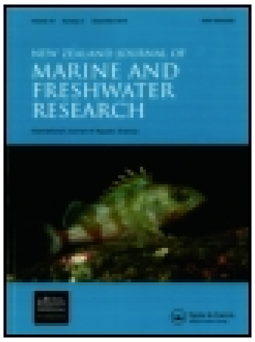

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COMPETITION AND INTERTIDAL ZONATION OF BARNACLES AT LEIGH, NEW ZEALAND

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ABSTRACT

Three species of barnacles (*Chamaesipho brunnea, C. columna,* and *Epopella plicata*) occupy a large part of the intertidal zone at Goat Island Bay, Leigh. Although settlement and growth patterns vary in the three species, intraspecific competition results mainly in reduced growth rates with increasing density. Smothering of earlier settled specimens occurs occasionally in *C. columna.* Competition and preferential predation by gastropods restrict *C. brunnea* to the upper shore. *Epopella plicata* and *C. columna* compete for settlement space. At the lower shore levels, competition from oysters, mussels, and algae reduces the rock space available for barnacle settlement.

INTRODUCTION

On certain shores, competition has been shown to be an important factor in bringing about the barnacle zonation observed (Connell 1961a, b), but at other shores its effect has not been apparent (Lewis 1957). The following assessment of the role of competition in barnacle zonation at Goat Island Bay was undertaken in conjunction with that of the effects of predation (Luckens unpublished 1966, 1975).

Observations were made on several shores in the Auckland area, but most of the experimental work was done on a reef near the Auckland University Marine Research Laboratory at Goat Island Bay (36° 16′ S, 174° 48′ E) near Leigh, on the east coast of the North Island, some 96 km (60 miles) north of Auckland, from 1964 to 1966. From June 1964 until June 1965 monthly visits were also made to Piha on the west coast near Auckland, these being a continuation of visits started in January 1962.

Settlement of barnacles on cleared rock, undisturbed surfaces, and artificial surfaces including perspex and concrete was noted, and their growth and development was kept under close observation. Photographs were taken regularly of selected areas to determine growth rates and mortality.

A general survey of New Zealand shores (Morton & Miller 1968), a survey of the Leigh area (Morton & Chapman 1968), the effects of temperature on barnacles (Foster unpublished 1965), and a discussion of barnacle breeding, settlement, and the effect of altered submergence times on barnacles at Goat Island Bay (Luckens 1970) contain further details of the zonation summarised in Fig. 1.

