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by
PENELOPE A. LUCKENS

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CONTENTS

Figures

Tables

Note added in proof: *Elminius plicatus* is now known as *Epopella plicata* (*see* Ross, A. 1970: Studies on the Tetraclitidae (Cirripedia: Thoracica): a proposed new genus for the austral species *Tetraclita purpurascens breviscutum*. *Transactions of the San Diego Society of Natural History 16:* 1–12; **and** Foster, B.A. in press: The Marine Fauna of New Zealand: Barnacles (Cirripedia: Thoracica). *N.Z. Oceanographic Institute Memoir 69*).

Settlement and succession on rocky shores at Auckland, North Island, New Zealand

PENELOPE A. LUCKENS

New Zealand Oceanographic Institute, Department of Scientific and Industrial Research, Wellington

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ABSTRACT

Seasonal settlement and temporal succession of organisms on both denuded rock faces and rocks immersed in pools were examined at three locations near Auckland. Information on the settlement times, location, growth rates, and density, etc., of more than 40 species was tabulated.

Settlement was found to occur at all seasons although numbers and species varied. Serpulids and some polyzoa settled in the summer, and algal species mostly in the winter. At each station one barnacle species settled throughout the year (*Chamaesipho columna* at Piha, *Elminius modestus* at Narrow Neck and West Tamaki Head), other species settling over a more limited season. Settlement of individual species differed on the two coasts; certain animals which settled throughout the year on the west coast (Piha) settled mainly in the spring on the east coast (*Perna canaliculus, Chamaesipho columna*). On the east coast mussels settled during winter and spring, oysters in summer and autumn.

Most of the organisms settled and grew on bare rock, either on newly cleared surfaces, or on bare areas on surfaces cleared up to 2 years before. *Perna canaliculus* settled only when there was protection from desiccation. The general pattern of seasonal settlement was similar each year, but the actual time and amount of settlement of any one organism varied from one year to the next. Time of settlement of one species at different levels on the same shore also varied.

Although the same species could be one of the early colonisers on one area, and the final dominant organism on another area, in general there was a replacement of short lived species by those having a longer life span. Many of these replacing organisms possessed growth characteristics such as limited powers of movement or surfaces not readily colonised by other species, which enabled them to smother earlier species but to avoid the same fate themselves.

Development on cleared areas often consisted of a cyclical progression in which there was a mosaic of patches of different ages, each of which was eventually removed in whole or in part, leaving bare rock to be resettled.

Zonation results from the interactions of many factors, both physical and biotic, and results in assemblages of species which are relatively permanent, although the actual organisms may be replaced at longer or shorter intervals.

INTRODUCTION

The intertidal zone separates a continuously submerged area from a continuously emersed one. The air/water interface produces gradients in light intensity, temperature, and humidity, which are affected by the rise and fall of the tide. Zonation of organisms results from their varying tolerances to the complex of physical and biotic factors, and although the basic zonation of any one area is stable, the numbers of individuals and species may fluctuate widely both seasonally and annually, despite the generally constant seasonal distribution of settling larvae.

In one of the earliest papers on New Zealand intertidal communities, Oliver (1923) described some of the more commonly encountered formations and associations. Later papers dealing with areas near Auckland include Beveridge & Chapman (1950) on algal zonation at the southern end of Piha, Chapman (1950) on algal zonation at Stanmore Bay, Dellow (1950) on intertidal ecology at Narrow Neck, and Dellow (1955) on marine algal ecology of the Hauraki Gulf. Morton & Miller (1968) described zonation at Lion Rock, Piha and at Narrow Neck. Except for the unpublished work of Dellow (1948) on settlement and succession at Narrow Neck, little was known of settlement seasons or levels of organisms at the three study beaches in 1962.

This study, involving the regular clearance of selected areas of rocky shore at three places over 2 years, was undertaken to provide a general picture of settlement and succession on northern New Zealand shores. It also produced data on growth rates, longevity, and inter- and intra-specific relationships.

THE EXPERIMENTAL AREAS

LOCATION AND PHYSICAL STRUCTURE

The areas in which experimental work was carried out are all within a 32 km radius of Auckland (Fig. 1). They were chosen for their contrasting conditions and ease of access, although their accessibility limited experimental work because it proved impossible to attach either wire screening or, in some cases, artificial settling surfaces to the rocks without subsequent interference.

Initially stations were set up at

(i) Piha,

(ii) West Tamaki Head, and

(iii) Narrow Neck and St. Leonard's Point,

but after the first year, work at Narrow Neck and St Leonard's Point was discontinued because of interference by the public.

PIHA

Piha, an ironsand beach 30 km west of Auckland and 14 km north of the Manukau Heads, was visited monthly throughout 1962 and 1963. On the exposed west coast, the site at Piha faces WSW into the prevailing south-westerly winds and a fetch of several thousand kilometres.

The rocky outcrops of Manukau Breccia at both ends of the beach consist of andesitic fragmental beds with intrusive dykes and minor interbedded flows (Figs 2, 3, 4). Three sites were studied, one (upper experimental level) in the *Elminius plicatus* (barnacle) zone high on the flat top of the reef, one (lower experimental level) on the southern slope of the reef, and one lower down the reef in the *Perna canaliculus* (green mussel) zone (Fig. 3).

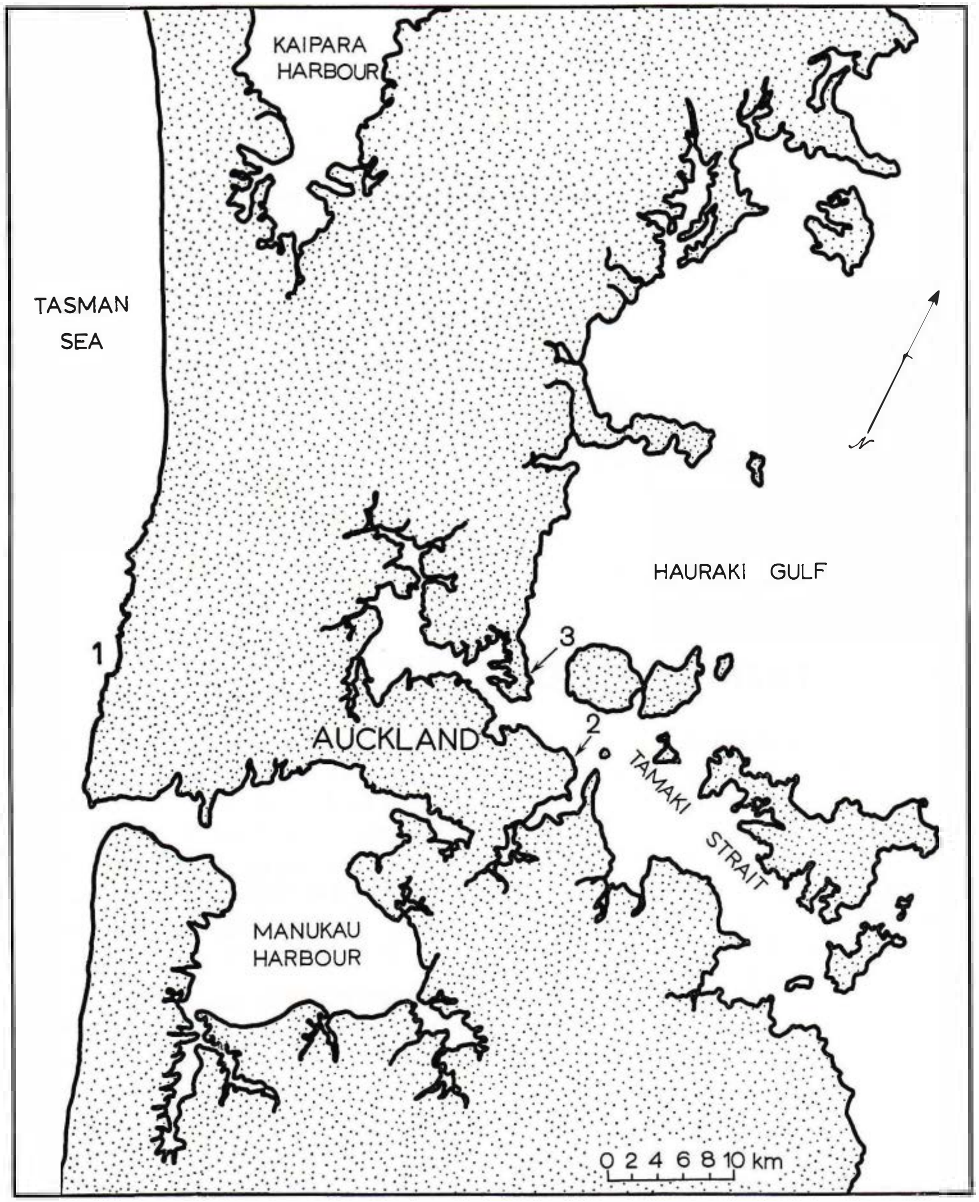


Fig. 1 The Auckland region showing the areas where the experimental work was carried out at (**1**) Piha, on the west coast; (**2**) West Tamaki Head; (**3**) Narrow Neck, on the east coast; together with part of the Hauraki Gulf and the Manukau Harbour.

At low tide the main areas of the reef are about 3 m above the extreme low water of spring tides (E.L.W.S.), the large flat platform to the north being separated from the experimental area by a steep-walled gully, 5–7 m across. The gully is occasionally filled with sand up to low water mark of neap tides (L.W.N.). The rocks to the west, which rise up to 2 m higher than the main part of the reef, extend southward and seaward protecting the southern slope of the experimental area from the full force of the surf. Te Waha Point protects the entire area from north-westerly storms. In winter when the reef is in the shadow of the point, algae grow at higher levels than in summer, and higher than in areas exposed to the sun.

During the year the sand level shows great and often rapid fluctuation. Sometimes a northward movement occurs along the beach depositing sand on the rocks at the base of the cliffs, and north of the gully where it accumulates. Sand height in the bay north of the reef is extremely variable and any sand washed on to the experimental area is eventually swept into the gully.

WEST TAMAKI HEAD

The sandstone reef (Fig. 5) where the experimental work was carried out is sheltered from heavy seas from the north and east by the islands of the Hauraki Gulf, and to the west and south it is protected by the mainland. The Tamaki River enters the harbour to the south-east of the reef, but the freshwater influence is not great.

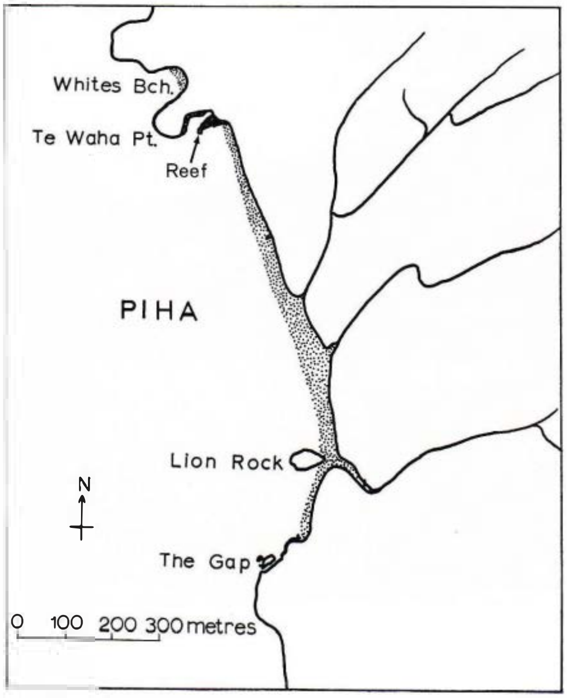


Fig. 2 The beach at Piha showing the location of the reef immediately south of Te Waha Point, where the experimental work was done.

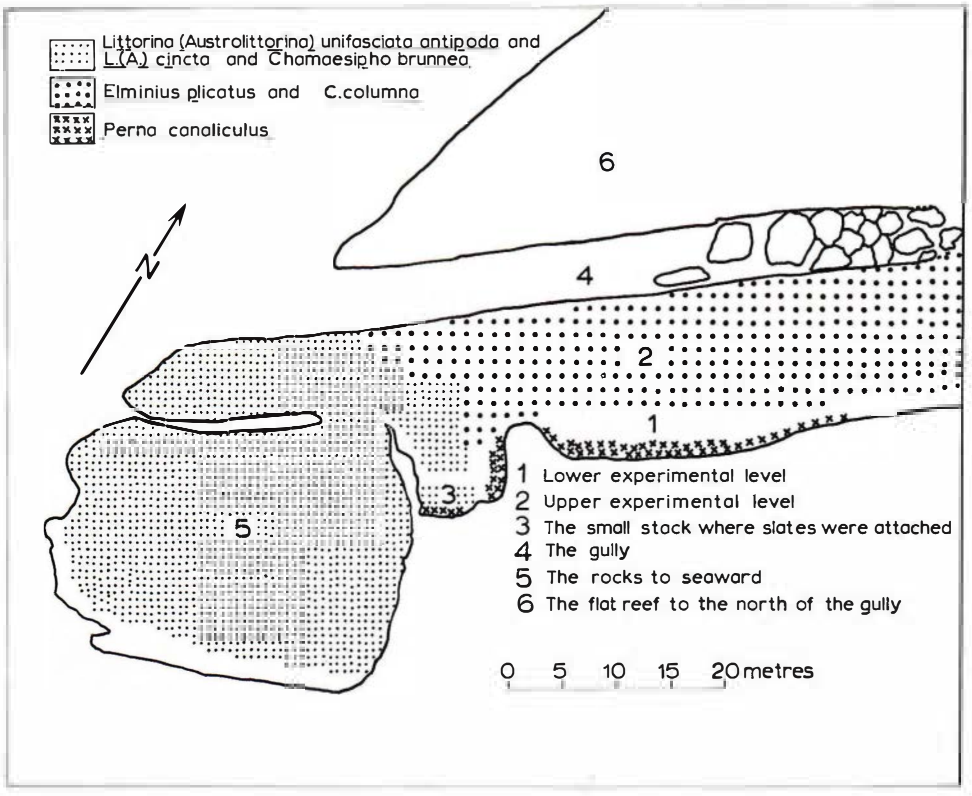


Fig. 3 A plan of the experimental area at the north end of Piha showing the distribution of the main organisms and the location of the experimental areas.

Fig. 4 The experimental area mapped in Fig. 3, photographed from the ridge to the north.

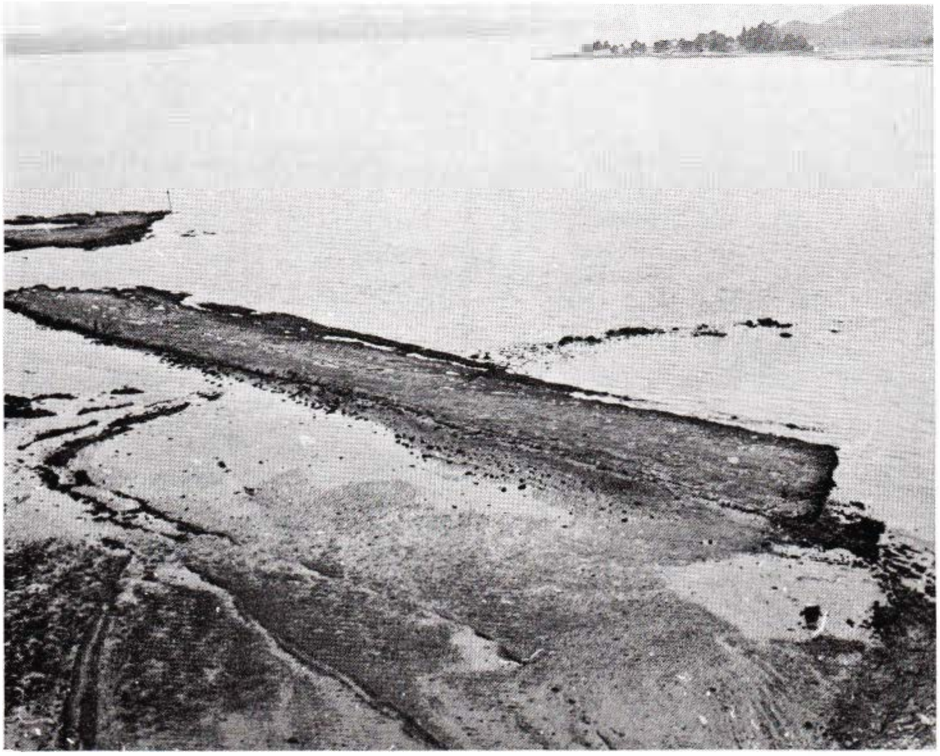


Fig. 5 The reef at West Tamaki Head viewed from the cliff top. The reef is about 230 m long and 25 m wide. The western (near) side of the reef rises almost vertically; the rest of the area consists of two gently sloping platforms separated by a somewhat steeper slope. A chain of pools extends along the upper platform and the lower platform is dotted by dark coloured areas of *Corallina officinalis* turf.

The reef, which was visited fortnightly at low spring tide from January 1962 to October 1963, is roughly rectangular, being 230 m long and 25 m wide at low spring tide. It is formed of Waitemata Sandstone and Parnell Grit, conformably interbedded. Brown ferric oxide has been deposited along some of the numerous joints of the rock, but on parts of the reef the sandstone blocks may be easily prised apart.

The highest point of the reef rises 1.5 m above Harbour Board Datum and is completely covered at each high tide. On the western side the reef falls almost vertically to a sandy mudflat dominated by the cockle *Chione stutchburyi*. From the wide platform with a chain of pools running roughly NNW parallel to the length of the reef, the rock surface slopes gently to the ENE to a level of 0.8 m, and then falls steeply to the surrounding sandy mudflat. On the northern half of the reef there is an abrupt slope 0.3 m high between the upper and lower platforms.

NARROW NECK AND ST LEONARD'S POINT

Narrow Neck Beach is about 4 km north of Auckland. The reef where the experimental work was carried out lies at the northern end of the beach and is divided into three main areas: (a) headland forming the northern end of the beach; (b) Crab Island, separated from the headland by sand; and (c) the main reef extending out from the shore for 250–300 m.

St Leonard's Point lies less than 1.5 km to the north. Dellow (1950) gives details of both the physical characteristics and zonation of the area.

TIDAL PHENOMENA

Auckland tides are semidiurnal with vertical ranges of 1.9 m at neap tides and 2.9 m at spring tides. In summer the lowest tides are at night, but in winter they are in the afternoon. Within the Hauraki Gulf and Waitemata Harbour, current velocities vary considerably, and are greatest off projecting headlands. The tidal levels for the Port of Auckland given in New Zealand tide tables (N.Z. Ministry of Transport, Marine Division 1973) are as follows:

M.L.W.S.	M.L.W.N.	M.S.L.	M.H.W.N.	M.H.W.S.
0.3 m	0.8 m	1.8 m	2.7 m	3.2 m

At Piha, Beveridge & Chapman (1950) found that the tidal range was approximately the same as at Auckland (3 m at average spring tides). Readings were restricted to calm days and were taken in a sheltered area. On most days the sea is rough and the surf is running.

TERMINOLOGY

Using the terminology of T.A. & Anne Stephenson (1949), the rocky shore can be divided into three main zones, two of which are only partly included intertidally. These zones are:

(a) Supra-littoral zone,
(b) Mid-littoral zone, and
(c) Infra-littoral zone.

Within these divisions each belt or zone is named after its chief characteristic – either organism or substrate.

GENERAL ZONATION PATTERN AT THE LOCALITIES SAMPLED

PIHA

Using the Stephenson system the following zonation is found at Piha:

Supra-littoral fringe
**Littorina (Austrolittorina) unifasciata antipoda*
†*L. (A.) cincta* (Littorinidae)

Mid-littoral zone
Chamaesipho brunnea (Chthamalidae)
C. columna (Chthamalidae)
§*Elminius plicatus* (Balanidae) (Balanoid zone)
‡*Xenostrobus pulex* (black mussel)
Perna canaliculus (green mussel)

Infra-littoral zone
Durvillea antarctica (bull kelp) (Laminarian zone)

*Formerly known as *Melarhaphe oliveri* and *Melarapha oliveri* and herein referred to as *Littorina antipoda* (see Rosewater 1970).

