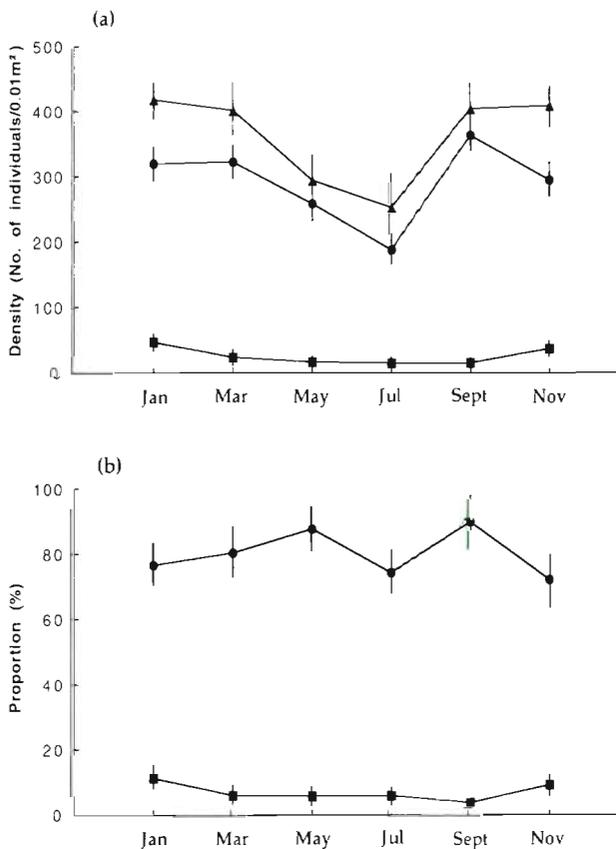
(a)

(b)

Fig. 6. Variation (±1 SD) in (a) the density of all invertebrate taxa (▲), polychaetes (●) and *Ophiactis kröyeri* (■) associated with the *Semimytilus algosus* bed; (b) the proportion of polychaetes (●) and *O. kröyeri* (■) among all invertebrate individuals found in the *S. algosus* bed

Mussel beds versus open space faunas

Some taxa were restricted either to mussel beds or to open rock surfaces, while others occurred in both habitats (Table 1). These faunal compositions varied very little throughout the year. Many taxa found on open surfaces were grazers such as keyhole limpets of the genus *Fissurella*, gastropods (*Tegula atra* and *Prisogaster niger*) and echinoids (*Tetrapigus niger* and *Arbacia incisa*). Filter-feeding anthozoans such as *Phymactis clematis* and *Phyllactis concinnata* also occurred in the open rock substrate, the former on exposed surfaces and the latter in cracks and depressions. In contrast, the *Semimytilus algosus* substrate supported a wide range of predaceous and detritivorous polychaetes and ophiuroids which were not found on open rock surfaces. It is also notable that juveniles of some taxa whose adults occurred in abundance on open rocks such as *P. clematis* and *T. atra* were commonly found in the mussel bed. On the whole, it is apparent that the *S. algosus* substrate had higher spe-

cies richness than open rock surfaces, due mainly to the occurrence of polychaete species which were completely missing in the latter.

The number of taxa associated with the *Semimytilus algosus* bed varied little throughout the year, with slightly lower numbers recorded in austral winter when the data from 15 quadrats were amalgamated (Fig. 5a). The absolute numbers of taxa are thought to be underestimated here, since the numerically most abundant group, a polychaete genus *Typosyllis*, is believed to contain at least 3 species which could not be distinguished in the present study. Nevertheless, the overall pattern of small variation in species richness of mussel-associated invertebrates is considered a valid observation. Amongst the mussel-associated taxa, the proportion of those restricted to this habitat was consistently high, being in a narrow range of 67 to 78% throughout the year (Fig. 5b). This was mainly due to the permanent presence of polychaete species in the *S. algosus* bed. In terms of density of individuals, the total density of all taxa reached a relatively low level from May to July, quickly recovering towards September (Fig. 6a). This was mainly due to fluctuations in the abundance of the most important taxa among mussel-associated invertebrates, polychaetes. The density of another taxon restricted to the *S. algosus* bed, the ophiuroid *Ophiactis kröyeri*, remained in the range 1470 to 4690 ind. m^{-2} throughout the year. Altogether, variation in the density of mussel-associated invertebrates was well within 1 order of magnitude. Finally, it is notable that the proportions of polychaetes and ophiuroids among all invertebrate individuals demonstrated little fluctuations, the former between 72 and 90% and the latter between 3.7 and 11% (Fig. 6b). Therefore, in terms of numbers of individuals, those taxa restricted to the mussel bed accounted for 80 to 94% of all invertebrates found in this habitat.