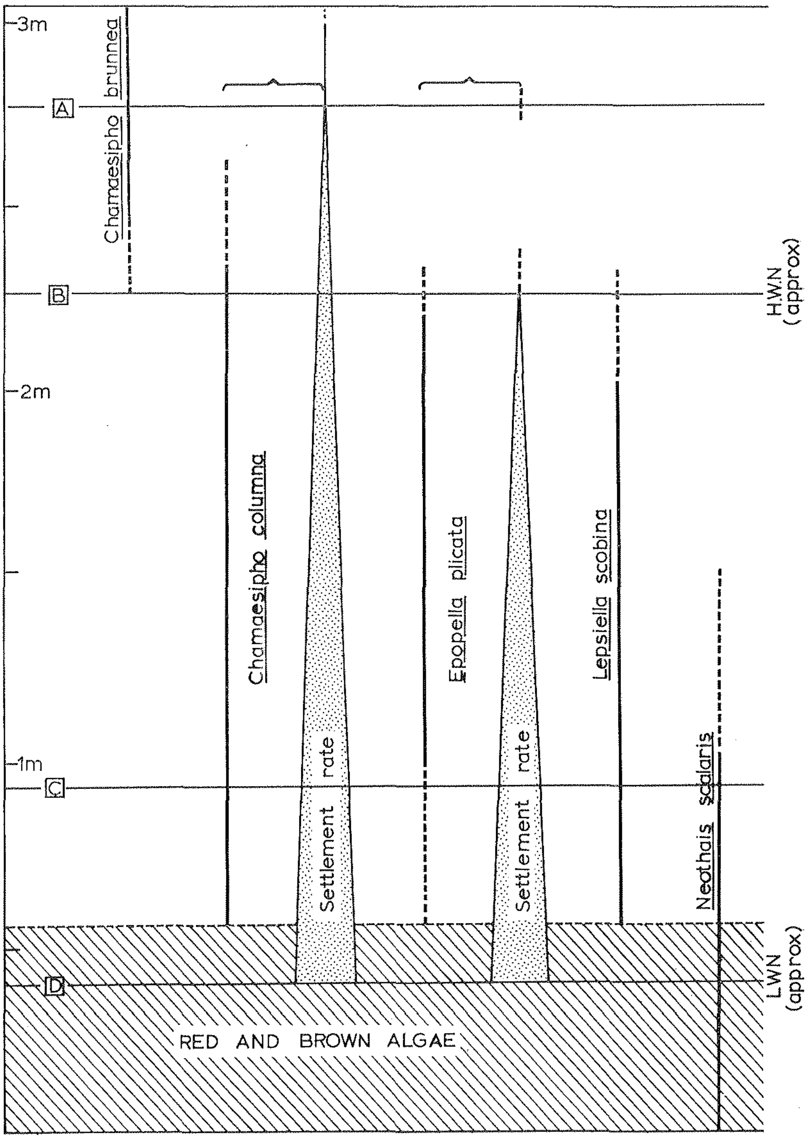

FIG. 1—Distribution of the three zoning barnacle species *Chamaesipho brunnea*, *Chamaesipho columna*, and *Epopella plicata*, and the gastropod predators *Lepsiella scobina* and *Neothais scalaris* on the experimental reef at Goat Island Bay, Leigh. A, B, C, and D are the positions of the four experimental levels. Settlement rates of *Chamaesipho columna* and *Epopella plicata* increase with increasing submergence time.

Increased submergence does not of itself result in increased mortality of any of the barnacles in the absence of predators and algal overgrowth (Luckens 1970). However, within the intertidal zone, the density of both predators and algae (Luckens 1974) tends to increase with increasing submergence times.

The settlement behaviour and the patterns of settlement of each species are first considered separately to show the importance of intra-specific competition, and then interspecific competition between different barnacle species and between barnacles and other organisms will be dealt with.

COMPETITION

Competition has been defined as "the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)" (Milne 1961). For a sessile, filter feeding rocky shore animals such as a barnacle, the most important requirement is space, primarily for attachment, but also as a place for feeding and reproduction. Each individual requires sufficient space to allow for secure attachment and continued growth, and competition for this can come from other specimens of the same species (intraspecific), or from other species (interspecific). The larger the amount of rock space occupied, the greater the volume of water available for filtering. Where other conditions such as wave action, angle of slope, aspect, and shore height are constant, the less dense the population the greater the space for secure attachment, and the more food available for each animal. However, the greater the amount of space around each specimen, the greater the likelihood of other organisms settling in the intervening area, i.e., spacing-out mechanisms reduce intraspecific competition, but can result in increased interspecific competition.

Since barnacles are sessile animals, their behaviour during settlement will be of great importance in determining what further interactions can occur during later growth. This will affect both competition, since only those organisms within the same immediate area can compete, and also reproduction, since barnacles are cross-fertilising animals.

To show that competition is occurring between two species or two individuals it is necessary to show that one is more successful in the absence of the other, e.g., that growth of one is faster, that its population density is greater, or that more individuals are able to settle, in the absence of the other species, than when the competing species is present. Since the discussion is here restricted to sessile intertidal animals, primarily barnacles, competition is restricted to competition for space.

Some overseas work (Connell 1961a, b) clearly demonstrated that the presence of individuals of one species results in the death of individuals of another species, and the action of interspecific competition can be regarded as proven. However, where the interaction is more subtle, careful measurements of populations in closely similar situations are necessary to establish that growth rates really differ and that competition is indeed taking place, and that the difference in growth rate is not due to some other factor.

With such filter feeding animals as barnacles, where the food supply is inadequate to maintain all the settled specimens at the same rate of growth, there is an increasing tendency for some specimens to flourish at the expense of the others. If there is a growth rate differential which varies seasonally between two species, the intensity of competition and the rate of elimination or reduction in growth rate of the slower growing species will also vary seasonally.

Where the distribution of adults differs markedly from that of the newly settled specimens, competition may be responsible for the difference, but predation or the effect of physical factors must be excluded before competition can be named as the causal factor. The possible distribution of each species in the absence of the other species has been determined using screened concrete frames at four levels on the shore (Luckens 1970).

OBSERVATIONS AND DISCUSSION

INTRASPECIFIC COMPETITION

Chamaesipho brunnea settles within the adult zone from late January to March at Leigh on rock or concrete surfaces near or between live and beneath dead specimens of the same species. Settlement on bare rock surfaces was gregarious and resulted in clusters of barnacles separated by uncolonised areas (Fig. 2). It has occasionally been reported as settling on other specimens of its own species or on *Epopella plicata* by Moore (1944) (as *Elminius plicatus*, see Ross 1970), but this has not been seen at Leigh. Although settlement was gregarious, newly settled specimens were spaced out, only becoming contiguous after a certain amount of growth had taken place. With continuing growth the groups of barnacles became fused into sheets and growth was mainly in an upward direction. Parietal plates of dead barnacles remained fused to the living ones around them, but as they were lifted off the rock surface by continued growth of adjacent ones, the space was either settled by cyprids or was gradually encroached upon by surrounding specimens.

Neither crushing, nor undercutting, nor smothering of live barnacles by others of this species was ever seen. Barnacles several years old are fused into almost continuous sheets whose apical plates may form a more even surface than the rock beneath them.