†Formerly known as *Melarhaphe cincta* and herein referred to as *Littorina cincta*.

‡Formerly known as *Modiolus neozelanicus*.

§Now known as *Epopella plicata* (see note on p. 4).

The species given in this system are those most prominent at their particular level on the shore. This does not mean that they are found only in this zone. For instance, the supra-littoral *Littorina antipoda* extends down to the *Elminius plicatus* zone where small specimens in particular are found at densities sometimes exceeding those found in the *Littorina* zone itself. *Chamaesipho columna* can be found associated with *C. brunnea*, on rocks in the *Xenostrobus* zone, and on *Perna canaliculus*.

The vertical distribution of the more common organisms in the experimental area is shown in Fig. 6. The classification of all organisms mentioned is given in the Appendix. The animal with the greatest vertical range is *Xenostrobus pulex*, which extends from the sand line or below, to the top of the reef (0–3 m). The levels where it is most abundant are:

(a) Among the *Elminius plicatus*. *Xenostrobus pulex* are densely packed on the top of the reef among the *E. plicatus*, especially in depressions which remain damp between tides. These patches are more prominent in the winter but are present throughout the year. At this level the smaller pools are lined with a turf of *Corallina officinalis*.

(b) Between the *Elminius plicatus* and the *Perna canaliculus* (lower experimental level). *Xenostrobus pulex* grows on and between the green mussel, *P. canaliculus*, and in areas where the green mussels have

Inset 1

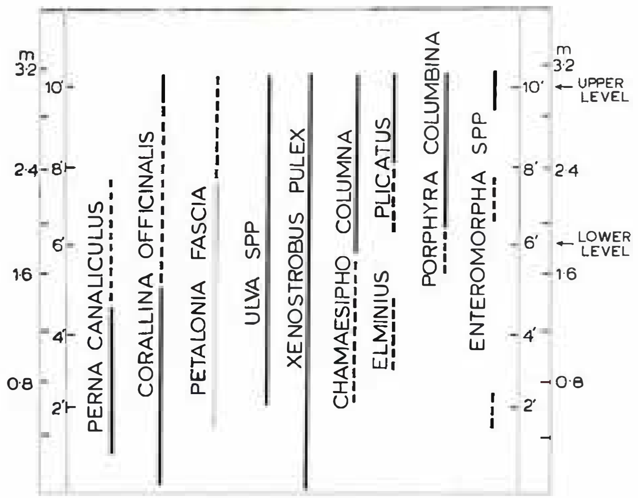


Fig. 6 The vertical distribution of the more common sessile organisms of the experimental area at Piha in relation to upper and lower experimental levels.

been extensively picked it forms a band, made up of a mosaic of patches of organisms of different ages.

(c) At and below the sand level. *Xenostrobus pulex* is one of the few organisms capable of surviving where the sand level fluctuates greatly but the sand never becomes densely packed.

Most of the upper surface of the reef (the upper experimental level) is covered with the barnacle *Elminius plicatus*. Other animals found with it include the barnacle *Chamaesipho columna*, the gastropods *Littorina antipoda*, *Risellopsis varia*, *Lepsiella scobina*, and *Cellana ornata*, and the mussel *Xenostrobus pulex*. The algae *Ulva* spp., *Porphyra columbina*, and *Enteromorpha* spp. are more common here on the *X. pulex* than on the *Elminius plicatus*, but lower down, on both *X. pulex* and *Perna canaliculus*, *P. columbina* and *Enteromorpha* spp. are replaced by *Petalonia fascia*. Between the lowest *X. pulex* and the *P. canaliculus* and also among and below the *P. canaliculus* is a cover of small red algae, including species of *Champia*, *Ceramium*, and *Laurencia*.

WEST TAMAKI HEAD

Distribution of the more common animals at West Tamaki Head is shown in Fig. 7. The dominant sessile animals on the upper platform are the barnacle *Elminius modestus* and the rock oyster *Crassostrea glomerata*. On this reef many of the oysters have been removed leaving only scattered specimens or small groups, rather than occuring as a dense belt as found on reefs such as Narrow Neck. Those oysters remaining are on the steeper parts, especially on the western face, and on small rocks projecting above the general level of the reef. These small rocks with their oyster shells shelter numerous predatory whelks (*Lepsiella scobina*) and the chiton *Sypharochiton pelliserpentis*, and smaller numbers of grazing gastropods (the catseye *Lunella smaragda* and the topshell *Melagraphia aethiops*). The cracks between the pieces of sandstone harbour *S. pelliserpentis* and *Lepsiella scobina* as well as large numbers of the anemone *Anemonia olivacea*. The limpet *Cellana ornata* is rare; prolonged searching produced only six specimens, all of which were more than 2 cm in length and heavily encrusted with *E. modestus*. At comparable levels on similar reefs, such as Narrow Neck, the numbers of *C. ornata* far exceed the numbers of *S. pelliserpentis*.

Corallina officinalis as well as turfing the sides of the pools and the larger cracks is the dominant alga on the lower platform of the reef, supporting and protecting a large and varied assortment of animals. Some, such as the gastropods *Lunella smaragda* and *Zeacumantus subcarinatus*, feed directly on the *C. officinalis*, others, especially rissoids (e.g., *Eatoniella (Dardanula) olivacea*), graze on epiphytic microscopic algae. Still other animals such as polychaete worms and amphipods use the *C. officinalis* merely as shelter, and feed on detritus or particulate matter. The bottoms of the pools are covered with an accumulation of silt, shell, and small rock fragments. Severe storms and rough seas remove much of this material leaving bare rock, but more debris soon accumulates. Large rocks are not common in the pools, but those placed there are not removed by storms.

On the lower slope to the east at a height of 0.6 m *Elminius modestus* is replaced by *Corallina officinalis* turf although still dominating at least 30% of the slope. Beneath the *C. officinalis* turf the sandstone is heavily bored by pholads. This boring continues below the *C. officinalis* to a level below 0.15 m, where the brown algae *Carpophyllum maschalocarpum* and *Ecklonia radiata* form a band extending below E.L.W.S. At these lower levels on all sides of the reef the oyster *Ostrea lutaria* is prominent together with sponges, ascidians, and polyzoa.

The steeper slope on the west shows a similar pattern. The upper half of the slope is occupied by *Elminius modestus* and *Crassostrea glomerata*. These are followed by *Corallina officinalis* turf, then *Ostrea lutaria*, sponges, ascidians, and polyzoa. *Ecklonia radiata* and *Carpophyllum maschalocarpum* are found on rocks embedded in the sand flat adjacent to the reef and on the reef itself. In several places the reef is undercut and here *O. lutaria* grows at a higher level.

Perna canaliculus is found as scattered individuals or small clumps and has a similar range to the *Corallina officinalis* turf except that it is not found in pools, and may extend to the *Ecklonia* level. The tube worm *Pomatoceros cariniferus* forms clumps on both the western face, and the steep slope between the upper and lower platforms. At the landward end of the reef specimens which probably settled between December 1962 and February 1963 occurred scattered in wide shallow cracks, but the specimens forming the clumps were several years old.

In the autumn and winter months the brown algae *Petalonia fascia* and *Scytosiphon lomentaria* settled on the upper and lower slopes, especially on portions kept damp by seepage, and *Colpomenia sinuosa* was prominent on the *Corallina officinalis* turf.

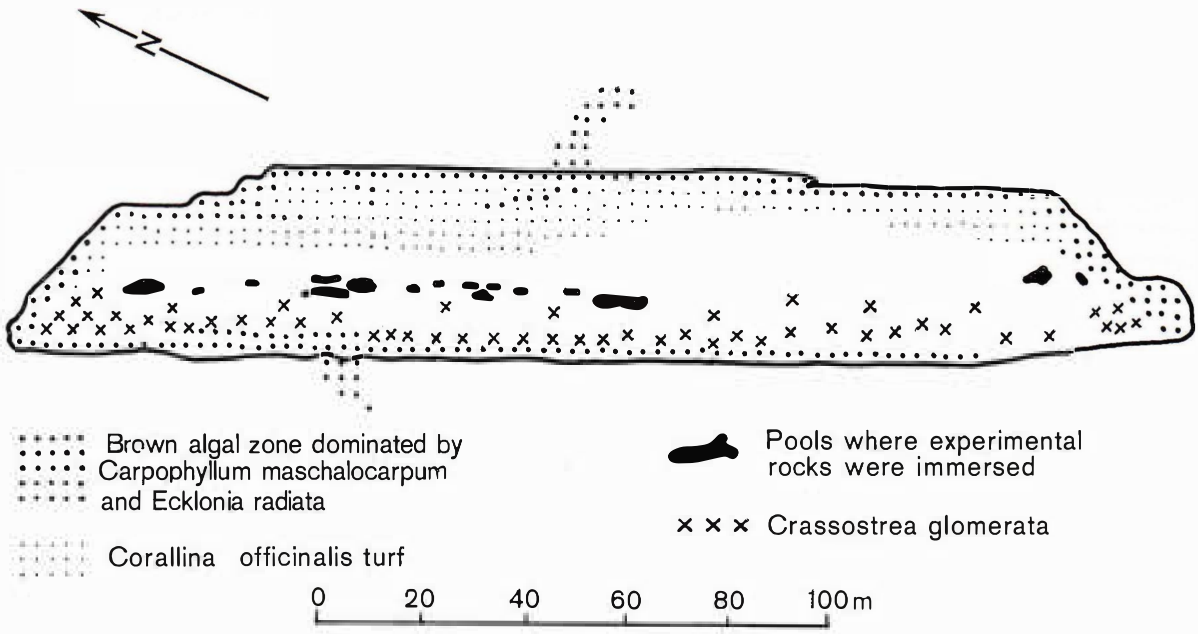


Fig. 7 A plan of the reef at West Tamaki Head showing the distribution of the main organisms, and the location of the pools where the experimental stones were immersed at fortnightly intervals. Unmarked areas include the upper platform and those parts of the lower platform covered by the barnacle *Elminius modestus* during most of the year.

METHODS

PIHA

(a) Clearing of rock surfaces

Areas were cleared monthly in the *Elminius plicatus* zone and on the southern slope of the reef, and observations made on the numbers and types of organisms settling on, or migrating to, these areas.

The surface layer of rock with its adhering organisms was removed using a bricklayer's hammer. The pattern of subsequent settlement did not appear to differ on squares where the surface layer of rock had been removed compared with squares where only the organisms had been removed.

(b) Artificial settling surfaces

During the second year 12.5 cm squares of slate were attached to two vertical rock faces to seaward of the experimental area, facing south and north respectively and adjacent to, but higher than, the cleared areas. Each slate had a central hole through which it was screwed on to the rock. Holes to take the screws were drilled by hand using masonry drills, and fitted with rawlplugs. This method of attachment permitted easy removal of slates for examination and their subsequent re-attachment. To reduce movement of the slate a rubber washer was placed between the slate and the screw head. Occasionally, baked clay plates were used instead of slate, the rubber washer then being omitted. In general, 38 mm ($1\frac{1}{2}$ in.) No. 10 stainless steel screws were used. These held well and any slate losses were usually due to slates splitting along lines of weakness, or to badly drilled holes which did not hold the plugs.

WEST TAMAKI HEAD

At West Tamaki Head three methods were used to study succession and colonisation.

(a) Clearing of rock surfaces at the seaward end of the reef

This was done with a bricklayer's hammer, a mattock, or a wire brush, the brush being sufficient to remove the surface rock layer on the lower slope of the reef once all larger growths had been cleared. The following surfaces were cleared.

(i) An almost vertical rock face on the western side of the reef. Here five vertical strips 0.3 m wide and approximately 1 m high were marked off and cleared.

(ii) The lower platform. A horizontal area just above the *Corallina officinalis* turf was marked out in squares and cleared. Later in the first year a sloping area in the *C. officinalis* turf below the first area was cleared.

(iii) The upper platform. To supplement the information on settlement on horizontal surfaces, several areas were cleared on the upper platform in the second half of the first year.

(b) Artificial settling surfaces

In the second year baked clay plates and slates were screwed on to the rock adjacent to all three cleared areas. These were removed and examined at fortnightly intervals.

(c) Rocks placed in pools and at low tide level

During each fortnightly visit after 5 April 1962 two or more rocks from the small beach behind the reef were placed in one of the 16 pools scattered along the upper platform. These rocks were usually partly embedded in shelly sand on the beach and were devoid of macroscopic algal growth. Since they were probably covered with a microscopic algal growth which might have affected subsequent settlement, some were scrubbed, and others sterilised with formalin or alcohol before they were placed in the pools. Examination of treated and untreated rock after 2, 4, and 6 weeks' immersion revealed no apparent differences in settlement rate or time among them. After this all rocks were left untreated. Each fortnight rocks were placed in a different pool, providing a sequence of emplacements, which was repeated throughout the experimental period to give several complete sequences. Examination of the rocks disclosed the general pattern of the process of colonisation, with reference to the length of immersion of the settlement surface.

NARROW NECK

(a) Clearing of rock surfaces

Areas were cleared in the *Corallina* zone on both horizontal and vertical rock faces, and on two rock surfaces originally cleared by Dellow in 1948.

(b) Artificial settling surfaces

These were used both in the barnacle zone and the *Corallina* zone but had to be abandoned because of continued interference.

(c) Rocks placed in pools and at low tide level

Rocks were placed at low tide level during the 12 monthly visits to the reef in 1962. They were raised up on small stones to prevent their sinking into the mud and smothering any animals on their lower surfaces.

SETTLEMENT SEASONS

A similar pattern of settlement occurred in both 1962 and 1963 at Piha and at West Tamaki Head (Figs 8, 9). Results from Narrow Neck (Fig. 10) are for 1962 only, but when compared with results from West Tamaki Head, settlement seasons of species occurring at both places were very similar. The different heights of the experimental areas at the two places makes direct comparison of all species impossible.

The number of species of several groups of organisms settling in each month was graphed for the three places (Figs 11, 12, 13), and shows some general trends common to both New Zealand and overseas shores. One of these, the summer settlement of serpulids (*Spirorbis* spp., *Hydroides norvegica*, *Pomatoceros cariniferus*) was previously noted by Coe & Allen (1937) and Skerman (1958, 1959); but Ralph & Hurley (1952) at Port Nicholson found that *Spirorbis* sp. and *Galeolaria hystrix* settled during all months of the year, without seasonal restriction. Fewer algae settled successfully in the warmer months. Coe & Allen working at La Jolla, California, also found a predominance of algae in the winter and spring months. The diatom *Navicula grevillei* was noted by Skerman (1958, 1959) in the winter and spring at both Lyttelton and Auckland, and by Hendey (1951) at Chichester Harbour. Settlement of the polyzoan *Watersipora cucullata* was restricted to the warmer months at Narrow Neck and West Tamaki Head and at other places in the Auckland Harbour (Skerman 1960). As noted by Skerman (1959) at Auckland, Moore (1944) at Auckland and probably further south, and Crisp &

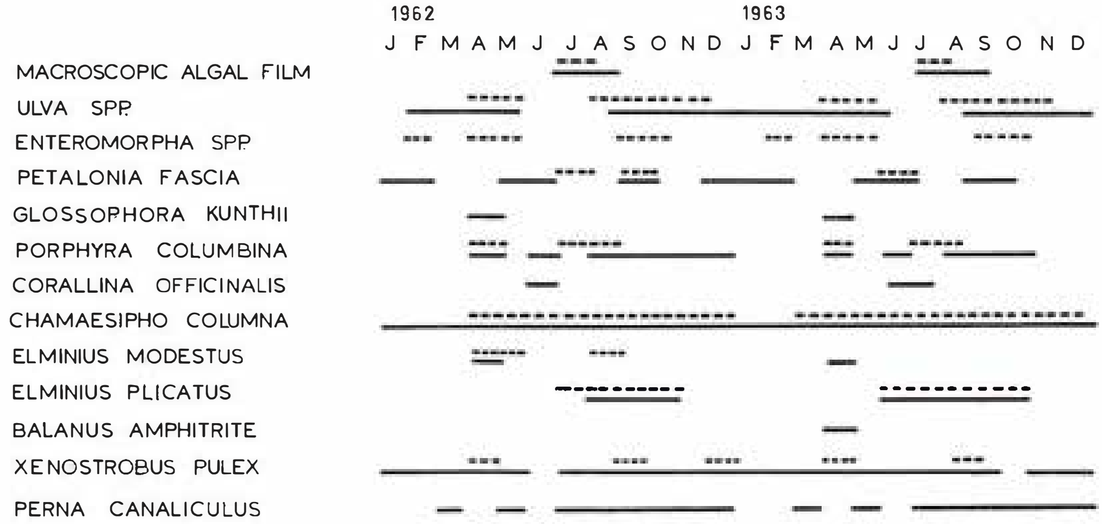


Fig. 8 The settlement seasons of the more abundant sessile organisms on the experimental areas at Piha during 1962 and 1963. Settlement at the lower level is shown by continuous lines and that at the upper level by broken lines.

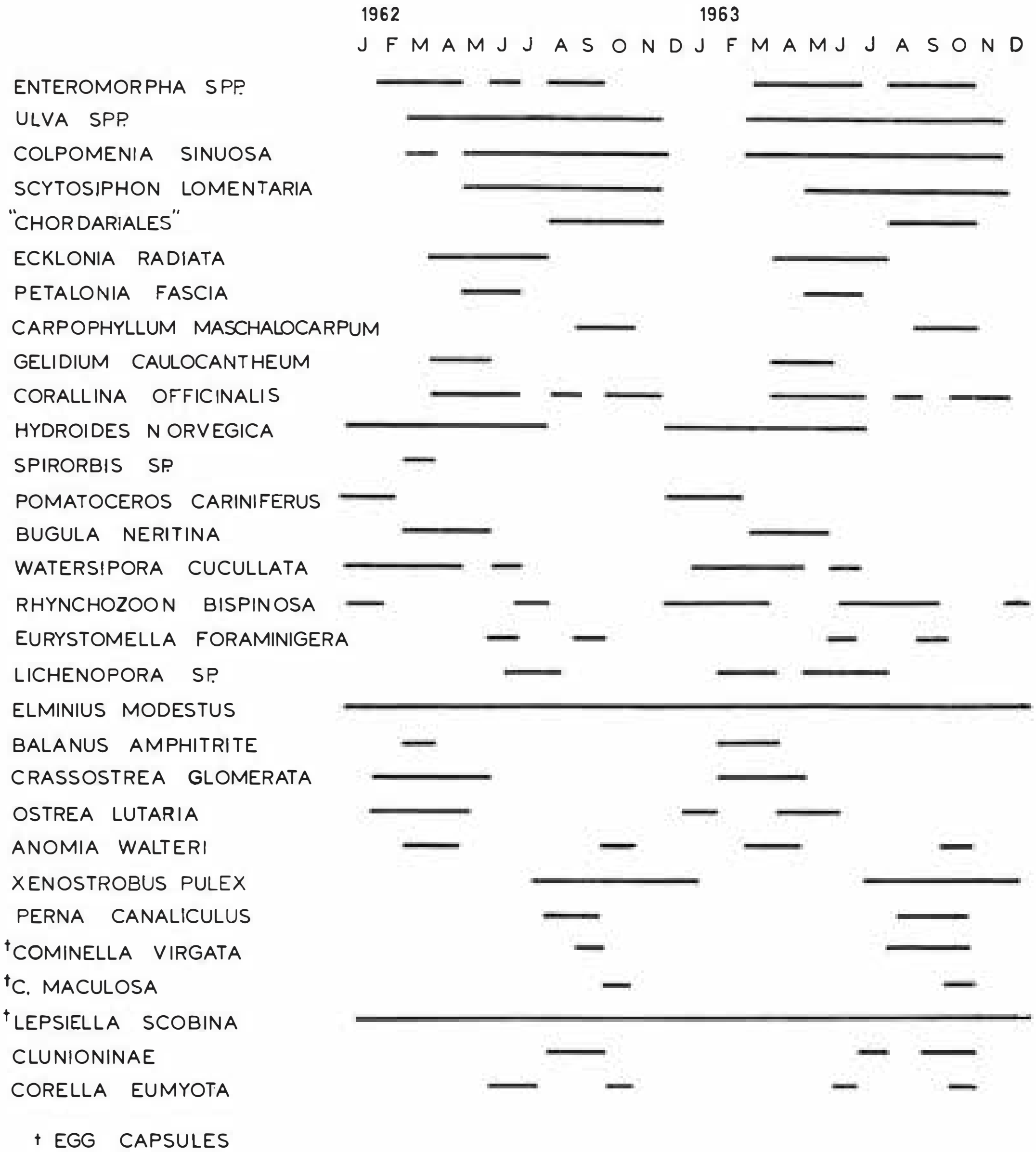


Fig. 9 The settlement seasons of the more common sessile organisms occurring on subtidal and intertidal surfaces at West Tamaki Head during 1962 and 1963. **Note:** *Anomia walteri* should read *Anomia trigonopsis*.