DISCUSSION

Spatial dominance by mussels has been experimentally investigated in a number of systems in North America, both intertidal (Dayton 1971, Paine 1971, 1974, Menge 1976, Peterson 1979, Paine & Levin 1981) and subtidal (Dean & Hurd 1980, Schoener & Schoener 1981, Chalmer 1982, Greene & Schoener 1982, Okamura 1986b). It has been suggested that early colonists can facilitate or inhibit the recruitment of later colonists (Connell & Slatyer 1977, Dean & Hurd 1980), though unequivocal quantitative data demonstrating both phenomena are sparse. In the present study there was an orderly succession by 3 filter-feeding taxa, from barnacles to the gallery-building *Phragmatopoma*

moerchi and finally to *Semimytilus algosus*. Experimental results suggest that barnacles were competitively eliminated by *P. moerchi* and the latter was outcompeted by *S. algosus*. It is interesting to note here that amongst the 3 taxa there appear to exist trade-offs between competitive ability and colonisation ability or the initial rate of colonisation.

Mechanisms of competition were clearly identified as overgrowth of late colonists and interference with filtering. *Phragmatopoma moerchi* individuals constructed their galleries directly over barnacle settlements (less than 2 mm tall), thus physically interfering with the filtering activities of barnacles. Similarly, colonisation by *Semimytilus algosus* over polychaete galleries increased siltation around their entrances. This became more pronounced as mussel settlement increased. Indeed, regular sampling of the mussel bed habitat revealed a substantial amount of sand and silt being trapped under the mussels, a situation which does not exist on exposed surfaces. Overall, later colonists were clearly competitively superior to earlier colonists and there was no evidence of inhibition by the latter on the former. Thus, the barnacle-*P. moerchi*-*S. algosus* relationships on a Peruvian rocky shore are similar to the *Chthamalus dalli-Balanus cariosus-Mytilus californianus* relationships on a North American rocky shore (Dayton 1971). On the other hand, there was no evidence of *S. algosus* colonisation being facilitated by barnacles or polychaetes, as was the case with *Mytilus* spp. colonising surfaces conditioned by barnacles, hydroids or tunicates (Dayton 1971, Dean & Hurd 1980, Okamura 1986b). It is possible that small-sized individuals of *Jehlius cirratus* do not alter the substrate surface textures sufficiently to enhance settlement of *S. algosus* larvae. Similarly, the presence of *P. moerchi* galleries made of sand grains do not significantly change the colonisability of a substrate by *S. algosus*. Thus, although *S. algosus* larvae were observed to settle preferentially on substrates already colonised by certain organisms, particularly algae of the genus *Polysiphonia* (cf. Seed 1969 in the case of *M. edulis*), neither positive nor negative interactions seem to occur with 2 filter-feeding early colonists. In a similar vein, colonisation by *P. moerchi* was neither inhibited nor facilitated by the presence of barnacles.

The above observation raises a question about the survival of barnacle and *Phragmatopoma moerchi* populations on the shores predominantly occupied by *Semimytilus algosus*. In the case of barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*, both are capable of colonising the shells of *S. algosus*, thus leading an epizoic life in the *S. algosus* bed. Small adult body sizes of these species (basal size generally less than 10 mm) are clearly advantageous in this respect, allowing

them to find a suitable microhabitat on *S. algosus* shells. This makes a clear contrast to larger species of barnacle such as *Balanus laevis* (basal diameter reaching 20 mm) which rarely occurred epizoically on *S. algosus*. Therefore, although *J. cirratus* and *N. scabrosus* are easily excluded from the primary rock surfaces by *S. algosus*, their populations can nevertheless persist epizoically with the mussels. It is possible that the substrate provided by *S. algosus* shells is less stable for colonising barnacles (i.e. *S. algosus* move about and may be dislodged, orientation to water currents may vary, the shell surface may peel off, etc.) than the rock surfaces, the increased surface area over the mussel bed may compensate for some loss of barnacle populations. Indeed, barnacles occur in abundance on the mussel bed throughout the year.