Chamaesipho columna settles throughout the year from the top of the *C. brunnea* zone to the top of the brown algal zone (at about low neap tide level), but both season and vertical extent of settlement vary widely (Luckens 1970). Survival of newly settled specimens above the adult limits is infrequent and brief. Settlement is greater on upward facing rock surfaces than on downward facing ones at any one level, but is

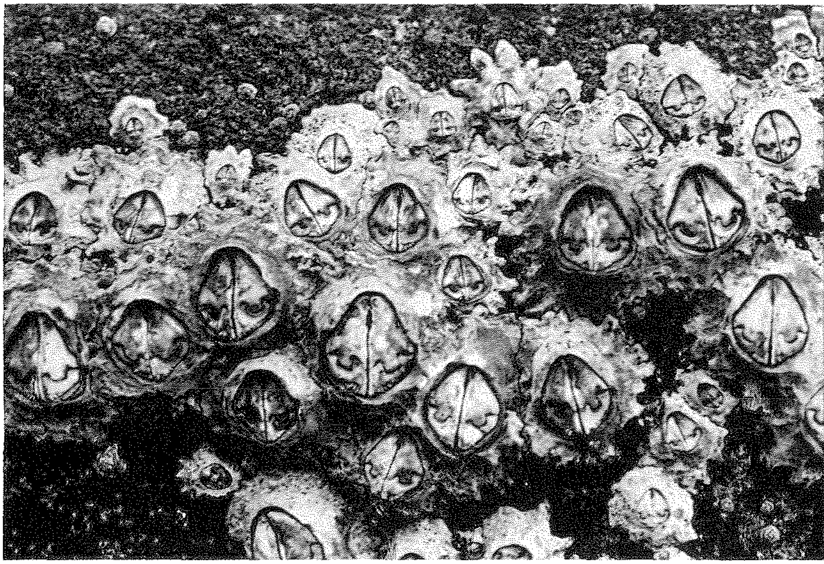

FIG. 2—Group of *Chamaesipho brunnea* with their bases often interdigitating and contiguous (approximately life size).

denser at lower levels on the shore. Dense but spaced settlements are common in the lower parts of the barnacle zone, and with continued growth these form sheets of greatly elongated fused individuals (Fig. 3). Settlement can occur on top of already settled specimens of the same or other species as easily as on bare rock surfaces.

Sparsely settled specimens on a glass plate at Piha grew faster than the crowded specimens on the surrounding rock. Attempts at Goat Island Bay, Leigh, to produce populations of the same age at varying densities on pitted perspex plates were foiled by continual dense settlements covering the complete plate.

Settlement on top of live barnacles may smother them as the upper barnacles grow over the apical plates of the lower ones. Undercutting of adjacent barnacles resulting in their death was not observed, and even in crowded sheets of barnacles none appear to be crushed to death.

Eggs and nauplii of *Epopella plicata* occur in the adult barnacle at all times of the year, but settlement is mainly from July to October and occurs over a wider shore range than that of the adults. On the experimental reef cyprids settled at the highest experimental level, adjacent to adults and newly settled *E. plicata* cemented there during the course of other experiments, but not at this level away from the experimental frames. Both those that were cemented there as newly settled specimens, and those that settled there naturally soon afterwards (perhaps induced to settle by the presence of others of the same species) died within a

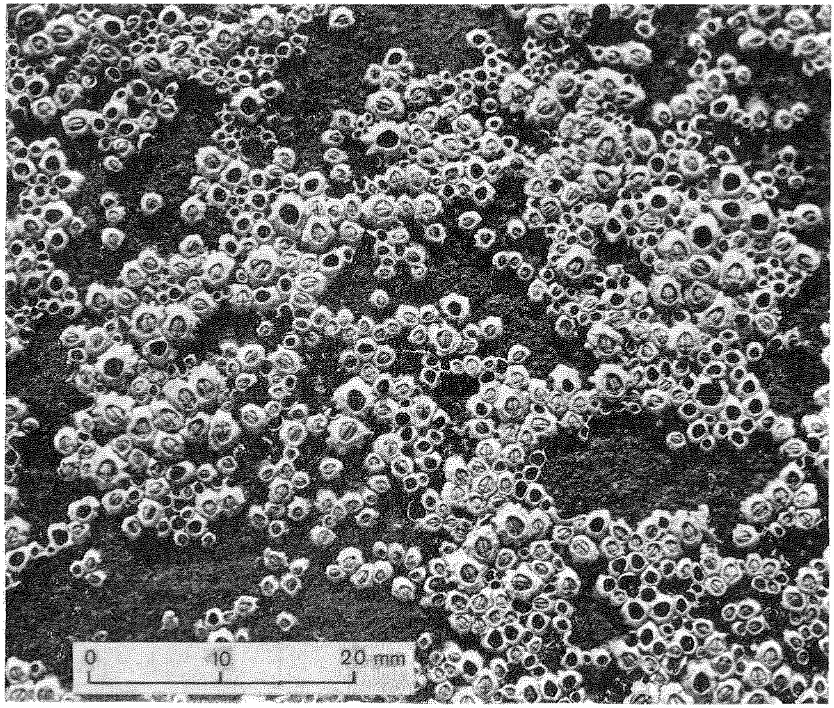

FIG. 3—Adult specimens of *Chamaesipho columna* – see also Figs. 4–6.

short time. Settlement is densest on the most recently cleared areas, but also occurs on more mature surfaces, with lowest settlement densities being recorded among mature populations at Piha.