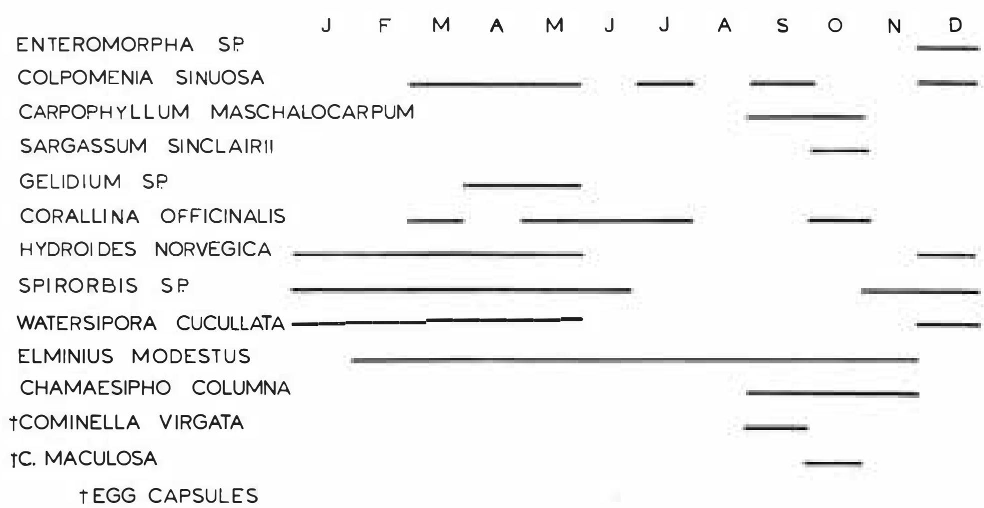


Fig. 10 The settlement seasons of the more abundant sessile organisms on intertidal surfaces at Narrow Neck during 1962. Most records refer to settlement within the *Corallina* zone.

Davies (1955) in Britain, *Elminius modestus* reproduced and settled at all seasons of the year.

On both coasts at Auckland there was at least one barnacle species settling throughout the year, this being *Chamaesipho columna* on the west coast and *Elminius modestus* on the east coast. At Piha a lack of suitable surfaces at low levels reduced the numbers of *E. modestus* below the point where settlement could be recorded as occurring throughout the year. In spring *C. columna* settled at Narrow Neck, and *Balanus amphitrite* settled at West Tamaki Head.

The Mytilidae and the Ostreidae settled at different times of the year. *Perna canaliculus* settled over a longer period on the west coast, but its time of greatest settlement on both coasts was from August to December. At the levels investigated on the east coast there was a clear division of settlement times, with *Ostrea lutaria* and *Crassostrea glomerata* settling from February to May and *P. canaliculus* and *Xenostrobus pulex* settling from August to December. Lower on the shore and subtidally on the east coast, *O. lutaria* appears to breed almost all the year. The saddle oyster *Anomia trigonopsis* belonging to an intermediate family, was found to settle at West Tamaki Head at the same times as both the Ostreidae and the Mytilidae.

The total number of species settling at the different sites is largely a reflection of the levels where observations were carried out. Work lower on the shore at Piha would have included many more species such as polyzoa, sponges, ascidians, and especially in the gully, numerous algae.

> All the information on settlement, growth, cause of death, etc., of all the species found at the three experimental areas is presented in Table 1, together with illustrations (Figs 14–48).

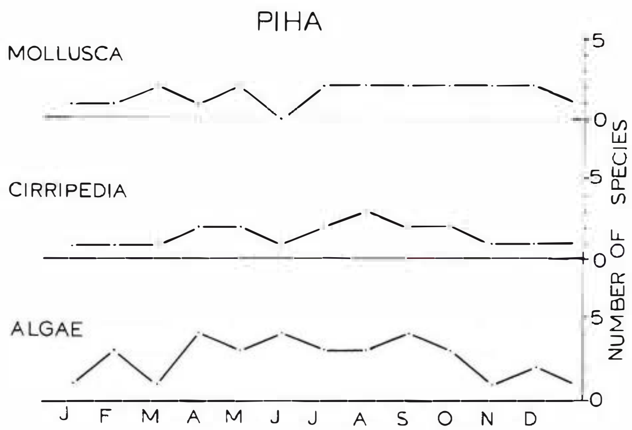


Fig. 11 The number of species settling monthly during 1962 in the more important groups of sessile organisms at Piha.

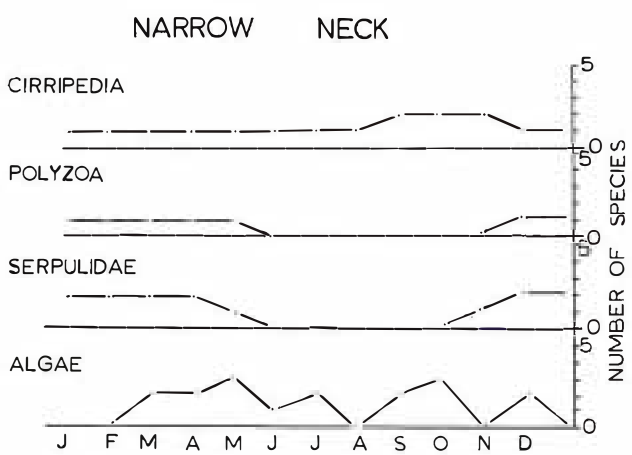


Fig. 12 The number of species settling monthly during 1962 in the more important groups of sessile organisms at Narrow Neck.

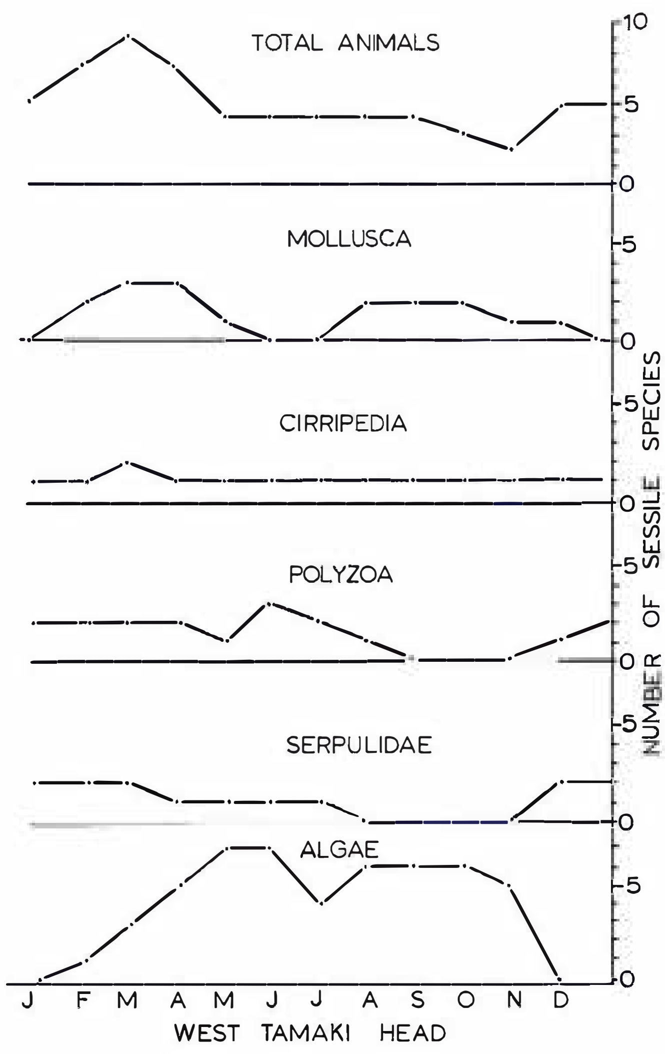


Fig. 13 The number of species settling monthly during 1962 in the more important groups of sessile organisms at West Tamaki Head.

Table 1

ORGANISMS SETTLING IN THE EXPERIMENTAL AREAS

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Macroscopic algal films			
SETTLING SEASON	Fine algal threads. July–August 1962, 1963.	Filamentous diatoms. June–December.	
SETTLEMENT LEVEL	Recently cleared, slow draining surfaces. Less apparent in 1963.	Densely on *Elminius modestus*. As a dark stain on rocks in pools.	
REMARKS	Covered newly settled *Chamaesipho columna* but did not harm them or restrict settlement.	Formed crust with silt which reduced barnacle settlement.	
***Ulva* & *Letterstedtia* spp.**		***Ulva* sp.**	
SETTLING SEASON	Most of year. September–May at lower level, April–November at higher level.	Autumn, winter, and spring.	
STAGE OF COLONISATION	Macroscopic plants any time after first 2–3 weeks of clearance.	On and between *Elminius modestus*.	
REMARKS	Grazed by *Littorina antipoda*, *Cellana ornata*, and *Lunella smaragda*. Frayed by surf at ends.	Marine chironomids common among mixed turf of *Ulva* sp. and *Enteromorpha* sp., feeding on algae.	
***Enteromorpha* spp.**			
SETTLEMENT TIMES AND CONDITIONS	February, April, May, September–October, more common at higher level and on poorly drained parts, particularly where there was a growth of *Ulva* sp. and *Xenostrobus pulex*, and grazing species were infrequent (i.e., areas which had been cleared several months before).	(a) small form less than 1 cm high present most of year on *Elminius modestus*. (b) larger form 3 cm high on upper surfaces of rocks in pools between February and November. Silt collected on and between plants but did not adversely affect growth.	December in *Corallina* zone, September and October on clay plates in barnacle zone at Crab Island.
Glossophora kunthii			
SETTLEMENT TIMES	April and May 1962 in small numbers at lower experimental level but forming a band 15 cm wide in the *Perna canaliculus* zone. Few plants seen in 1963.		
Chordariales		Forms dark brown irregularly shaped patches up to 1 mm thick on clay plates and rocks in pools, persisted for months but did not produce fruiting bodies.	
Myriogloia lindaueri			August–September at mid-tide level on rocks where sand had been recently removed by storms. Not on experimental areas.
Petalonia fascia (*figure 14*)			
SETTLEMENT TIMES	July, September at higher level. January, February, May, June, September, and December at lower level.	May and June.	
SETTLEMENT AREAS	Experimental areas cleared more than two months previously, surrounding reef slopes.	Above *Corallina* zone on poorly drained areas.	
SURVIVAL	2–4 months.		
FORM	12 or more unbranched straps 1 cm × 8–12 cm arising from a common base. Leathery.	Singly or in 2s and 3s, 1.5–20 cm × 15–20 cm. Thin and membraneous. Could attach to rock at distal tip and form further strap.	

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Scytosiphon lomentaria			
SETTLEMENT TIMES		June–August.	
SETTLEMENT AREA		On rocks in pools and on flat, poorly drained areas above the *Corallina officinalis* turf.	
Colpomenia sinuosa			
SETTLEMENT TIMES		March, May, June, July on rocks in pools.	March–May, July, September, December.
OCCURRENCE		Found at all times but more prominent in cooler months. At all levels on reef but restricted to pools and crevices at higher levels.	Cleared areas in *Corallina* zone. Rocks in brown algal zone. Any stage from newly cleared rock.
SIZE		1–40 mm diameter.	3–9 mm diameter after 1 month.
Leathesia difformis			
SETTLEMENT TIMES		May–November.	
SETTLEMENT AREA		Upper platform.	
Ecklonia radiata			
SETTLEMENT TIMES		April–July.	
SETTLEMENT AREA		Submerged rocks. Artificial pool on upper platform.	
SIZE		20–25 cm at 6 months.	
REMARKS		Removed by *Lunella smaragda* grazing.	
Durvillea antarctica	Fertile plants December 1962. No settlement on experimental areas.		
Carpophyllum maschalocarpum			
SETTLEMENT TIMES		Spring 1962.	July, September, October.
SETTLEMENT AREAS		Rocks in brown algal zone. NOT on rocks in pools.	Horizontal cleared areas in *Corallina* zone, tops of rocks in brown algal zone. Cleared rock surfaces below *C. officinalis* turf on Crab Island.
Sargassum sinclairii			
SETTLEMENT TIMES			September.
SETTLEMENT AREAS			As for *Carpophyllum maschalocarpum*.
Porphyra columbina			
SETTLEMENT TIMES	April–November at lower level. April–August at higher level.		

Fig. 14 Young specimens of *Petalonia fascia* growing at the lower experimental level at Piha, mixed with *Ulva* sp. and growing above a layer of *Xenostrobus pulex*. Calipers set at 5 cm.

Inset 2

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Corallina officinalis			
SETTLEMENT TIMES	June below lower level and on gully walls.	April–November on lower platform and rocks in pools.	March, May–August, October on cleared areas in *Corallina* zone and rocks at low tide mark.
GROWTH, ETC.	Paint stage only developed.	Many sporelings died at a diameter of up to 5 mm. Vegetative reproduction from tips of fronds touching rock as well as spores.	Up to 7 sporelings/cm². Turf 2–3 mm high by end of fourth month.
Porifera	Sponges all found below experimental levels.	As at Narrow Neck. *Hymeniacidon perlevis* grew on to rocks from adjacent colonies.	A small unidentified spiny sponge fairly common under rocks. Also a keratose sponge forming thin patches.
Coelenterata: Anthozoa	Not colonising cleared rock areas.	Two spp. of *Sagartia* moved on and off rocks in pools. (a) greyish or colourless up to 10 mm high. (b) Green and orange striped 16–18 mm high. Often the first animals to appear on the rocks in pools but usually migrated adults, not settling larvae.	
Coelenterata: Hydrozoa	*Sertularia bispinosa* and *Sertularella* sp. settled on *Perna canaliculus* where they formed a suitable substrate for the settlement of *P. canaliculus*.	Hydroids abundant on rocks in pools, particularly between July and September. The largest, most conspicuous, being a species of *Plumularia*. When hydroids were abundant eolid nudibranchs (*Facelinella* spp.) were often found together with their spawn bands.	
Watersipora cucullata *(figures 16, 20, table 2)*			
SETTLEMENT TIMES		December–June on submerged rocks, sometimes within 24 hours of immersion. Settlements after April died before reaching 5 mm diameter.	December, January, March–May. Similar to West Tamaki Head. Forms black-brown crusts over the rock surface often with orange edges. Prominent in the intertidal zone.
REMARKS		Slowly spreading from the Port of Auckland (Skerman 1960) Tends to grow over surrounding organisms (*see figure 16*).	
Rhynchozoon bispinosa *(figures 15, 16)*			
SETTLEMENT TIMES		June, July, December, January, March.	
SETTLEMENT AREAS		Lower sides of rocks in pools and among brown algae low on the shore.	Under rocks at low tide.
SETTLEMENT DENSITY		1–250 colonies/rock (lower surface only).	
REMARKS		Crowded colonies grow more slowly than spaced colonies (*figure 15*). Smothers many surrounding species and inhibits the growth of *Botryllus schlosseri* (*figure 48*). Colonies circular in outline.	

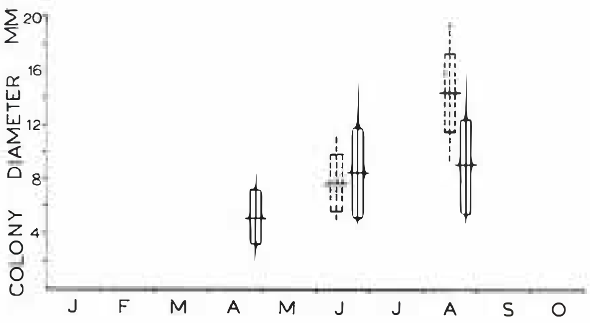


Fig. 15 Growth rates of *Rhynchozoon bispinosa* settled at the same time on two different rocks, between January and October 1962. The dotted lines are the colony diameters from a rock with only 12 colonies and the solid lines refer to a rock with numerous, crowded colonies.

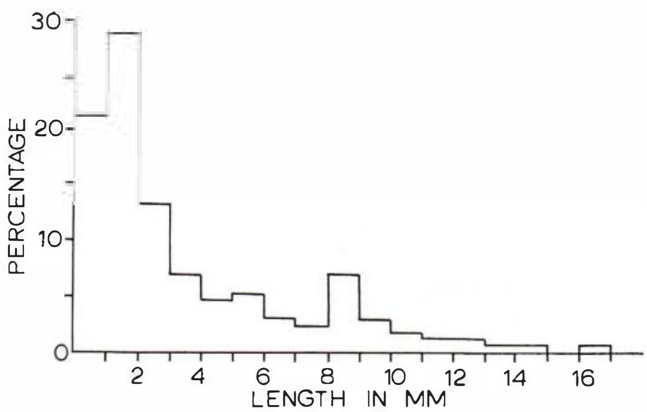


Fig. 17 The length of the *Hydroides norvegica* on a rock immersed in a pool at West Tamaki Head for one month (7 February–8 March 1962). There appear to have been at least two settlements. In Sydney Harbour there is a fortnightly periodicity of *H. norvegica* settlement coinciding with the spring tides (Dew & Wood 1955).

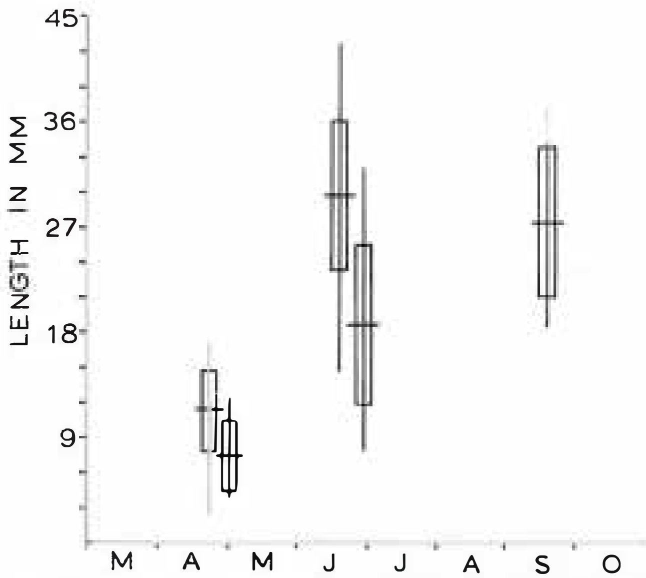


Fig. 18 Growth rates of *Hydroides norvegica* on the lower side of a rock immersed in a pool at West Tamaki Head, between March and October 1962.