Phragmatopoma moerchi, on the other hand, seems incapable of leading an epizoic life on the shells of *Semimytilus algosus*, mainly because its tubes are relatively large (reaching 40 mm in length) and cannot easily be accommodated on the mussel shells. In consequence, its population tends to exist as isolated patches of colonies often established at the periphery of a mussel bed. Thus, *P. moerchi* is truly excluded by *S. algosus* aggregations and needs peripheral refugia to maintain its population.

It was observed that *Semimytilus algosus* has 2 different ways of filling a spatial gap: (1) colonisation by recruiting young larvae ('plantigrades') and by drifting individuals detached from substrata elsewhere; and (2) gradual lateral movement of individuals at the edge of a mussel bed. The former is a less predictable process, being dependent upon factors such as seasonality, current conditions and chance. This was demonstrated in a rather slow (initially at least) colonisation of denuded rock surfaces (Fig. 1), taking 5 mo to reach 20% cover since *S. algosus* first appeared. In contrast, lateral migration of individuals at the periphery of a mussel bed occurs constantly, as shown by a steady decrease in gap size (Fig. 4) throughout the year. In terms of the rate of filling a gap within a mussel bed, the latter process was much faster than free colonisation from drift. The expansion rate observed (1.2 cm mo^{-1}) is comparable to the value obtained for *Mytilus californianus* on the Pacific North American coast (1.5 cm m^{-1}; Paine & Levin 1981). Indeed, if edges were left and lateral migration were allowed in the first experiment, the 10 × 10 cm quadrat would have been completely closed in less than 5 mo, probably preventing the establishment of *Phragmatopoma moerchi* colonies. Such a situation was observed for those gaps left after the regular sampling of *S. algosus*-associated fauna; these were very rapidly closed, generally in less than 3 mo. As this is an 'edge effect', it is natural that this mode of colonisation assumes more importance as

gap size becomes smaller. Therefore, gaps of different sizes may be affected differently by free colonisation and lateral migration (Paine & Levin 1981).

In addition to the dynamics of sessile organisms which occupy the primary rock surface, the present study has revealed a substantial number of taxa which were closely associated with the *Semimytilus algosus* bed. In particular, polychaetes form an important group, consistently accounting for a large proportion of the invertebrate fauna in terms of both species diversity and the number of individuals. Free-ranging predatory polychaetes require protection from predators and pounding waves in the form of an intricate matrix of mussels, which also harbour polychaetes' prey organisms. Similarly, detritivorous polychaetes as well as ophiuroids utilise detrital material accumulated in the *S. algosus* bed; apart from mussel beds, they normally occur in protected microhabitats of unexposed shores, particularly under stones. Without mussel cover, both the consumers and their resources will be lost. The bare rock surface, on the other hand, supports a range of organisms which are restricted to that habitat, particularly grazers, though the (potential) number of such taxa appears smaller than the mussel-associated fauna. In this context, whether subtropical South American rocky shores possess a relatively depauperate fauna of grazing taxa in comparison to rocky shores elsewhere is unknown. Nevertheless, it should be stressed here that juveniles of taxa in which the adult occurs on free rock substrates were often found in the *S. algosus* bed, suggesting that the latter serves as a nursery ground for many taxa.

These observations point to the importance of mussel beds as a habitat for a wide range of infaunal organisms (cf. Tsuchiya & Nishihira 1985, 1986, Seed & Suchanek 1992) which will inevitably disappear if the habitat is lost. This aspect of the dynamics of mussel beds has received less attention in earlier studies on the community structures of mussel-dominated rocky shores where emphasis tended to be placed on a decline in species richness as mussels monopolise space. A decline may be evident if attention is focused only on a certain range of grazing and filter-feeding taxa. The mussel beds add 3-dimensional structures to essentially 2-dimensional rock surfaces, vastly increasing the habitable space which is buffered against waves. As a result, 'spatial gaps' on the rocky shore habitat are filled not only by *Semimytilus algosus* but also by many other taxa. This implies that species richness is bound to decrease if mussel beds are removed by predators such as starfish [cf. the South American sun-star *Heliaster helianthus* (Lamarck) occurs commonly in the study site (Tokeshi 1989, 1991, Tokeshi et al. 1989, Tokeshi & Romero 1995)] and wave actions.

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