Although sometimes settling as a dense sheet on rock surfaces, *E. plicata* more commonly forms clusters (Fig. 4), with barnacles settling upon the parietal plates of older specimens of the same species. Except for a reduction in growth rates with an increase in the population density, the barnacles do not appear to affect each other adversely. As the barnacles in the clump grow, each spreads out as best it can, until it is difficult to see where each barnacle begins and ends without dissecting the clump. In spite of this complexity, direct overgrowth and smothering does not seem to occur.

Epopella plicata that settled on a cleared rock surface during the winter of 1962 at Piha were larger than the largest individuals in the surrounding natural populations by the summer of 1965. The natural population appeared to be fully grown when the adjacent rock surface was cleared, to grow very little in the next 2.5 y, and to be more crowded than the barnacles which settled on the cleared rock surface.

Not only do fewer barnacles settle among mature clusters of *E. plicata*, but also those that do grow more slowly than others on cleared

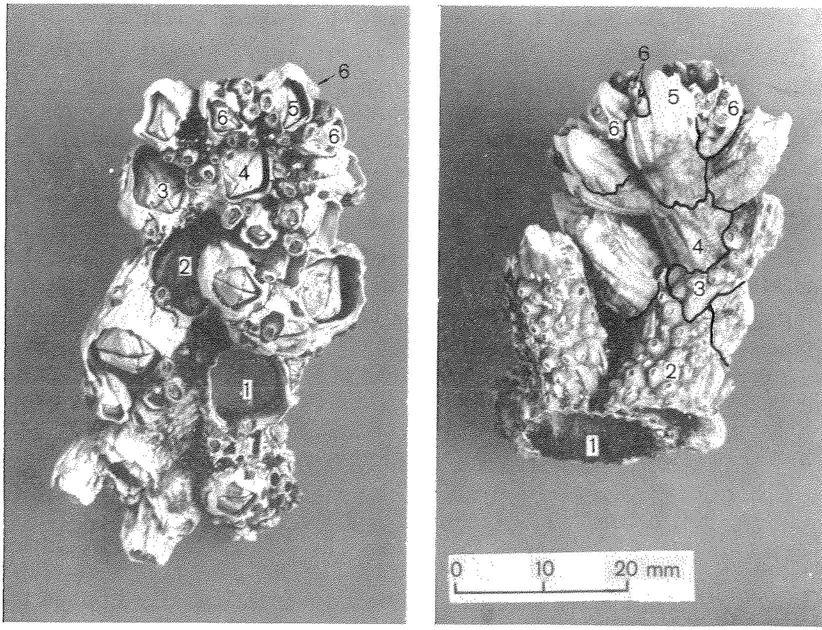

FIG. 4—Apical (*left*) and side (*right*) views of a clump of 30 *Epopella plicata* of which only one specimen (large empty barnacle marked 1) was completely attached to the rock surface. The settlement sequence of barnacles supporting the uppermost specimens is numbered in both views, and the base of each *E. plicata* is outlined in black in the side view. Specimens of *Chamaesipho columna* on the upper part of the clump show the typical grey colour of light-exposed specimens, but those within the clump are much paler.

rock areas nearby. Non-breeding barnacles are known to grow at a faster rate than breeding specimens, but as the less crowded barnacles were still close enough to breed, the increased growth rate could not be due to absence of breeding. This difference in growth rate implies that either intraspecific competition is limiting growth in the older population, or that total food supply has increased.

Intraspecific competition does not cause appreciable mortality among settled *E. plicata*, but results in lower settlement among adult populations and in reduced growth rates with increasing population density.

Elminius modestus, a fast maturing, continuously breeding species, can settle at any time of the year to form dense, even layers over rock, wood, iron, other barnacles, settled invertebrates, and even algae, both intertidally and subtidally, when cyprids are available in sufficient concentrations. With continued growth in dense settlements, hummock formation (Barnes & Powell 1950) occurred 8–10 weeks after settlement in the warmer months, but settlement between and on top of the barnacles of the hummock still continued.

COMPETITION BETWEEN *Chamaesipho brunnea* and *C. columna*

The normal overlap zone of *Chamaesipho brunnea* and *C. columna* settlement is 0.3 m deep and is immediately above the upper middle experimental level. *Chamaesipho brunnea* did not settle lower on the shore than this on the experimental reef, even when pieces of rock bearing groups of adult barnacles were cemented at lower levels. *Chamaesipho columna* occasionally settled right to the top of the *C. brunnea* zone, but these specimens quickly died.

In the overlap zone, *Lepsiella* predation is usually negligible, but occasionally during the winter numbers of large *C. brunnea* are eaten.

Because *C. brunnea* does not settle readily on other barnacles, the presence of *C. columna* greatly reduces its settlement. *Chamaesipho columna* settles during most of the year at Leigh, but *C. brunnea* settles in late summer only, so the former species has considerable advantage in colonising bare patches of rock, unless these patches become bare immediately before a settlement of *C. brunnea*.