Fig. 16 Polyzoans and *Hydroides norvegica* on the lower side of a rock immersed in a pool. The dark colonies are *Watersipora cucullata*, the small, pale colonies with the radial ridges and lower rims are *Lichenopora novaezelandiae*, and the large and small, pale colonies with the stippled surface are *Rhynchozoon bispinosa*.

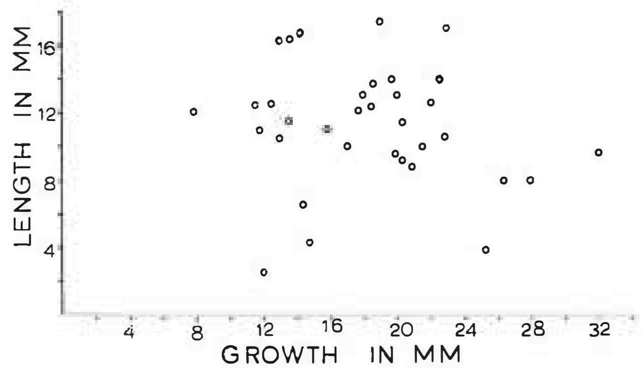


Fig. 19 The relationship between the length of *Hydroides norvegica* tubes and their subsequent amount of growth. The original length bears little relation to the amount of growth in the following months, although there is a tendency for the largest specimens to grow more than small ones in terms of absolute increment.

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Eurystomella foraminigera			
SETTLEMENT TIMES		Winter and spring.	
SETTLEMENT AREAS		Lower sides of experimental rocks in pools.	Under rocks at low tide.
SETTLEMENT DENSITY		Up to 6 colonies/rock. Colonies not regularly circular.	
Lichenopora novaezelandiae			
SETTLEMENT TIMES		June–August 1962. February, March, May–July 1963.	
SETTLING AREA		Under rocks in pools and at low tide.	Under rocks at low tide.
REMARKS		Settles in groups of 3–12. Forms small raised white cushions with radiating ridges, surrounded by a narrow rim.	
Bugula neritina			
SETTLEMENT TIMES		February–May.	
SETTLING AREA		Rocks in pools, low level rock surfaces, subtidally on rocks and *Carpophyllum maschalocarpum*.	
Hydroides norvegica (*figures 17, 18, 19* on p. 19)			
SETTLING SEASON		December–July 1962. December–June 1963.	December–February, April, May.
SETTLING AREA		Upper and lower sides of rocks in pools.	*Corallina* zone.
SETTLING DENSITY		Rocks up to $2/cm^2$, platform up to $8/cm^2$.	
SURVIVAL		Upper surface rocks up to 2 months. Lower platform up to 1 month.	Up to 3 months.
MAXIMUM SIZE AT 4 WEEKS		17 mm (*see figures 17, 18, 19*) (cf Skerman 1959).	
CAUSES OF DEATH		(a) dehydration (intertidal surfaces). (b) smothering (rocks in pools). (c) predation by *Taron dubius*.	
Pomatoceros cariniferus (*figures 20, 21, 22*)			
SETTLING SEASON	September–November 1962.	December–February.	
SETTLING LEVEL	Low tidal clay plates, high level slates.	Lower platform and western face (*figures 20, 22*). Rarely on upperside submerged rocks.	
SURVIVAL		Up to 1 year.	
GROWTH RATES		(*see figure 21*)	
***Spirorbis* sp.**			
SETTLING SEASON	September–December.	March 1962.	November–June.
SETTLING AREA	Clay plates below *P. canaliculus* beds; south face of gully.		*Corallina* zone and rocks in the brown algal zone.
SETTLEMENT DENSITY			$3.5/cm^2$.
Idianthyrsus quadricornis			
SETTLEMENT	Occasionally on backs of clay plates on vertical rock faces		

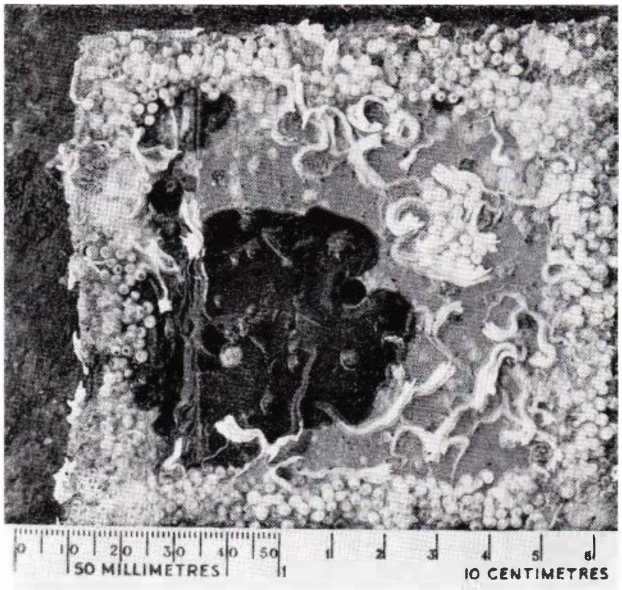


Fig. 20 The under surface of a clay plate attached to the western face at West Tamaki Head, showing one large and several small colonies of *Watersipora cucullata*, good settlement and growth of *Pomatoceros cariniferus*, and numerous egg capsules of *Lepsiella scobina*. Settlement of *P. cariniferus* is better on clay plates than on slates, possibly because of their better water-retaining qualities.

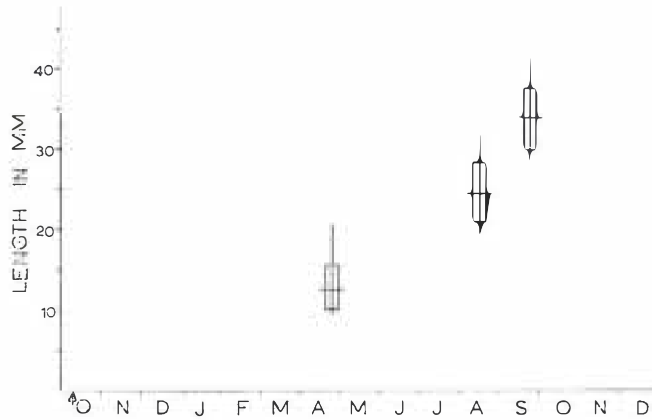


Fig. 21 (above) Growth rates of *Pomatoceros cariniferus* calculated from measurements of the specimens on the clay plate from West Tamaki Head shown in Fig. 20, between October 1962 and December 1963.

Fig. 22 Part of a clump of *Pomatoceros cariniferus* on the western face at West Tamaki Head close to the experimental areas. Photographed 4 October 1963.

Perna canaliculus (*figures 23–30*)

	PIHA	WEST TAMAKI HEAD	NARROW NECK
SETTLING TIMES	All year. Maximum July to December.	July to October.	
SETTLING AREA AND DENSITY	Greatest density on *Sertularia bispinosa* and other hydroids, then finely divided algae (*Ceramium* sp.) on older mussels, among byssus threads, and *Xenostrobus pulex* (*figure 23*) (Havinga 1956).	*C. officinalis* turf on lower platform. Cracks near pools.	
GROWTH RATES	(*see figure 24*)	(*see figure 26*)	
LENGTH AT 1 YEAR	70 mm.	20–55 mm or 35–40 mm.	
SIZE AT SEXUAL DIFFERENTIATION	30–40 mm.	30–40 mm.	
MAXIMUM SIZE	80 mm (Powell 1961, 172 mm).		
AGE AT DEATH	1 year.	1 year.	
LENGTH WHEN 20 MM HIGH	40 mm (average) (*figures 25, 27, 28*).	35 mm (average) (*figures 26, 28*).	
PREDATION	Humans, *Dicathais scalaris*.	Humans.	
ENCRUSTING SPECIES	*Balanus amphitrite*, *Elminius plicatus*, *E. modestus*, *Chamaesipho columna*, hydroids, *Ceramium* sp., *Ulva* sp., *Petalonia fascia.*		
BORING SPECIES	*Cryptophialus melampygos* and *Penetrantia irregularis* (*see* Silen 1956).		

Fig. 23 On the west coast *Perna canaliculus* is found in beds on the lower shore but the density of these varies widely and is often related to their accessibility. At Piha where they are heavily picked an irregular cover consisting of scattered clumps of mussels is most common.

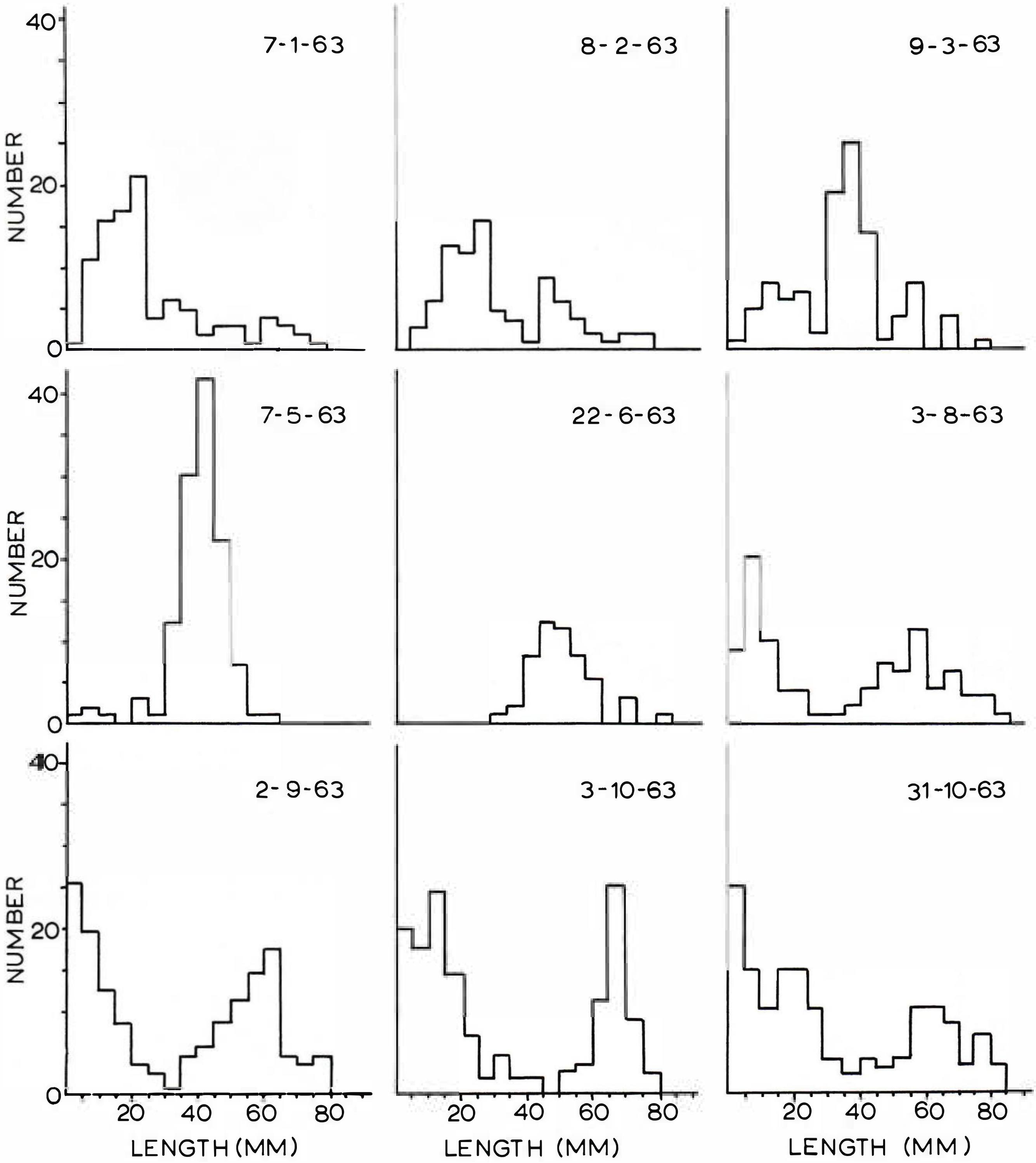


Fig. 24 The length distribution of *Perna canaliculus* collected from below the lower experimental level at Piha during 1963. Results given as the absolute numbers found in each 5 mm size class. The absence of individuals longer than 85 mm is a reflection of human collection which is most intense in the summer months and in May.

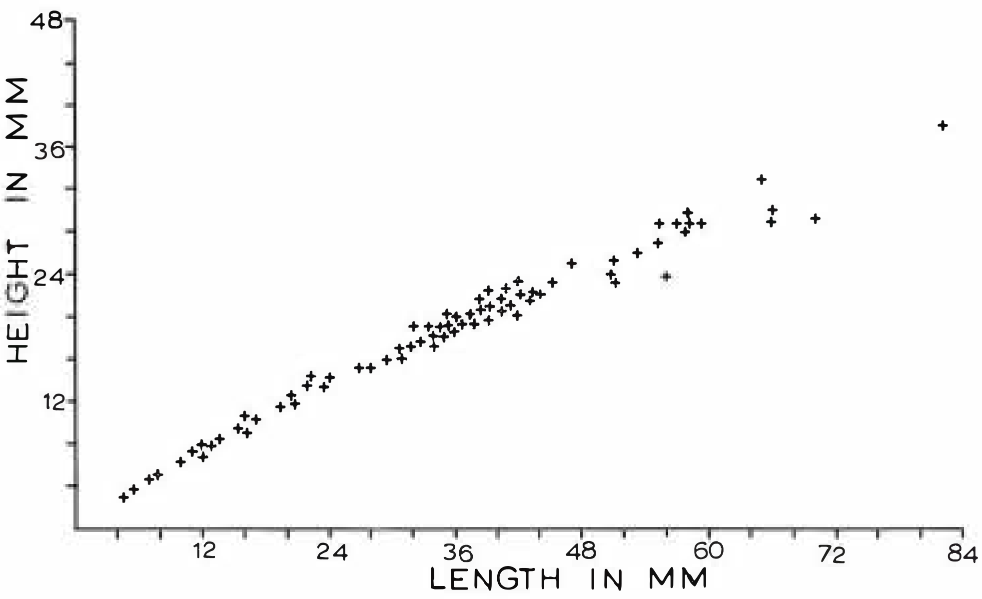


Fig. 25 The ratio of length to height in specimens of *Perna canaliculus* from Piha.

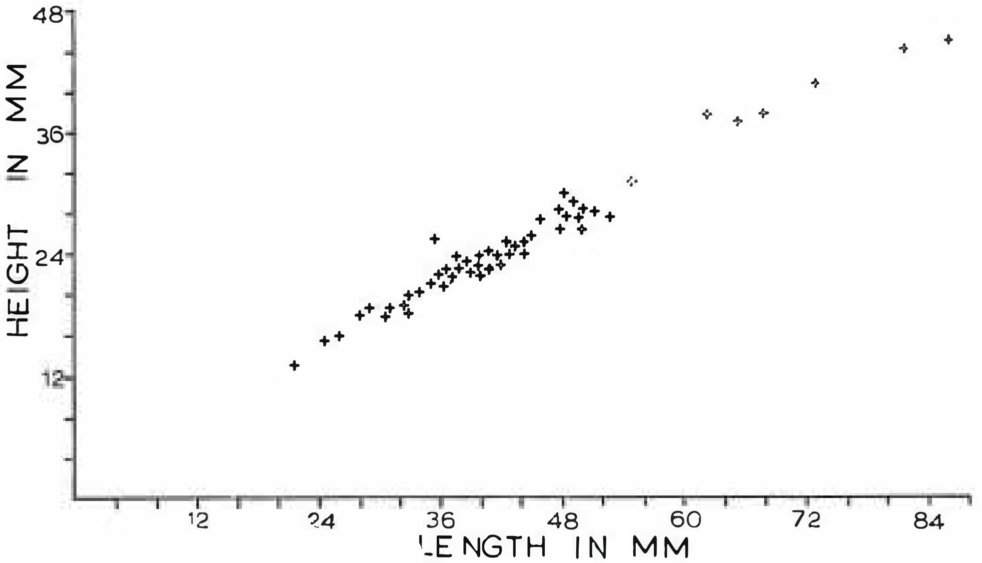


Fig. 26 The ratio of length to height in specimens of *Perna canaliculus* from West Tamaki Head. Growth is slower and settlement occurs over a more limited period here than at Piha. Most of the specimens are about one year old, but the six largest ones are of unknown age.

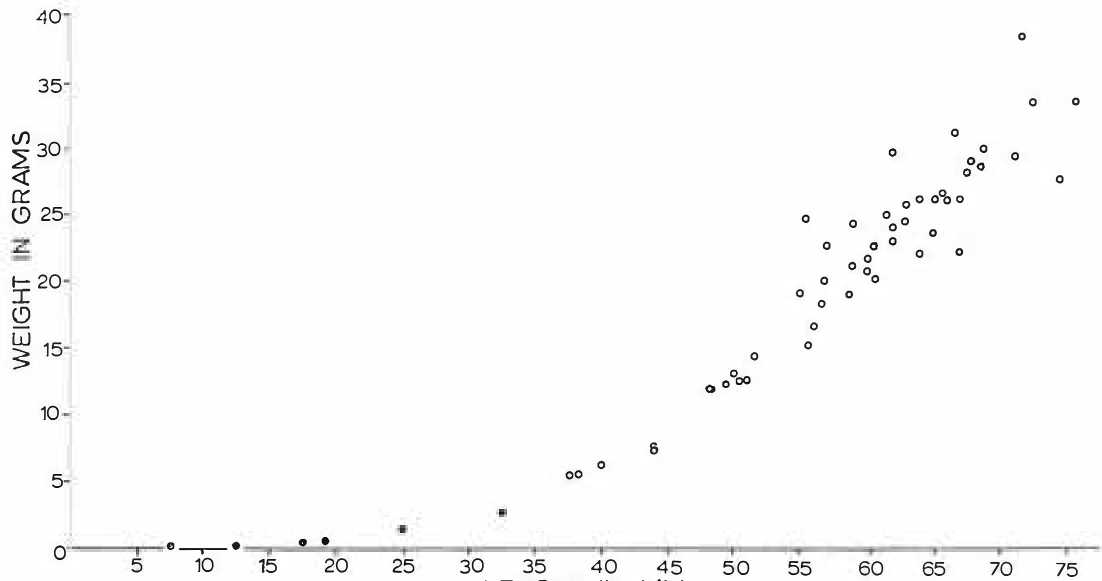


Fig. 27 The ratio of length to weight in specimens of *Perna canaliculus* from Piha. The solid circles showing lengths less than 35 mm are of averaged weights. (Weight is total weight of animal, shell, and retained water.)