The overlap area is well above the maximum development of *C. columna* and below that of *C. brunnea*. When protected from predation, large numbers of *C. columna*, particularly juveniles, die from desiccation and the adverse effects of salinity changes at this level (Luckens 1970). Growth rates are lower here than further down the shore. Although the *C. columna* here forms merely the upper fringe of its total population, the combined effect of its presence and predation are perhaps sufficient to limit the *C. brunnea*. However, settlement of *C. brunnea* does not occur below this level on the experimental reef at Goat Island Bay.

When groups of large *C. brunnea* were cemented inside cages at the two lowest experimental levels on the shore, where silting did not occur they became densely settled by *C. columna*. The *C. brunnea* had already formed a continuous sheet, and the settlement and growth of the smaller species on top of this sheet resulted first in difficulty in feeding and then in smothering for the larger species.

COMPETITION BETWEEN *Chamaesipho brunnea* and *Epopella plicata*

These two species normally show very little overlap, since any *E. plicata* above the upper middle experimental level at Leigh were usually confined to crevices. The effects of emersion limit the *E. plicata* to areas of the experimental reef below H.W.N. level, so it is not necessary to consider competition between these two species as important in limiting either the upward extension of the *E. plicata* or the downward extension of *C. brunnea*.

On the more exposed north-eastern sides of Goat Island, the ranges of these species overlap, and the barnacles grow mixed in a crowded jumble. In exposed situations such as this, *Lepsiella* are much less numerous and lack of predation may be responsible for the *C. brunnea* being lower on the shore. Alternatively, the exposure may have raised the upper limits of the *E. plicata*. It was neither possible to make regular

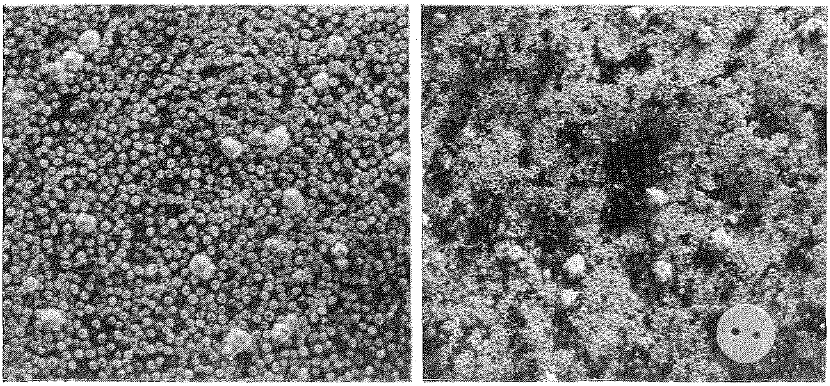

FIG. 5—Two areas where *Chamaesipho columna* and *Epopella plicata* have settled together. *Left* – An early stage when some *E. plicata* are still attached to the rock surface (average diameter of smaller species 1 mm). *Right* – A later stage when the *C. columna* have formed a continuous sheet, with most of the *E. plicata* attached over the top of smothered *C. columna. Xenostrobus pulex* have also settled on and among the *C. columna* and are likely to smother the barnacles as they grow (button diameter 12.5 mm).

observations nor to observe settlement on cleared rock at these wave-exposed situations, so the correct alternative could not be established.

COMPETITION BETWEEN *Chamaesipho columna* and *Epopella plicata*

The distributions of these two barnacles overlap completely on the experimental reef (see Fig. 1). However, differences in density and proportions are found at different levels and on different shores. Both species settle more densely at lower levels than at higher ones, and both breed throughout the year, but settle irregularly, although at Goat Island Bay *E. plicata* has a much more restricted settlement season than *C. columna*.

Settlement of *Epopella plicata* was greatly increased on areas of rock cleared just prior to settlement, compared with rock surfaces cleared earlier, which already bore a scattering of *C. columna*. This competition for space continues where the two species have settled together. *Chamaesipho columna* are smothered by *E. plicata* growing over them. Where the *C. columna* are dense, and form a continuous sheet soon after settlement, this smothering process results in the *E. plicata* growing on top of a layer of the smaller barnacle, and attached to the rock only where they settled first (Fig. 5). Such insecurely attached specimens are easily dislodged.

If the *C. columna* are scattered and the *E. plicata*, while smothering some of them, still remain firmly attached to the rock surface, the result will be a reduced density of *C. columna* growing between larger *E. plicata*. This reduction of density is soon compensated for by further settlement of *C. columna* on the *E. plicata*. The turnover in individual numbers is much higher in the smaller and shorter lived *C. columna*, but this is compensated for by its earlier breeding, and its greater ability to settle on small, already partly settled areas of rock. Once *E. plicata* has settled where there are no predators and the density of *C. columna* is low, it can live for at least 5 y.

The outcome of competition between these two species appears to depend on such chance factors as the amount of bare rock available at the time when each species is settling, and the numbers of cyprids available for settlement.

The restriction of numerous large *E. plicata* to the band between the two middle experimental levels is related to predation.

Although competition tends to be thought of as an active process, it is simply the outcome of a series of events which may but need not always be interdependent, e.g., a newly settled specimen of *E. plicata* surrounded by *C. columna* grows at a rate dependent on food supply, temperature, etc., but usually not related directly to the smaller barnacles around it. As it grows it increases in volume and basal diameter. This may involve its growing over surrounding barnacles, but it does this in the same way that it would grow over a nearby rock projection. Unlike *Balanus balanoides* (Connell 1961a), none of the barnacles at Leigh killed surrounding specimens by undercutting them and lifting them off the rock surface. With *B. balanoides* whether it overgrows, undercuts, or crushes surrounding barnacles depends on their relative growth rates and the firmness of their attachment. These vary seasonally with *Balanus* and *Chthamalus*, but in *Epopella* and *Chamaesipho*, although further work may reveal some seasonal variation affecting interspecific competition, this has not yet become apparent.

COMPETITION BETWEEN BARNACLES AND OTHER ANIMALS

On well-drained, sunny, intertidal rock surfaces, barnacles are often the most numerous animals, but where surfaces are shaded or slow to drain other sessile animals (and algae) may also thrive. Such damp conditions favour the growth of various mussels, commonly the small, black mussel *Xenostrobus pulex* (formerly *Modiolus neozelanicus*, see Wilson 1967) at Leigh, Piha, and West Tamaki Head, but with the green-lipped mussel *Perna canaliculus* abundant at the lower levels at Piha.

On gently sloping sandstone reefs at the western end of Goat Island Bay, *Xenostrobus pulex* settle between and around both *Chamaesipho columna* and *Epopella plicata*. With growth and further settlement, small islands of *X. pulex* form, often centred on a somewhat larger specimen or group of *E. plicata*. *Chamaesipho columna* beneath the *X. pulex* usually become smothered by silt accumulating among the byssus threads. Large specimens of *E. plicata* often survive surrounded by a sheet of mussels. Small patches of mussels may persist for months, but large patches attached firmly to the rock only at their extreme edges and to occasional live *E. plicata* within the patch, and usually separated from

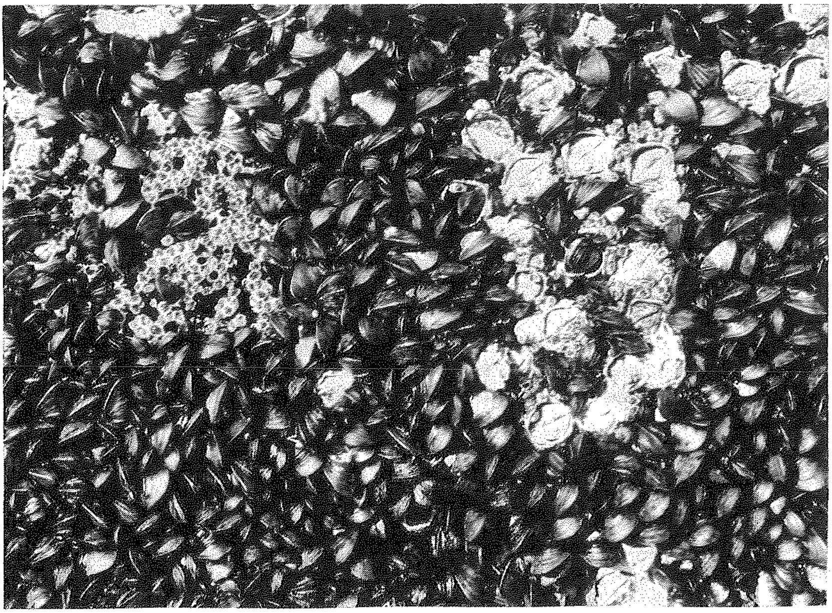

FIG. 6—Settlement and growth of *Xenostrobus pulex* on and among *Chamaesipho columna* and *Epopella plicata* has smothered most of the barnacles except those on raised areas or those tall enough to reach above the *X. pulex* carpet (average diameter of smaller barnacles approximately 2 mm).

the rock by a layer of silt and dead barnacle plates, can be quickly ripped from the rocks by heavy seas if the continuity of the patch is broken. The more uneven the underlying surface, the more securely are the mussels attached.

At Piha *X. pulex* was most abundant in hollows, cracks, crevices, and other surface irregularities. Rock surfaces one month after the removal of all growth often showed a pattern of *C. columna* on the smoother, raised parts, and *X. pulex* on the damper, more creviced parts. The presence of barnacles increased the likelihood of *X. pulex* settlement, and on smooth surfaces settlement was often delayed until barnacles had settled. The growing mussels then soon smothered the barnacles (Fig. 6).

Although *X. pulex* occurred on some parts of the reef at West Tamaki Head, Auckland Harbour, at all times of the year, it became the dominant organism on the upper reef flat in summer 1962–63 (Luckens unpublished 1964). Settlement among the dense cover of *Elminius modestus* began in late July and continued until October. In spite of an almost complete cover of mussels, many barnacles survived for several months, but eventually they were smothered by a continuous carpet of mussels underlain by silt. Further growth of the mussels forced the carpet into ridges 2–8 cm high. In February 1963 a period of afternoon low tides and hot weather, with crushing by children walking on the reef, killed some of the *X. pulex*. A period of rough seas then removed almost all the *X. pulex*. and many of the dead barnacles as well.