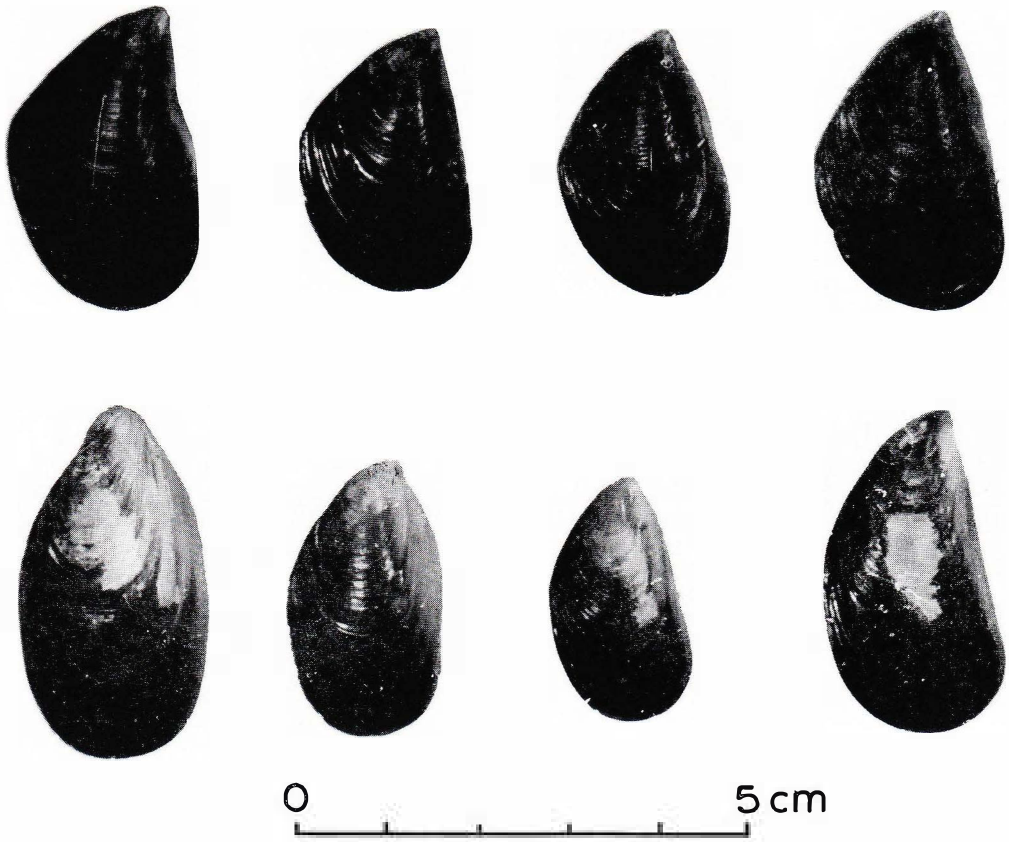


Fig. 28 Specimens of *Perna canaliculus* from West Tamaki Head (upper) and Piha (lower) to show the difference in shell shape.

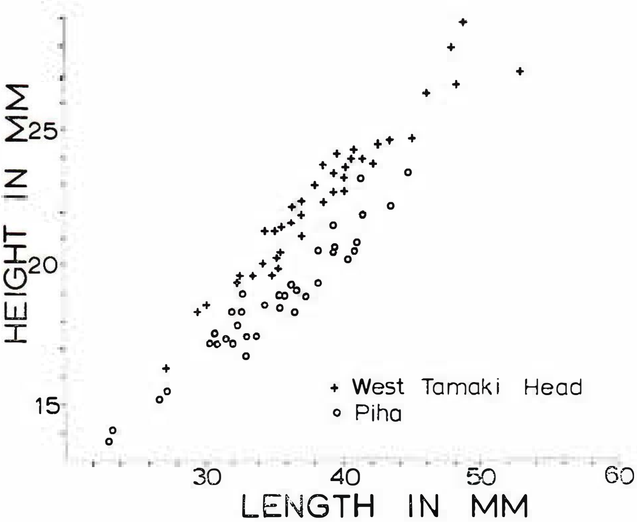


Fig. 29 The ratio of length to height in specimens of *Perna canaliculus* from Piha (o) and West Tamaki Head (+) showing the slight but distinct difference in proportion between the two samples (*see also* Fig. 28).

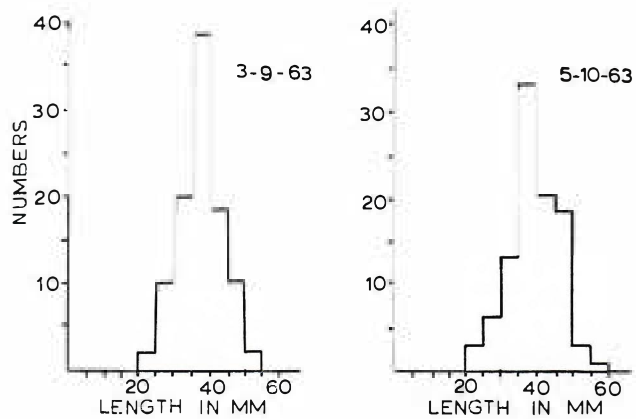


Fig.30 The length distribution of *Perna canaliculus* from West Tamaki Head, sampled when the mussels were 11 months old (3 September 1963) and 12 months old (5 October 1963).

Inset 3

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Xenostrobus pulex (*figures 31–35*)			
SETTLEMENT TIME	All months of year at lower level. January, April, September, December at higher level.	July–October on upper platform.	
SETTLEMENT PATTERN	Settlement most abundant in rock hollows, cracks, and crevices, also between barnacles and older *Xenostrobus pulex*. Delayed on smooth rock or plates at higher levels until barnacles had settled and grown to 2–3 mm diameter (*figure 31*).	Between barnacles, even on apical plates. Successive settlements growing to form a continuous carpet smothering the barnacles, and accumulating silt between the mussels and the rock surface.	
GROWTH	(*see figure 33*)		
GROWTH RATE	Faster at higher temperatures (*see figure 34*) and lower on the shore.	Mussel carpet forced up into ridges 2–8 cm high by continued growth. Silt helps prevent crushing by people walking on reef in summer (*see figure 32*).	
SEXUAL DIFFERENTIATION	Apparent at 8–10 mm long. Male gonad white-cream, female gonad orange-brown. Sex ratio 1:1.		
MAXIMUM SIZE	(*see figure 34*)	August (1.5 mm), October (2.5 mm), January (11 mm) on rocks in pools.	
CAUSES OF DEATH	(a) high air temperatures and low spring tides in afternoon particularly at higher levels and landward end of reef. (b) heavy seas remove sheets of *X. pulex*, particularly where a layer of sediment has built up between the rock and the mussels and only peripheral mussels are attached directly to the rock. (c) Predation. The gastropods *Lepsiella scobina* and *Dicathais scalaris* and the rock cod *Acanthoclinus quadridactylus*. (d) Crushing by people walking on the reef. Also important in that it breaks the surface continuity of the mussel carpet enabling the sea to get under and remove large unattached areas of mussels.	(a) high temperatures and afternoon low spring tides in summer. (b) Rough seas in February 1963 removed almost all of mussel carpet (together with many dead barnacles). (c) Predation by *Lepsiella scobina*, which was abundant on the reef but actual feeding was not seen. (d) Crushing by people walking on reef in summer.	

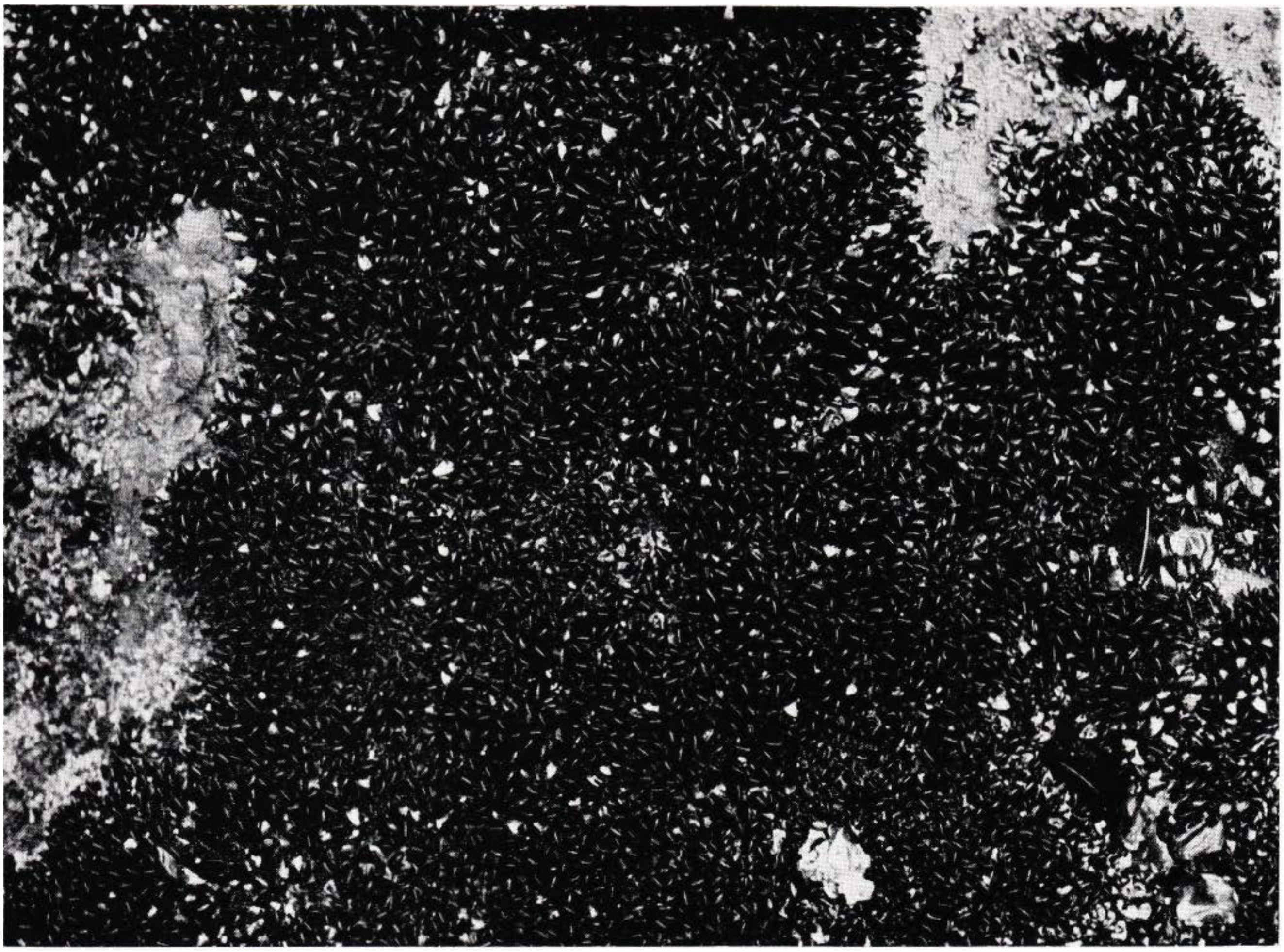


Fig. 31 (above) The cover of *Xenostrobus pulex* on one of the cleared areas at the lower experimental level at Piha.

Fig. 32 The dense carpet of *Xenostrobus pulex* developed on the upper platform at West Tamaki Head from larvae settling on and between the *Elminius modestus.* Rough seas in February 1963 removed all the *X. pulex* and most of the dead barnacles beneath them

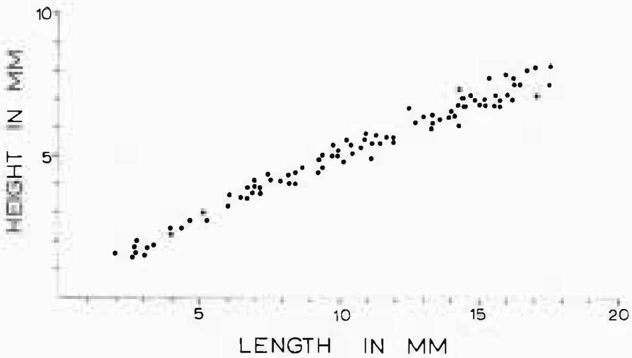


Fig. 33 The ratio of length to height in a sample of *Xenostrobus pulex* from Piha.

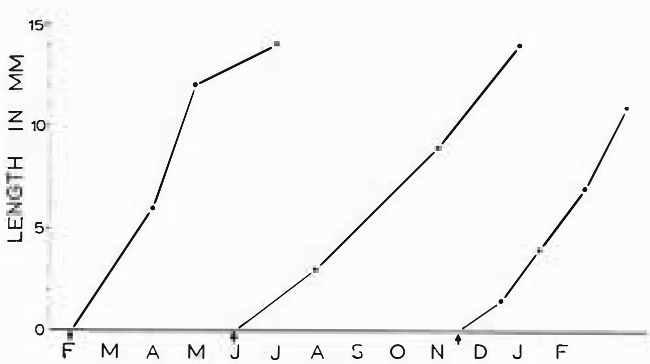
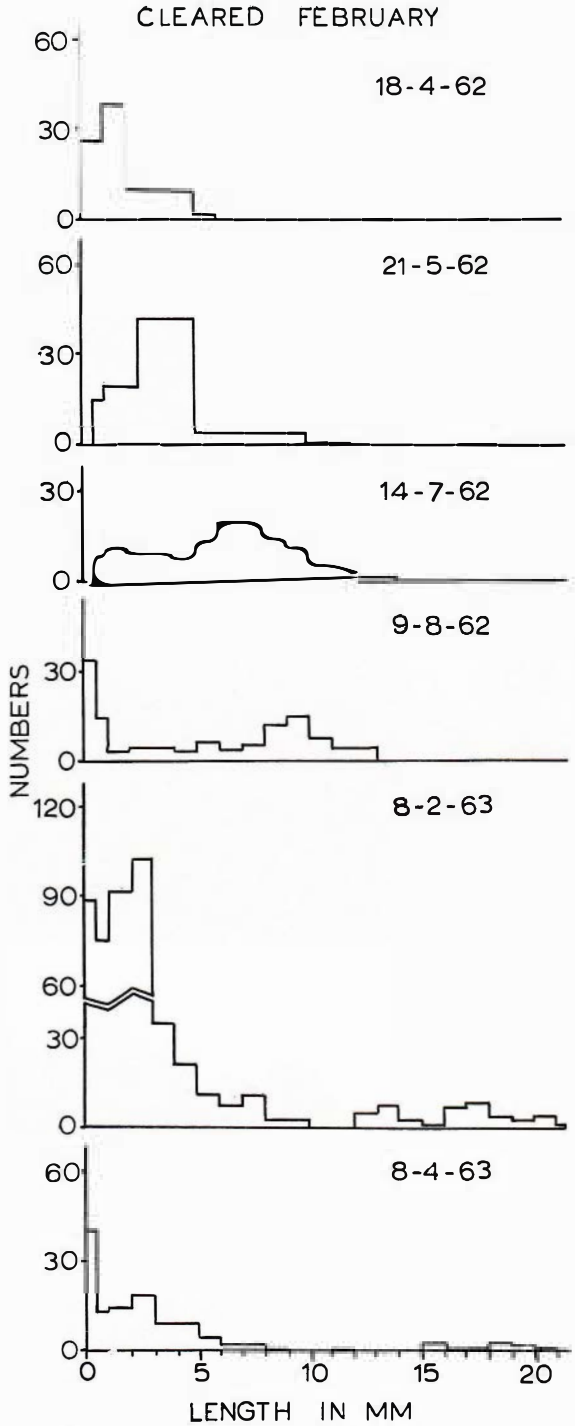
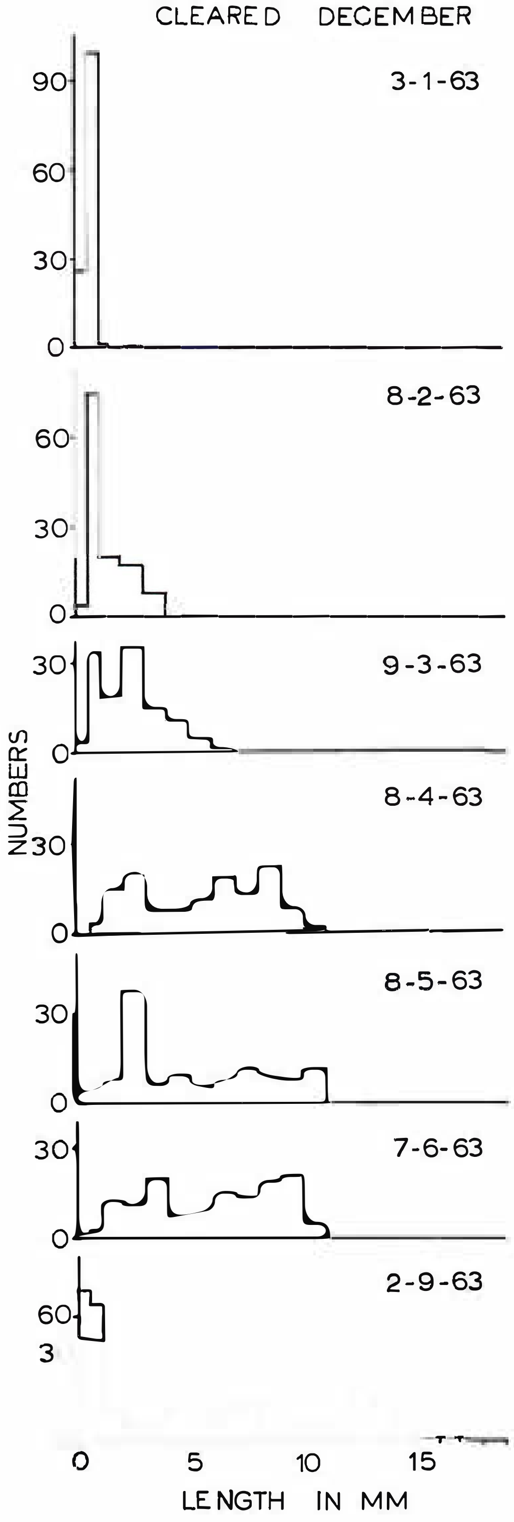


Fig. 34 Maximum growth rates of *Xenostrobus pulex* which settled at the lower experimental level at Piha at various times of the year, between February 1962 and February 1963. (Settling time indicated by arrows.)

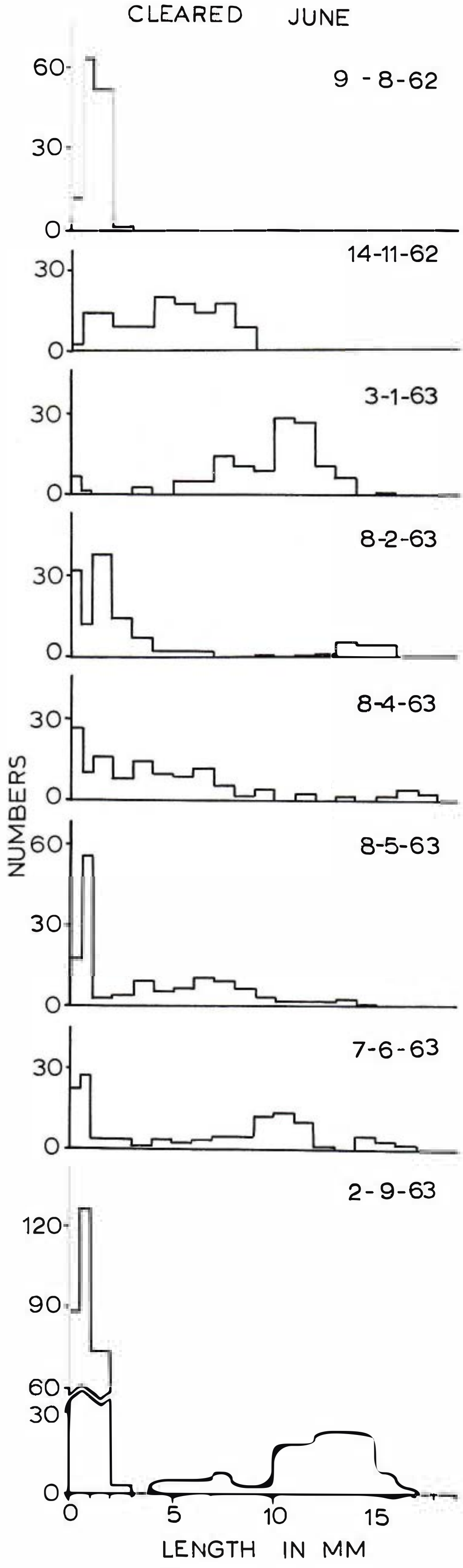


(a)

Fig. 35 a–c The length distribution of samples of *Xenostrobus pulex* from three areas at the lower experimental area at Piha cleared in February, June, and December 1962 and sampled for varying periods of time after clearance. The growth of successive settlements can be followed through the samples.