Where Auckland rock oysters *Crassostrea glomerata* occurred with either *C. columna* or *E. modestus*, they were often found to have smothered the barnacles. The oyster spat settled among the barnacles, and as they increased in size, they grew out over the nearest barnacles, which were killed. If the barnacles were dense around the oysters, so that little rock surface was left exposed, the attachment of the oysters became less secure with time. Attached to the rock surface only where they have settled first, and separated from the rock by a layer of dead barnacles, the oysters were easily removed. This process was hastened where other animals such as polychaetes and small molluscs were able to insinuate themselves between the oyster shells and the rock.

COMPETITION BETWEEN BARNACLES AND ALGAE

In the absence of grazing animals, the volume of algal production usually increased with decreasing shore height. However, both the weight and diversity of grazing animals increased lower on the shore, resulting in the restriction of algae to certain levels. An increase in dampness, especially if accompanied by an absence of grazing animals, generally resulted in an increased amount of algae. This intensified the competition between the algae and the sessile animals.

Among the highest barnacles (*C. brunnea*), blue-green algae, some lichens, and red algae such as *Gelidium* spp. occurred on and between the barnacles. On the open rock surfaces, they rarely killed the barnacles but merely inhibited settlement of cyprids. In crevices, especially on shaded rock faces, *Gelidium* sometimes grew completely over the *C. brunnea* and effectively restricted its cirral extension.

Epopella plicata appeared to compete with algae only on shaded or poorly drained faces, where it already showed a high mortality rate from predation and smothering by *X. pulex*. The algae *Ulva* spp., *Splachnidium rugosum*, and *Scytothamnus australis* only occasionally killed the barnacles directly, by growing across the apical plates, but they contributed indirectly to barnacle mortality by providing shelter for predators and lodgment for silt and mussel larvae. As the algae were usually seasonal, and as the dead barnacles with the algae were removed periodically by rough seas, there was little restriction of barnacle settlement.

Chamaesipho columna occurs among both *C. brunnea* and *E. plicata*, but being smaller is more affected by algal competition.

Inside experimental frames at the two lower levels from which grazing animals were excluded, retention of silt between algal thalli was responsible for the deaths of *C. brunnea*, *C. columna*, and small *E. plicata*.

The best evidence for direct interspecific competition for space was between *Elminus modestus* and *Corallina officinalis* at Narrow Neck, Auckland (Luckens unpublished 1964). Here, areas of rock cleared of *Corallina* turf were settled by *E. modestus* and *C. officinalis*. As they grew, the barnacles were smothered by the *Corallina* paint growing up and over them. Further growth resulted in a sheet of *Corallina* turf once more. At Goat Island Bay, *Corallina* paint smothered *C. columna* in small shallow pools, but on the reefs where most of the experimental work was carried out, *Corallina* was not common.

Except for this last example, interspecific competition between barnacles and algae occurred mainly on shaded faces, poorly drained areas, and in crevices. Such areas represented only a small part of the barnacle zone. The poorly drained areas, with their cyclic successions of organisms and the baring and recolonisation of the rock surface, contrast strongly with most of the barnacle zone, where the pattern of zonation appears to have stabilised.

SETTLEMENT AND GROWTH PATTERNS IN *Chamaesipho brunnea*

Chamaesipho brunnea is a barnacle of the upper intertidal zone, extending well above extreme high water of spring tides on wave-exposed shores. At these raised levels, the number of possible competitors is few, but the physical conditions are severe and fluctuating. Growth is relatively slow when compared with species living lower on the shore, but many specimens are at least 10 y old. Specimens more than 2 or 3 y old are usually fused into almost continuous sheets whose apical plates may form a more even surface than the rock beneath them. Although *C. brunnea* on the shore will readily extend their cirri when water is poured over them, it is difficult to induce them to extend their cirri in an aquarium unless they are exposed to a vigorous and preferably air-entrapped stream of water. On the shore much of their food is extracted from the thin layer of water from surge and spray. Most shells are oriented so the aperture is transverse to the main back and forth movement of the water, and thus the cirri can strain particles from water moving in either direction.

Fused sheets of barnacles are better able to withstand the impact of heavy masses, whether waterborne or human, than are isolated specimens, but where most food is extracted from a thin, flowing sheet of water, a further factor assumes importance. Any specimen which is raised relative to the surrounding surface whether it be of rock or barnacles, may be raised wholly or partially out of at least some of the water flow. Thus its food intake will be lowered relative to those specimens forming an even sheet. Within such an even sheet the food supply will be shared out automatically in such a way that all the specimens grow upward at a similar rate. If this hypothesis is true, then the formation of even sheets of barnacles would be most common at those levels where most of the food is extracted from thin sheets of moving water, i.e., the highest levels on wave-exposed coasts. This would also explain the extreme low-conical shape of isolated specimens at the highest levels, and the lack of settlement on older specimens.

In fact, food supply mainly restricted to that present in thin sheets of splash and spray would provide a somewhat self-regulating system, favouring specimens at or below the general level, and reducing the food supply of those above the general level.

SETTLEMENT PATTERNS IN *Chamaesipho columna*

Its smaller size and its range from high to low water neaps tend to reduce the significance of the sheet-forming behaviour of this species, which, when it settles densely, is somewhat similar to that of *C. brunnea*. However, unlike *C. brunnea*, it settles readily on other barnacles either of its own or (more usually) of other species as well as on rocks, mollusc shells, wood, iron, etc. Its much smaller size means that it will be likely to occupy a somewhat damper microclimate than surrounding larger species.

SETTLEMENT PATTERNS IN *Epopella plicata*

Epopella plicata is found from high water neaps down to the brown algal zone. Although young specimens, particularly at low levels, may form contiguous groups, they rarely form the continuous sheets so characteristic of the two species of *Chamaesipho*, nor do they appear to settle densely enough to grow into hummocks as both *C. columna* and *Elminius modestus* do. Instead, *E. plicata* is usually found as a scatter of individuals and clumps. While hummocks develop from one dense settlement of barnacles (although they may be augmented by later settlements), clumps develop from subsequent settlements on previously settled individuals. Both clumps and hummocks increase the surface area and the filtering potential of the group. Morton (Morton & Miller 1968) has stated that with hummock formation "the turbulence may increase and with it the access to food supply", and this would also apply to clump formation.

Earlier in this paper it was noted that specimens of *Epopella plicata* surrounded by *Xenostrobus pulex* tended to grow taller and narrower than nearby specimens which had the *X. pulex* removed from around them. Within the main *E. plicata* zone, most of the *E. plicata* attached directly to the rock surface, whether as isolated specimens or as the basal specimens of clumps, are decidedly more tubular in proportions than isolated specimens of *Chamaesipho* or *Elminius modestus*, even when potentially smothering species such as *X. pulex* are absent.

The tendency of *Epopella plicata* to settle on the distal parts of the parietal plates of already settled *E. plicata* seems to be accentuated where *Chamaesipho columna* are present. It has been noted that *E. plicata* settle more densely on rock surfaces in the absence of *C. columna*. Although *C. columna* also settle on *E. plicata*, in the presence of *C. columna*, *E. plicata* are more likely to settle on older *E. plicata*, if these are available, than on the rock surface.

Clump formation in *E. plicata* seems more pronounced on steeply sloping surfaces than on horizontal ones. As most of the observations have been carried out at beaches heavily frequented by people at least in the summer, this could be related to the higher chance of clumps on horizontal surfaces being dislodged by accidental crushing or kicks.

SUMMARY

Among sessile animals which filter their food from the sea, competition is primarily for space to settle and grow. Intraspecific competition is not a major cause of mortality in either *Chamaesipho brunnea* or *Epopella plicata*, but their settlement and growth patterns differ. Crowded *C. brunnea* form a fused sheet of barnacles, but crushing, smothering, and undercutting of live specimens does not occur. *Epopella plicata* form clumps by settling on already settled specimens, but do not smother each other. *Chamaesipho columna*, by settling on top of already settled sheets of the same species, can smother them, but this is not common. Crowded populations of both *C. columna* and *E. plicata* have reduced growth rates compared with adjacent less crowded populations.

Interspecific competition between *C. columna* and *C. brunnea* may restrict *C. brunnea* to the upper levels of the shore at Leigh. *Chamaesipho columna*, with its longer settling time and ability to settle on other barnacles, has an advantage over *C. brunnea*, but this latter species is much more resistant to desiccation. At lower levels on the shore, competition pressure of *C. columna* against *C. brunnea* is increased by an increase in the settlement rate of *C. columna* and by the preferential predation of *C. brunnea* by the thaisid gastropod *Lepsiella*.

Distributions of *C. columna* and *E. plicata* overlap completely. The two species compete for space during both settlement and growth. *Epopella plicata* can smother *C. columna*, but where the latter are dense, *E. plicata* usually become insecurely attached. Increasing density of *Lepsiella* favours the survival of *C. columna* where *E. plicata* is also present.

Both the mussel *Xenostrobus pulex* and the rock oyster *Crassostrea glomerata* smother *C. columna*, *Elminius modestus*, and small *Epopella plicata*. *Xenostrobus pulex* growth is greatest on poorly drained reefs, where barnacle zonation is replaced by a mosaic of areas showing cyclic successions of organisms and bare rock.

Competition between barnacles and algae is intensified by poor drainage. Often algae and *X. pulex* occur together in competition with barnacles.

At Narrow Neck, however, competition between *Elminius modestus* and *Corallina officinalis* occurred on both vertical and horizontal cleared rock surfaces. *Elminius modestus* settled first, but was smothered by *Corallina* paint. *Corallina* turf developed from the paint and soon covered the area completely.

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