CLEARED DECEMBER
3-1-63
8-2-63
9-3-63
8-4-63
8-5-63
7-6-63
2-9-63
NUMBERS
LENGTH IN MM

(b)


CLEARED JUNE
9 - 8-62
14-11-62
3-1-63
8-2-63
8-4-63
8-5-63
7-6-63
2-9-63
NUMBERS
LENGTH IN MM

(c)

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Chlamys zelandiae			
SETTLEMENT TIME		September–December.	
SETTLEMENT AREA		Under rocks in pools.	
SETTLEMENT DENSITY		Up to 3/rock.	
Anomia trigonopsis (*figure 36*)			
SETTLEMENT TIME		March, April, October.	
SETTLEMENT AREA		Reef surface 0.6–1.2 m. Under rocks in pools. Beneath slates on horizontal or vertical surfaces.	
SETTLEMENT DENSITY		Up to $15/dm^2$ in March and April.	
SURVIVAL		3–9 months.	
GROWTH RATE		(*see figure 36*)	
Ostrea lutaria (*figures 37, 38*)			
SETTLEMENT TIMES		February–April 1962. January, April, May 1963.	
SETTLEMENT AREA		Under rocks in pools.	
SETTLEMENT DENSITY		Up to $16/dm^2$ in March and April.	
SIZE AT 4 WEEKS		5 mm diameter. *cf.* Hollis (1963), Skerman (1959) (*see figure 37*)	
SURVIVAL		4–12 months (4–5 cm long).	
SHAPE		(*see figure 38*)	
Crassostrea glomerata			
SETTLEMENT TIMES		January–May.	
SETTLEMENT AREA		Western face.	
LENGTH OF 0+ YEAR GROUP 28–1–63		39.0 max; 26.1 mean; 14.0 min. (mm)	
LENGTH OF 0+ YEAR GROUP 18–10–63		18.0 12.4 7.0	
LENGTH OF 1+ YEAR GROUP 18–10–63		47.5 38.0 29.5	
CAUSE OF DEATH		(a) predation by *L. scobina*. (b) dislodgment by waves of specimens which had grown over and smothered the *Elminius modestus* beneath them and consequently were insecurely attached.	
Anchomasa similis and ***Pholadidea spathulata***			
SETTLEMENT TIMES		July–August 1962; May, October 1963.	
SETTLEMENT AREA		In soft rocks in pools. Suitable soft rocks were not always available.	
SIZE OF HOLES BORED		*A. similis* settled in July–August 1962 had bored completely through 20 cm of rock leaving holes 1.9 cm in diameter in November 1962.	
SETTLEMENT PATTERN		Settlement often heavy on a small area of rock but could have been related to surface texture or larval aggregation.	

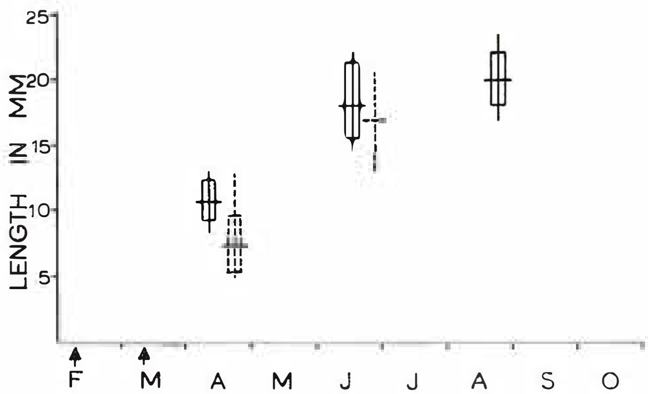


Fig. 36 The growth of *Anomia trigonopsis* settled on rocks immersed in pools (at the arrowed dates) at West Tamaki Head, between February and October 1962. The specimens represented by the solid lines were still alive in early December, but the sample shown as a dotted line was dead by July.

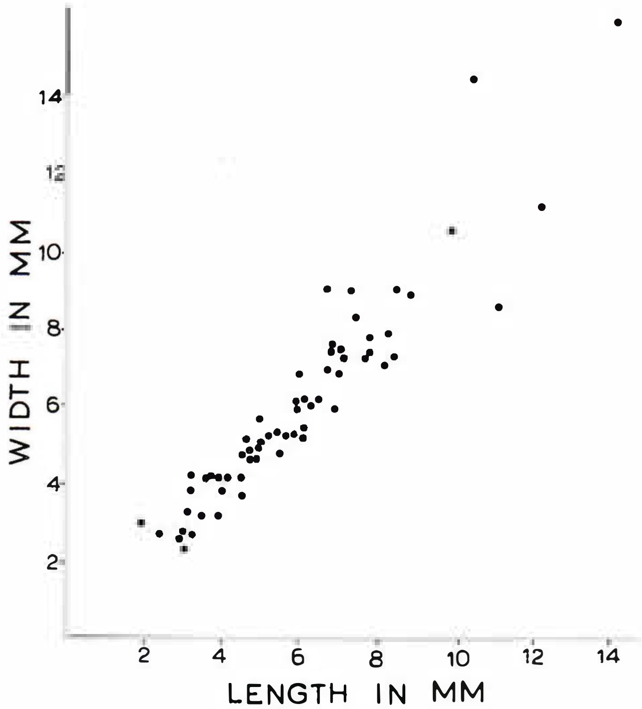


Fig. 37 The relationship between length and width in a sample of *Ostrea lutaria* from the lower side of a rock immersed in a pool two months previously at West Tamaki Head.

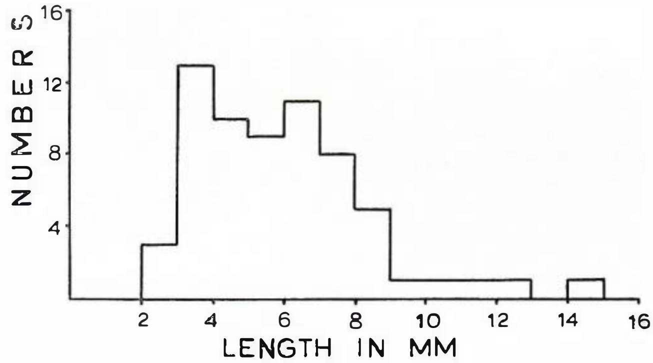


Fig. 38 The length distribution of *Ostrea lutaria* from the lower side of a rock at West Tamaki Head after two months immersion. Most of the individuals were dead a few weeks later.

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Elminius modestus *(figures 39, 40)*			
SETTLEMENT TIME	April, May, August, September.	Throughout year.	All year. February–November in *Corallina* zone.
SETTLEMENT AREA		Western face, upper and lower platforms, upper and lower surfaces of rocks in pools.	Oyster zone to below E.L.W.S.
SETTLEMENT PEAKS		Mid winter and early spring (this corresponds with the peak in the numbers of barnacle nauplii and cyprids in plankton tows in the Waitemata Harbour (Jillett, pers. comm.).	
SETTLEMENT DENSITY		Up to 45/cm² (*see figure 39*).	
GROWTH RATES		Higher in warmer months and low on shore.	
SIZE AFTER 2 WEEKS		April to October 1 mm diameter. November to March 2 mm diameter.	
SIZE AFTER 4 WEEKS		April to October 1 mm diameter. November to March up to 8 mm diameter.	
HUMMOCK FORMATION (*cf.* Barnes & Powell 1950, Knight-Jones & Moyse 1961)		Occurs 8–10 weeks after settlement in warmer months on lower platform.	
SIZE OF BARNACLES IN HUMMOCK		Max. diameter 7–8 mm. Average diameter 2–5 mm.	
DENSITY WITHIN HUMMOCK		12–16/cm².	
CAUSES OF DEATH		(a) Predation by *Lepsiella scobina* on barnacles larger than 2 mm diam. usually by boring through apical plates but through parietal compartments where space was restricted (*figure 40*). (b) Smothering by *Xenostrobus pulex* in late spring and summer on upper platform. (c) Smothering by oysters, polyzoans (*Watersipora cucullata*, *Eurystomella foraminigera*, and *Rhynchozoon bispinosa*), ascidians (*Botryllus schlosseri* and *Corella eumyota*), sponges, and hydroids.	(a) Smothering by *Corallina officinalis* paint within three months of settlement by *C. officinalis*.
LIFE EXPECTANCY	Up to 1 year.	Up to 1 year.	Up to 1 year.
BREEDING SEASON	All year.	All year.	All year.

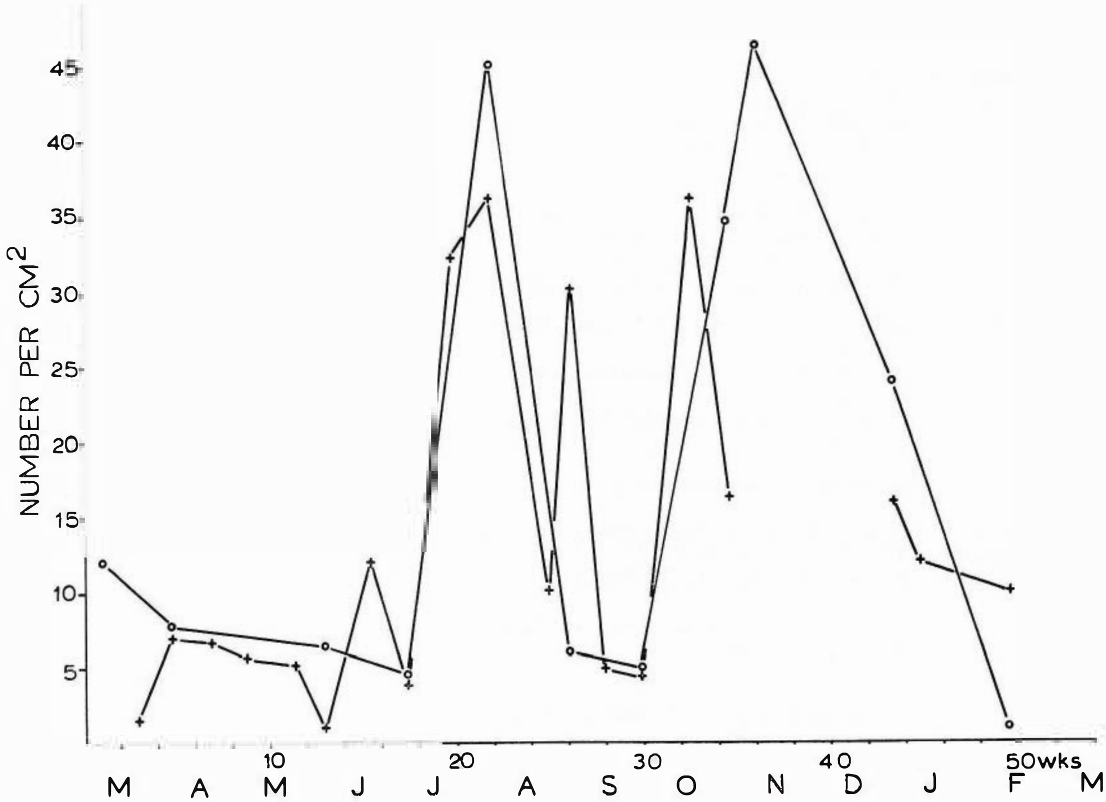


Fig. 39 The numbers of *Elminius modestus* settled per square centimetre on cleared rock surfaces on the lower platform at West Tamaki Head, two weeks (+–+) and four weeks (O–O) after clearance, between March 1962 and March 1963.

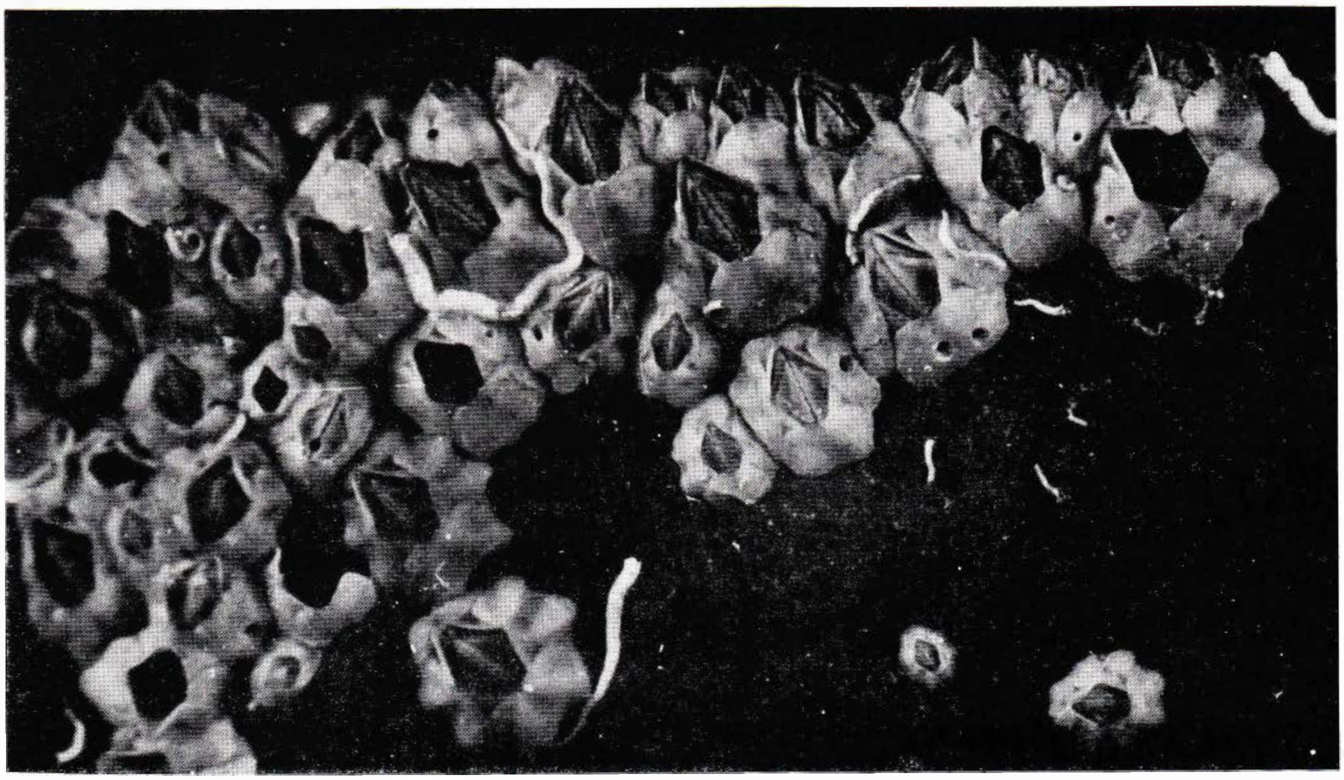


Fig. 40 *Elminius modestus* settled on the back of a slate attached closely to a rock face at West Tamaki Head; they have been bored in both their apical plates and parietal compartments by the predatory whelk *Lepsiella scobina*. Barnacles settled on the open rock surface are usually bored in their apical plates by *L. scobina*, but behind slates where space was limited and parietal areas were more accessible these parietal areas were bored by the *L. scobina*.

PIHA | WEST TAMAKI HEAD | NARROW NECK

Elminius plicatus *(figures 41–45)*

SETTLEMENT TIME	Most of year, particularly July to November at higher level and August to November at lower level in 1962, but July to November at all levels in 1963.
SETTLEMENT LEVELS	From the *Perna canaliculus* beds to the top of the *E. plicatus* zone. On wave-exposed rocks settlement also occurred up to 1 m above the upper level of the *E. plicatus* zone.
SETTLEMENT DENSITY	Lower level: up to 90/dm^2 on areas cleared one month previously. Up to 60/dm^2 on areas cleared two months previously. Up to 5/dm^2 on areas cleared three months previously.
GROWTH RATE	Decreases with increasing height on shore.
SIZE AT 4 MONTHS AFTER SETTLEMENT	Sample from *P. canaliculus* beds 9–10 mm basal diam. *(see figure 41).* Sample from lower level 7.5 mm (av.) basal diam. *(see figure 43).* Sample from higher level 8.2 mm (av.) basal diam. *(see figure 44).*
SHELL SHAPE	Higher levels tall and tubulo-conical – orifice slightly smaller than base. Low-levels – low conical shell with base much larger than orifice. Low-level specimens surrounded by *Xenostrobus pulex* grow tall. *E. plicatus* can avoid smothering by *X. pulex*.
AVERAGE LENGTH OF LIFE OF THOSE SURVIVING FIRST MONTH	(a) on *P. canaliculus* 4–6 months. (b) lower experimental level 8–9 months. (c) upper experimental level up to 1 year.
BASAL DIAMETER AT MAX. AGE	(a) on *P. canaliculus* beds 10 mm. (b) lower experimental level 13 mm. (c) upper experimental level 23 mm *(figure 42).*
CAUSES OF DEATH	(a) on *P. canaliculus* beds — (i) Predation by *Dicathais scalaris* and fish (also starfish in more exposed mussel beds). (ii) Dislodgment by wave action or people. (*E. plicatus* with a membraneous base is much more easily removed than *Balanus* which has a calcareous base firmly cemented to the mussel shell).

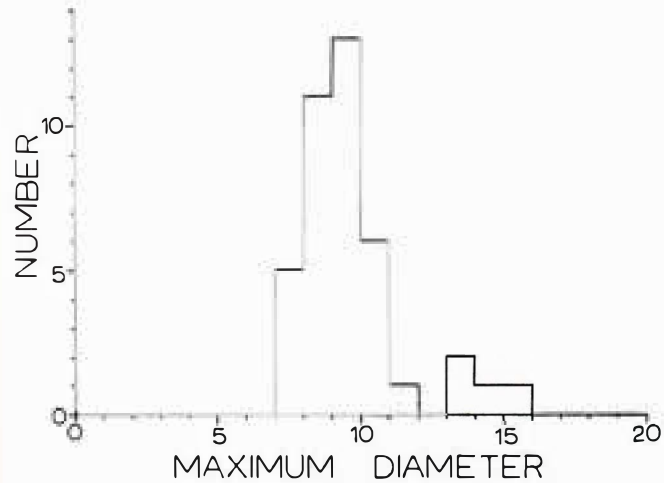


Fig. 41 The size (maximum basal diameter, mm) distribution of *Elminius plicatus* growing on *Perna canaliculus* below the lower experimental level at Piha.

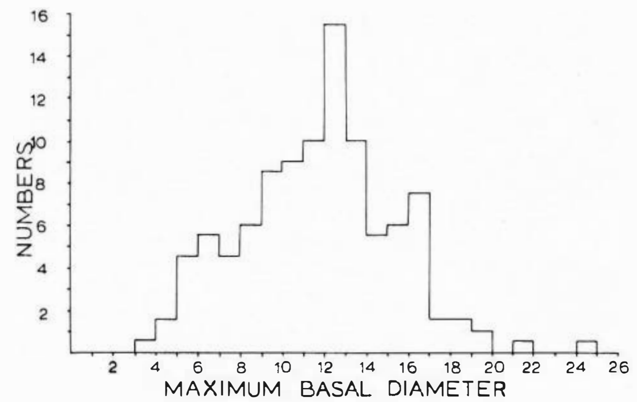


Fig. 42 Size distribution (maximum basal diameter, mm) of the adult population of *Elminius plicatus* (i.e., that present before the start of the experimental work) at the upper experimental level at Piha.

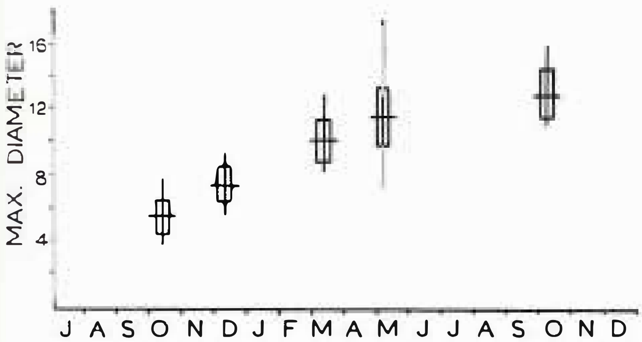


Fig. 43 Growth rates of *Elminius plicatus* at the lower experimental level at Piha, from July 1962 to December 1963. Diameter in mm.

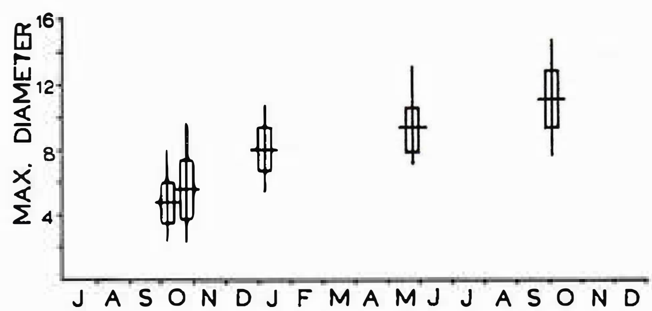


Fig. 44 Growth rates of *Elminius plicatus* at the upper experimental level at Piha, from July 1962 to December 1963. Diameter in mm.

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Elminius plicatus CAUSES OF DEATH (CONTINUED)	(b) Lower experimental level — (i) Smothering by *X. pulex*: as early as the third month when *X. pulex* settles earlier than *E. plicatus*: where *E. plicatus* settles several weeks before *X. pulex* smothering had not occurred when the *E. plicatus* were six months old (and tubulo-conical) *(figure 45)*. (ii) Predation by *Dicathais scalaris*. In May 1963 many dead 9-month old *E. plicatus* were found with rose-purple markings on their intact apical plates. These were presumed to have been smothered by *D. scalaris* (*see also* Luckens 1966, Connell 1961). (iii) Crushing by people walking on the reef. Spaced out barnacles not surrounded by *X. pulex* are particularly affected since a solitary barnacle is subject to a greater weight. (iv) Insecure attachment. *E. plicatus* which had grown over and smothered surrounding *Chamaesipho columna* were easily detached. (c) Upper experimental level— (i) Damage by people walking on the reef as the barnacles were neither densely settled nor strong enough to resist the pressures applied. (ii) Smothering by *X. pulex* is less important at this level. *E. plicatus* settled on other *E. plicatus* are safe from smothering by *X. pulex*. (iii) Predation. Once *E. plicatus* reach 5–8 mm in diameter they are too large to be bored by *L. scobina*. *D. scalaris* is rare at this level.		
Chamaesipho columna	*(figures 46, 47)*		
SETTLEMENT TIMES	All year at lower experimental level. April–January at higher experimental level.	No settlement, no adults.	August–November.
SETTLEMENT RANGE AND SUBSTRATES	From H.W.S.-L.W.S. on rock and *E. plicatus* at higher levels and on mussels, barnacles, and gastropods at lower levels.		Oyster and barnacle zones on cleared rock and baked clay plates.
DENSITY OF SETTLEMENT	Up to 120/cm², usually 30–50/cm². At a density of 80–90/cm² the specimens are contiguous at a diameter of 1–1.5 mm. Dense settlements occur at least once a month and may be related to tide cycle — probably greatest at spring tides.		Up to 70/cm² on lower edge of plate (October, 4 weeks). 30/cm² on cleared rock in oyster zone (August). Up to 12/cm² lower edge of plate in barnacle zone (September, 2 weeks).
RUGOPHILIC SETTLEMENT	Tends to settle in grooves, depressions, scratches on slates, grooves in stainless steel screws, pits in perspex plates.		
SETTLEMENT ON BLACK AND CLEAR PITTED PERSPEX PLATES ON VERTICAL SURFACES	Both sides of black perspex and outer side of clear perspex bore similar number but numbers were greatly reduced on inner side of the clear plate, with only one-fifth of the pits occupied, mostly by one barnacle each. The three other surfaces had 75% of holes occupied by up to seven barnacles each *(figure 46)*.		

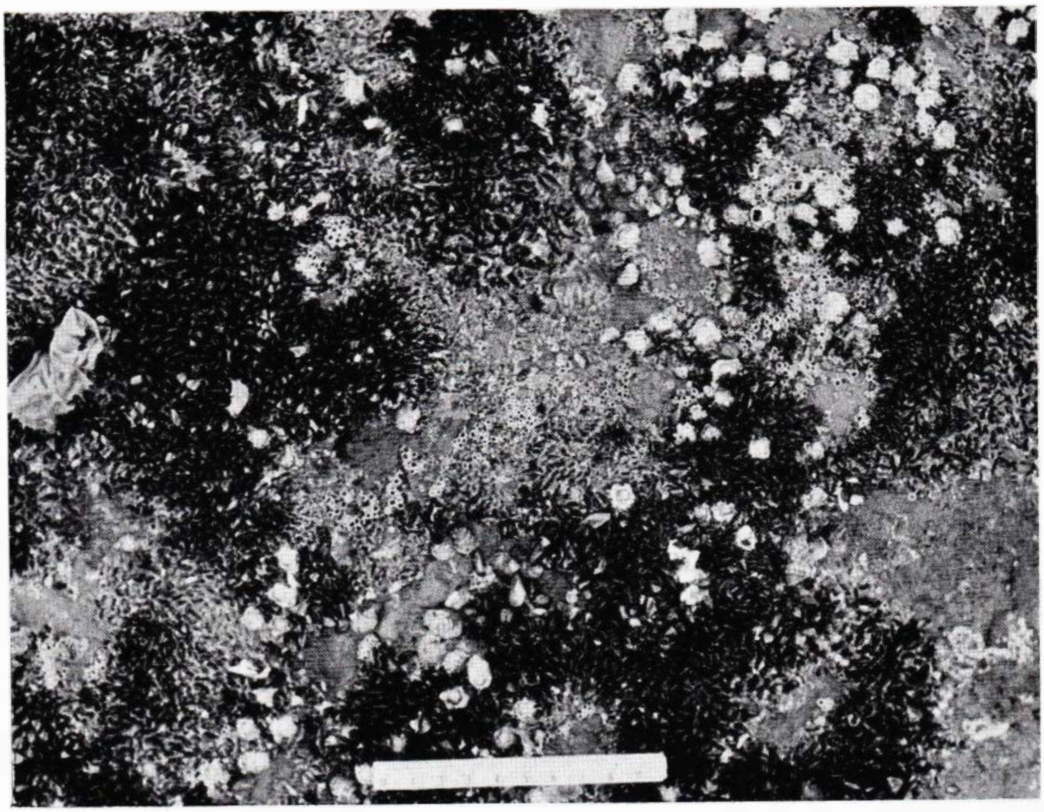


Fig. 45 *Elminius plicatus* surrounded by *Xenostrobus pulex* at the upper experimental level at Piha. Numerous *Lepsiella scobina* and dead *Chamaesipho columna* are also present. Scale 10 cm long.

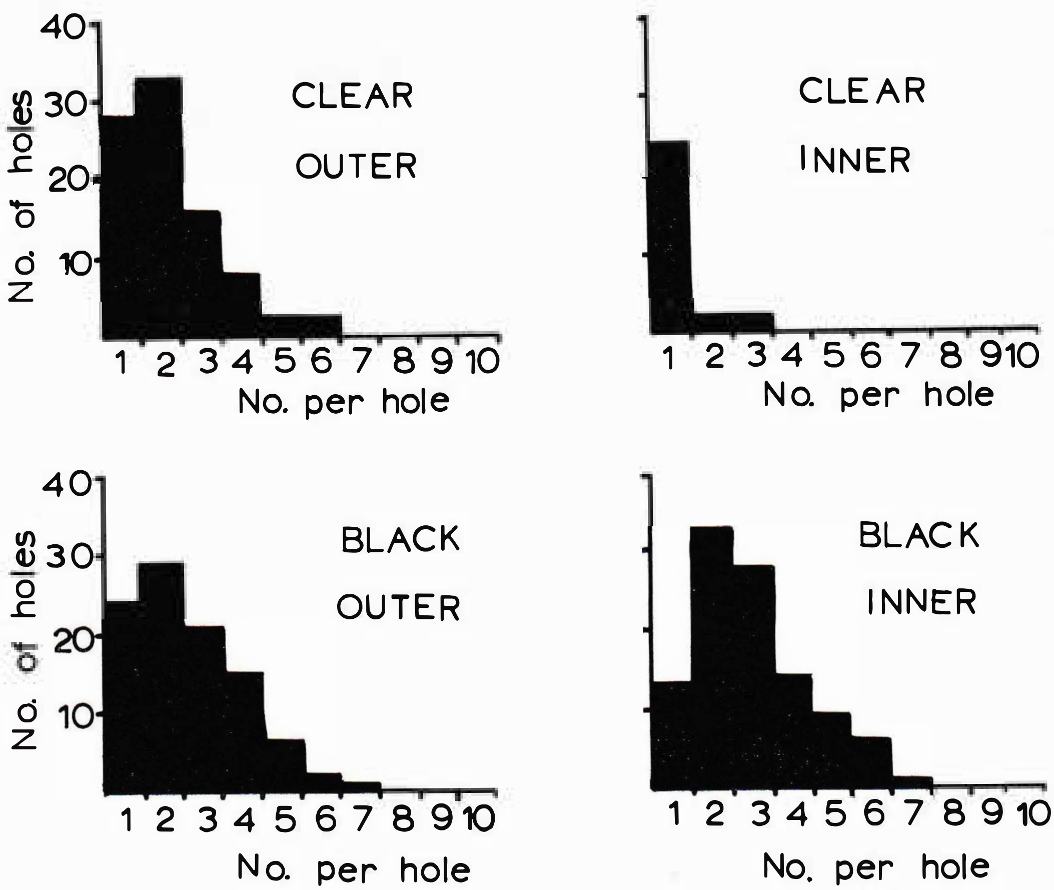


Fig. 46 The number of *Chamaesipho columna* settling in pits drilled on both sides of clear and black perspex plates. The inner side refers to that side nearest to and facing the rock to which the plate was attached. (Piha upper level.)

Chamaesipho columna *(continued)*

SETTLEMENT ON VERTICAL SLATES — Greater on outer side with most barnacles restricted to the edges of the inner side. Settlement reduced and restricted to the lower edge on north facing, high level slates in summer due to differential heating of the slate. During winter settlement was similar on slates facing north and south. Growth faster where settlement density lower *(figure 47)*.

GROWTH RATE ON SLATES — AVERAGE DIAMETER OF CONICAL FORM ON SLATES EXPOSED AUG.–OCT. 1963

South face		North face	
Inner	Outer	Inner	Outer
2.65 mm	1.85 mm	1.45 mm	1.30 mm

Barnacles on south face have longer feeding time.

SIZE AT 10–12 MONTHS, ISOLATED SPECIMENS — 4–4.5 mm basal diameter on both north and south faces.

DIAMETER AT 7–8 MONTHS IN FUSED SHEETS — 1–3 mm.

CAUSES OF DEATH —
(a) Smothering by *Xenostrobus pulex* was common at the lower level, and more rapid here than at higher levels, but occurred wherever both the species occurred.
(b) Predation by *Lepsiella scobina* was more important at the higher level and on barnacles larger than 2 mm diameter. The numbers of *L. scobina* on the experimental areas at the upper level rose as the barnacles increased in size. With a density of six *L. scobina*/dm^2 the proportion of live *C. columna* larger than 2 mm diameter fell to 5–10%. This density was reached four months after settlement in summer.
(c) Overgrowth by *Elminius modestus* (on the *P. canaliculus* beds) and *E. plicatus* on the lower and upper experimental levels.

SURVIVAL — Up to 2 months at lower experimental level (*X. pulex* smothering).
Up to 6 months at upper level (*L. scobina* predation).
Up to 10 months on slates higher on the shore. At higher levels where predators are absent specimens at least a year old are found.

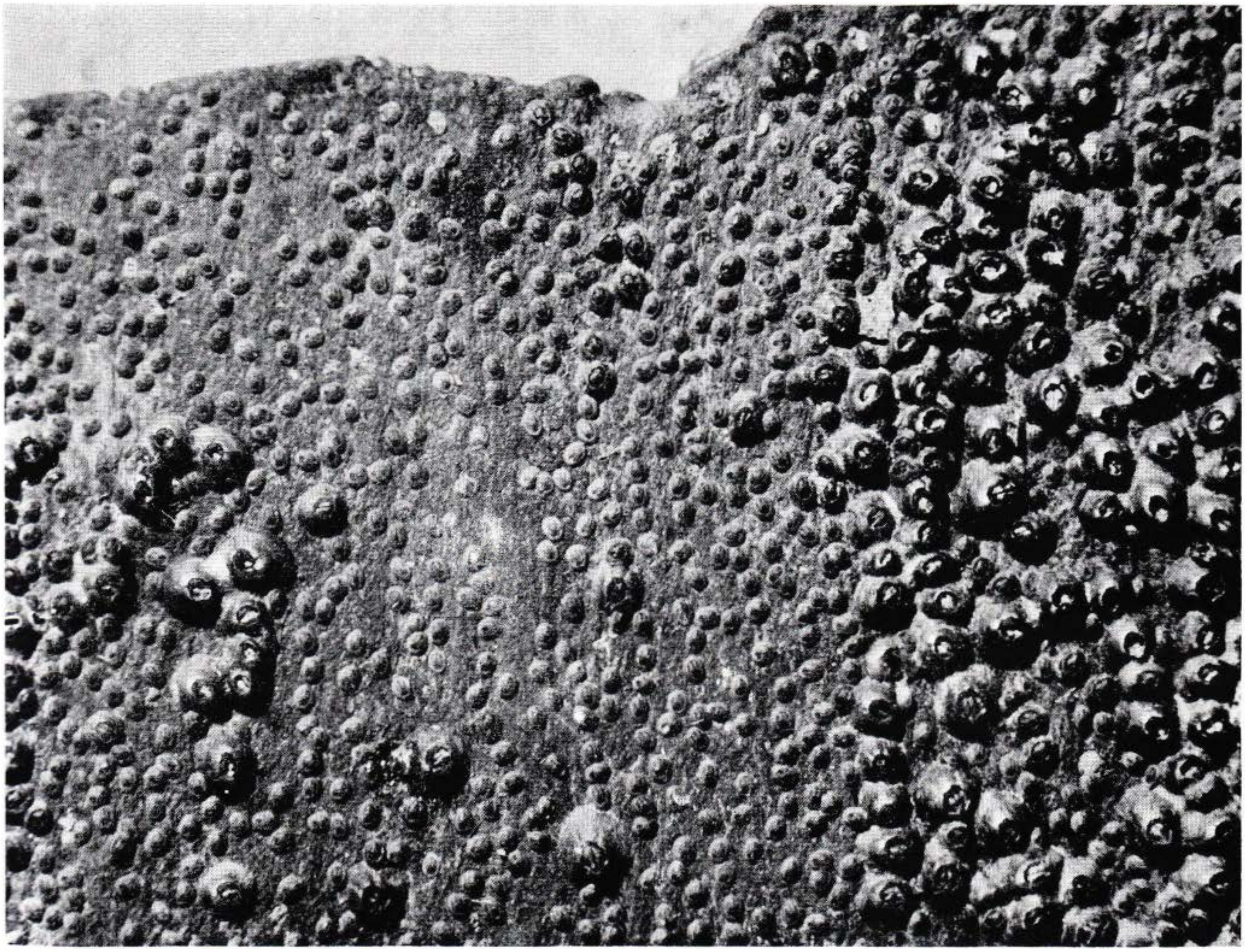


Fig. 47 Part of a slate exposed at Piha showing both newly settled and older *Chamaesipho columna*. The newly settled specimens are about 0.5 mm long.

	PIHA	WEST TAMAKI HEAD	NARROW NECK
Corella eumyota			
SETTLEMENT TIME		June, July, October. 1962 winter settlement heavy. 1963 spring settlement heavy.	June, July, October. 1962 winter settlement heavy. 1963 spring settlement heavy.
SETTLEMENT LEVEL		Restricted to lower surfaces of submerged rocks.	Restricted to lower surfaces of submerged rocks.
SURVIVAL		Up to 6 months.	Up to 6 months.
Microcosmus kura			
SETTLEMENT LEVELS		Lower sides of rocks in pools and beneath slates on lower platform.	Lower sides of rocks at low tide level.
SETTLEMENT TIMES		Winter.	Winter.
Botryllus schlosseri *(figure 48)*			
SETTLEMENT TIMES		Irregular throughout year.	
SETTLEMENT AREA		Upper and lower surfaces of rocks in pools.	
REMARKS		Its high growth rate enabled it to cover large areas of the rocks, smothering many species with the noticeable exception of the polyzoans *Lichenopora novaezelandiae* and *Rhynchozoon bispinosa* (*see figure 48* and *cf.* Goodbody 1961).	

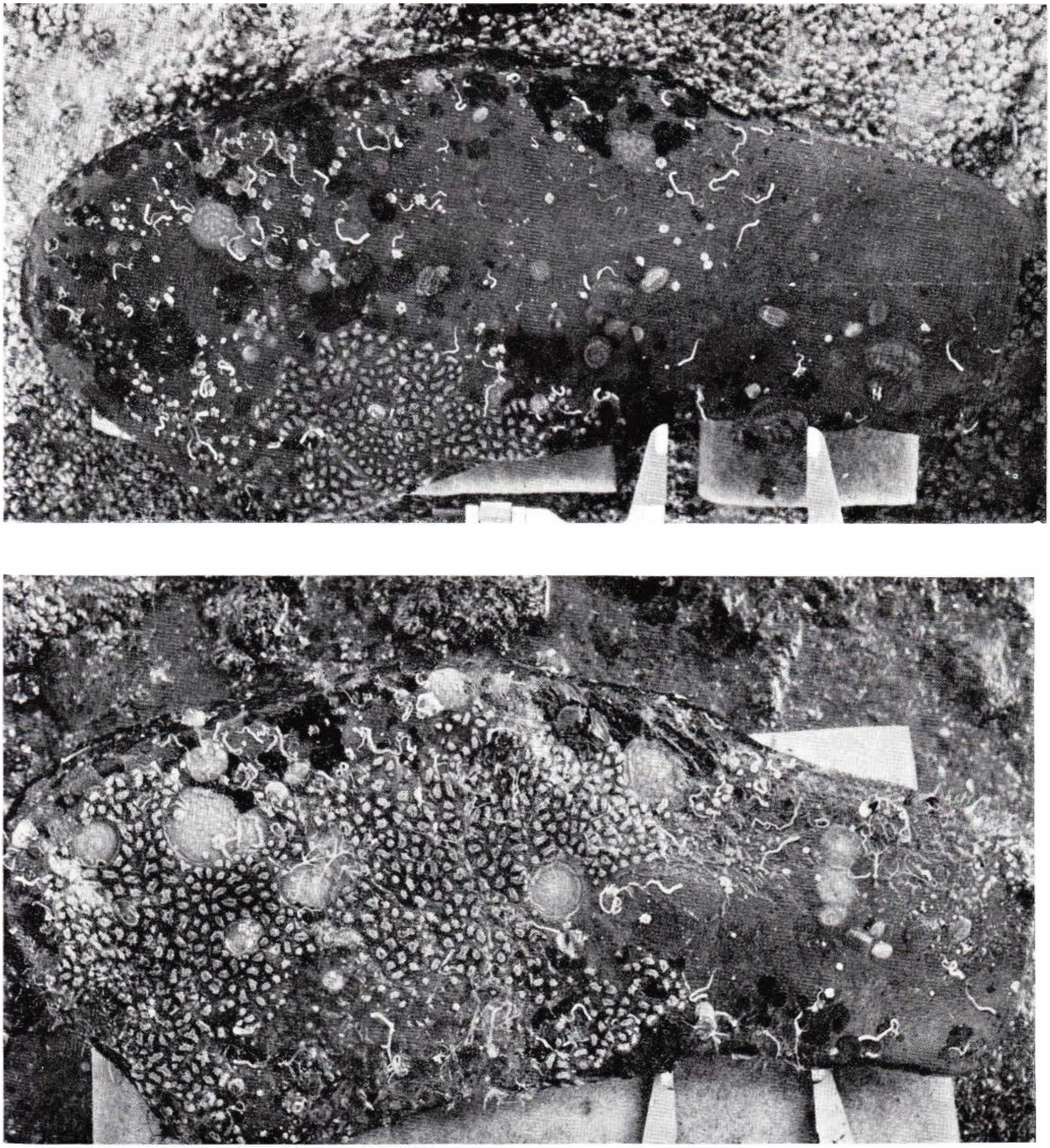


Fig. 48 Two photographs of the same rock from a pool at West Tamaki Head showing the development and spread of a colony of the compound ascidian *Botryllus schlosseri*. Although most of the animals were smothered by the advance of the compound ascidian, the circular, pale colonies of the polyzoan *Rhynchozoon bispinosa* were not overgrown by the ascidian, and in some way were able to prevent its advance across them. Other animals visible include the barnacle *Elminius modestus*, the tubeworm *Hydroides norvegica*, and the polyzoan *Watersipora cucullata*. Calipers set at 5cm.

FACTORS AFFECTING SETTLEMENT OF SOME OF THE ORGANISMS

As well as the length of time an area has been cleared, the amount of rock surface remaining unoccupied affects the organisms settling. Many organisms which settle on freshly cleared surfaces will also settle on any area where unoccupied rock space still exists. On non-toxic surfaces more species appear to settle on the bare rock areas than on already settled areas; these species include serpulids, sabellariids, encrusting polyzoans, barnacles, and oysters. On a toxic surface the first animals which settle are those which can tolerate high concentrations of heavy metal toxins and these form a surface on which other organisms can settle. Such pioneer organisms include the encrusting polyzoan *Watersipora cucullata* and certain barnacles, although the barnacles may be malformed.

The organisms which settle on the cleared areas can be divided into three groups:

(a) those settling only on clean (but filmed) surfaces;

(b) those settling on both clean and already-colonised surfaces;

(c) those settling only on already-colonised surfaces. SEE *Perna canaliculus* (b) (ii) p. 43.

These groups may each be further subdivided into those organisms surviving more than one year after settlement, and those surviving less than one year. Some organisms may fall into more than one of these divisions or subdivisions.

(a) Those organisms settling only on clean surfaces

(i) *Organisms surviving less than one year**

Most of the organisms encountered on all three shores can be included in this category. However, some are present at only certain stages of colonisation, whereas others, although individuals are relatively short-lived, are constantly replaced by members of the same species. At Piha most of the *Chamaesipho columna* individuals survive less than one year, but certain areas, such as parts of the upper level, are dominated by *C. columna* almost continuously from first settlement. On parts of the reef at West Tamaki Head, especially the western face and the lower platform where *Xenostrobus pulex* does not become dominant, *Elminius modestus* settles continuously on bare patches, and within all the dead *E. modestus* compartments, thus maintaining the barnacle cover. Because these species settle on clean surfaces, the dead valves become detached either before others settle in their place, or they are dislodged by the growth of young barnacles.

*Length of survival is considered in terms of the average life span of those individuals of each species surviving beyond metamorphosis.

At certain levels above M.H.W. these same species may be found only at an early stage in the sequence of colonisation. *Chamaesipho columna* at the lower level at Piha is often prominent in the first months after clearance before it gives way to *Xenostrobus pulex*. At Narrow Neck in the *Corallina* zone, *Elminius modestus* settled on the cleared areas but was overgrown by *Corallina officinalis*. The death of an organism settling on a clean surface may not be due to predation or smothering; at West Tamaki Head, *Hydroides norvegica* settled densely on the lower platform but died within a month, perhaps because of dehydration.

The encrusting polyzoans, *Watersipora cucullata* and *Rhynchozoon bispinosa* survived more than one year on certain rocks but not on all rocks, and here it is not the individual animals which have continuity but the whole colony.

The growth rate and settlement density of *Watersipora cucullata* varied seasonally as can be seen from Table 2.

Table 2 Number and diameter of *Watersipora cucullata* colonies on rocks immersed in pools at West Tamaki Head.

Dates	*Number/dm² and diameter of colony* 2 mm	2–5 mm	5–10 mm	*Max. diam.* mm
23.1.62–21.2.62	48	268	22	12
7.2.62– 8.3.62	88	90	21	8
8.3.62– 5.4.62	19	4	–	5
24.3.62– 5.4.62	168	–	–	2
3.5.62– 2.6.62	140	–	–	2

The dates given are the date on which the rock was immersed, and the date on which the colonies were measured and counted. Larger colonies originating from earlier settled larvae were more likely to persist over the winter and to start growing again in October and November. Colonies less than 5 mm in diameter did not survive the winter.

On the east coast both simple and compound ascidians appeared to settle on clean rock. The simple ascidians, of which the commonest was *Corella eumyota*, were capable of smothering other organisms in their immediate vicinity. The growth and development of the compound ascidian *Botryllus schlosseri* was rapid, and it could cover much of one rock within 2 or 3 months of settlement. However, settlement was restricted to the rock surface and did not occur on other organisms. *Ostrea lutaria* and *Anomia trigonopsis* also settled on clean surfaces.

(ii) *Organisms surviving more than one year*
Most of the organisms in this category are related to those in the previous one, but simply differ from them in having a longer life span. Some examples are *Elminius plicatus* at the upper level at Piha, and *Crassostrea glomerata* and *Corallina officinalis*.

(b) Those organisms settling on both clean and already-colonised surfaces

(i) *Organisms surviving less than one year*
Xenostrobus pulex is perhaps the best example in this group. At Piha it commonly settled between barnacles but was also found settling on bare rock. Young *X. pulex* also settled among older specimens. At West Tamaki Head hydroids of several kinds, but particularly *Plumularia* sp., were found at all stages of colonisation. Sometimes they were the only sessile organisms to be seen on newly-immersed rocks, but they could also be found growing on and between previously settled species. On all shores most species of algae were found on both clean and already-colonised surfaces. Many of the algae would grow on rocks, shells, plates, and other algae.

(ii) *Organisms surviving more than one year*
Perna canaliculus was at first thought to settle only on areas already colonised. However, at West Tamaki Head in November and December 1963 several newly-settled mussels were found on the western face, attached to the bare rock surface behind a slate. When all the areas where *P. canaliculus* had settled were compared they were all found to protect the young mussels from desiccation. *Perna canaliculus* can alter its position slightly and then re-attach itself by new byssus threads.

The organisms settling on colonised areas can either move slightly to avoid smothering, e.g., *Perna canaliculus* and *Xenostrobus pulex*, or they have "stems" which lift them above the surface partially or completely, e.g., hydroids, the polyzoan *Bugula neritina*, and many algae. *Perna canaliculus* does not appear able to compete successfully with a thick growth of non-calcareous algae, which tends to smother it, without offering sufficient support or attachment surface. Bokenham & Stephenson (1938) reported that mussels (*Mytilus* spp.) tended to settle when algal growth was reduced or absent. This would explain the absence of *P. canaliculus* settlement at the lower level at Piha on newly-cleared areas which were often densely covered with *Ulva* spp., *Porphyra columbina*, and *Petalonia fascia*. Some settlement did occur among older *X. pulex*. The stiffer thallus of *Corallina officinalis* would provide suitable anchorage for the byssus threads and would not smother the *P. canaliculus*.

On subtidal plates *Perna canaliculus* settles only on mature surfaces, usually those colonised by simple ascidians (Morton & Miller 1968). Here again there is a firm surface for byssus attachment. Growth is rapid and complete smothering of the mussels does not often occur. The orientation of the mussel shell, with the aperture away from the substrate, together with its power of limited movement, helps delay or prevent smothering.

It appears that the settling larvae of most animals do not discriminate between rock surfaces, barnacle plates, molluscan shells, or serpulid tubes as such. These all present a relatively smooth hard surface for attachment. Surfaces covered by silt or a fuzz of fine algal growth often discourage settlement of barnacles and rock oysters whereas fibrous surfaces may encourage mussel settlement. Some animals such as *Elminius modestus* settle on surfaces placed at any angle between vertical and horizontal, but others are restricted to, or settle more densely on, surfaces of a certain angle. On the rocks at West Tamaki Head, where surfaces with all possible orientations were available for settlement, some species were restricted to surfaces oriented in certain directions. Here results are not necessarily related only to surface angle, because light, silting, and possibly other factors were different on the upper and lower surfaces. Animals restricted to the lower surface included the bivalves *Chlamys zelandiae* and *Ostrea lutaria*, the ascidians *Microcosmus kura*, and *Corella eumyota*, the bryozoans *Eurystomella foraminigera*, *Lichenopora* sp., and *Rhynchozoon bispinosa*, and sponges. Algae were mainly restricted to the upper surface and the sides but here light was probably the important factor. Organisms found on both upper and lower surfaces included *Elminius modestus*, *Watersipora cucullata*, *Botryllus schlosseri*, *Hydroides norvegica*, and hydroids.

Because few animals settle on a mat of fine algae, or on silted surfaces, surface texture and microtopography is very important to some organisms, for example, those settling in specialised habitats, such as on certain algae (Nishihira 1965, 1966). At West Tamaki Head the hardness and grain size of the rocks were the most important factors influencing pholad settlement. Both the physical characteristics (rugosity, pitting, cracks) and the chemical characteristics (presence or absence of tanned proteins and "settling substances") of the rock surface can affect the settlement of barnacle larvae, particularly when the larval numbers are low (Knight-Jones & Moyse 1961).

On hard surfaces immersed in the sea competition is often for space. Intertidally where zones composed mainly of one species are common, mechanisms including aggregation at the time of settlement may be of great importance. Aggregations of one or a few species are often found on uniform and stable substrata; where the surface is not uniform, or becomes partly cleared by silting or abrasion the fauna will be a varied and changing one. Rocks immersed in pools are subject to movement by waves and, together with the general rock surfaces, can become buried by silt or sand or suffer scouring by sand.

The rocks at Narrow Neck and West Tamaki Head are examples of this unstable substrate. Except for *Corallina officinalis* and encrusting polyzoa all the species found there survived for less than one year after settlement. Such a short survival time provided bare rock surfaces for settlement during most of the year.

CHANGES OBSERVED AFTER CLEARANCE OF THE EXPERIMENTAL AREAS

PIHA

(a) The *Perna canaliculus* zone below the lower experimental level

This was cleared in February and March 1962. One month after clearance a cover of algae, especially sea lettuce (*Ulva* sp.) and *Corallina officinalis* "paint", was present together with *Xenostrobus pulex*, hydroids, and two specimens of the chiton *Guildingia obtecta*. During the second month red algae increased both in size and number of species and by the end of the third month they formed an almost continuous carpet interrupted by two areas of *Corallina officinalis* paint occupied by *G. obtecta*. *X. pulex* and hydroids were still present.

By the end of the eighth month, after a heavy settlement of *Perna canaliculus* on surrounding areas, small green mussels were located on the cleared area. Except for the lack of adult *P. canaliculus* the cover resembled that on the surrounding rock surfaces. Compared with areas cleared at the same time at the lower experimental level the *Xenostrobus pulex* were slightly smaller at this level in the *P. canaliculus* zone.

The successive stages found and the order in which they occurred were:

(i) *Ulva* sp. and *Xenostrobus pulex* with grazing *Guildingia obtecta*.

(ii) Small red algae with *X. pulex* and hydroids.

(iii) Red algae, *X. pulex*, hydroids, and *Perna canaliculus*.

(iv) The characteristic *P. canaliculus* zone with an algal carpet and epizoics such as hydroids and barnacles.

At a point further along the reef two plates were attached on a cleared patch in the *Perna canaliculus* zone below the lower experimental area. Although settled lightly by *P. canaliculus* the plates became overgrown both by growth of the mussels which settled on the plates and by growth and lateral movement of those on adjacent areas. Given time, and good settlements of *P. canaliculus* these should eventually predominate on the shore at this level. The scattered *P. canaliculus* already present with their byssus threads and attached "mussel beard" can act as nuclei from which settled mussels can spread outwards.

(b) Lower experimental level

A primary algal film was the first stage in colonisation of denuded rock surfaces at the lower experimental level (Daniel 1955, Skerman 1956) and was followed by settlement of *Chamaesipho columna* and *Xenostrobus pulex* (Fig. 50). At the end of the first month the predominant

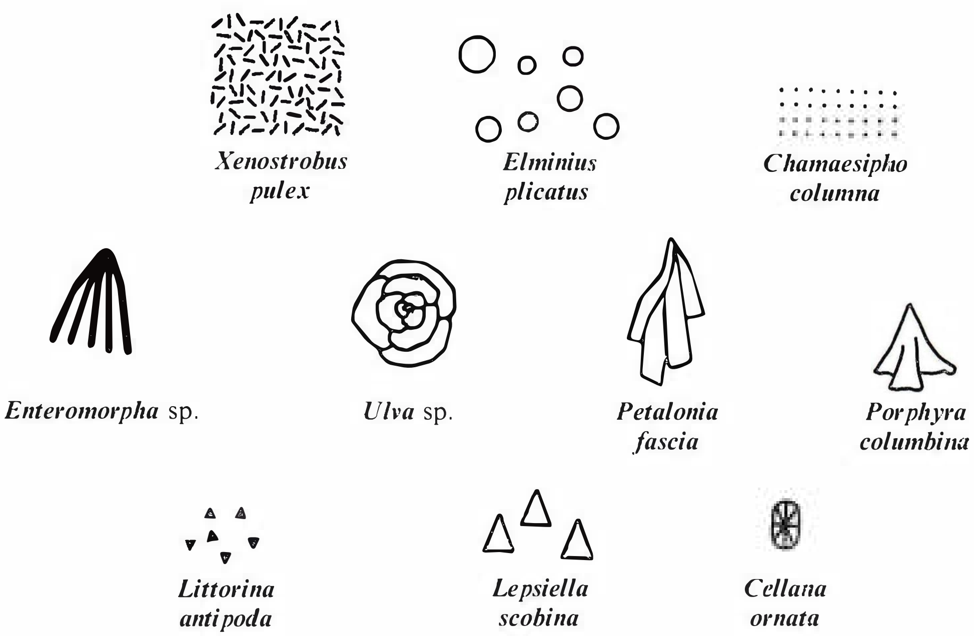
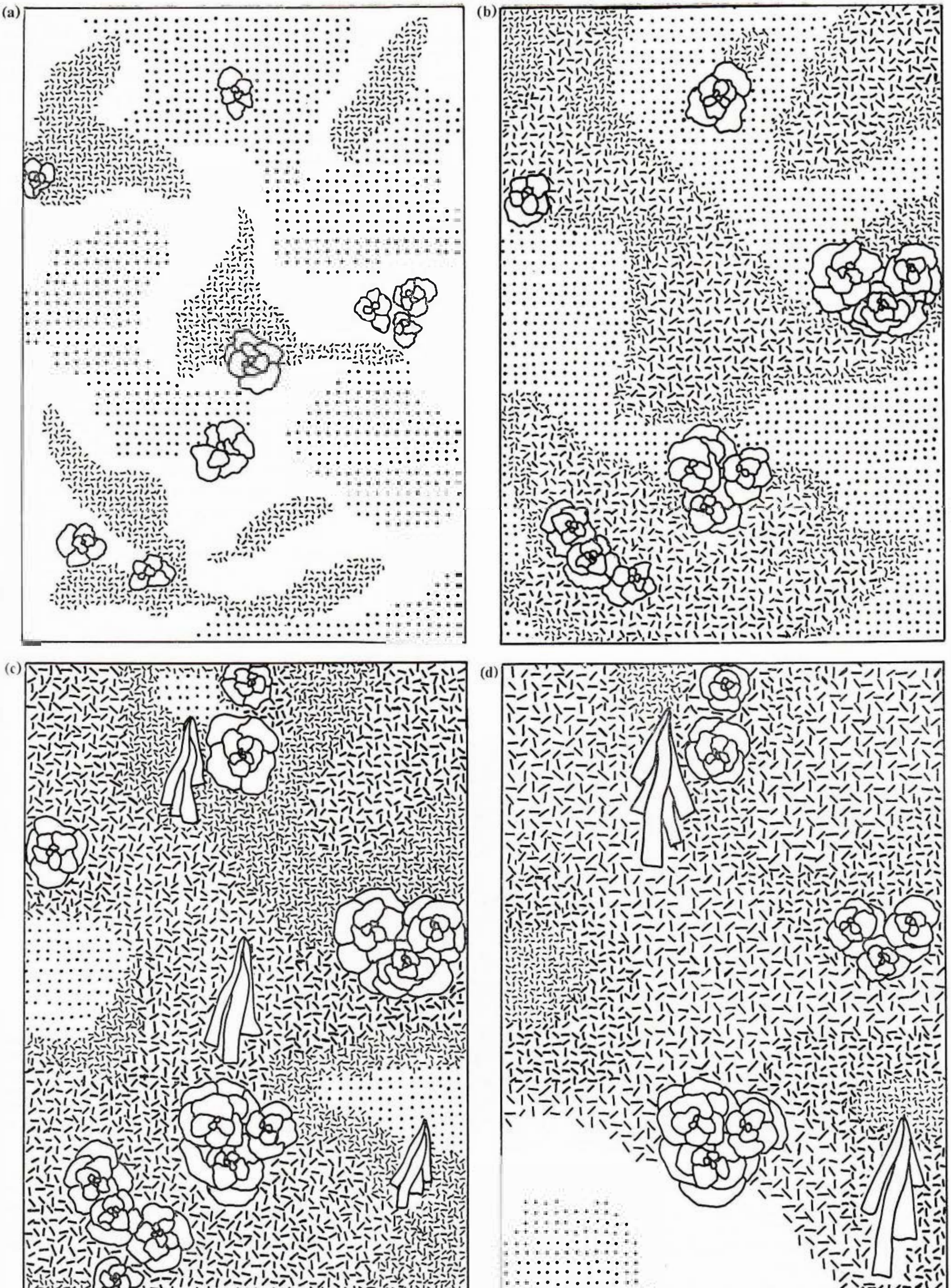


Fig. 49 A key to the symbols used in the succession diagrams for Piha (Figs 50, 52, 54).

Fig. 50 *(opposite)* Succession at the lower experimental level at Piha where *Elminius plicatus* did not settle. Area cleared in February 1962; diagrams were made from observations in March (a), April (b), May (c), and June (d) 1962. Initial settlements of *Chamaesipho columna* and *Xenostrobus pulex* were followed by growth, expansion, and further settlement of the mussels, together with sporelings of *Ulva* sp. and *Petalonia fascia*. Further settlements of barnacles occurred when bare rock was available. (*see* Fig. 49 for key)


(a)
(b)
(c)
(d)

species was either *C. columna* or *X. pulex*. From the end of the first month there was settlement of *Ulva* spp., *Porphyra columbina*, and *Petalonia fascia* (Table 1).

These were accompanied occasionally by the green algae *Enteromorpha* sp. and *Letterstedtia* spp. On all the squares, *Xenostrobus pulex* with growth and sand accumulation, tended eventually to smother the *Chamaesipho columna*, thus becoming the dominant organism. The accumulation of sand beneath the *X. pulex* masked any irregularities of the rock surface, and produced a smooth carpet of densely packed *X. pulex*. This carpet was not directly attached to the rock surface except at its edges, and was readily stripped from an ever-widening area once a break occurred in its surface. Predation by rock cod, *Acanthoclinus quadridactylus*, or damage by people were means by which such breaks occurred.

These exposed rock surfaces were rapidly recolonised by *Chamaesipho columna* and *Xenostrobus pulex*. Thus, within each square there developed a mosaic, each showing a similar pattern of colonisation, but at a different stage. This development of a mosaic led to the obliteration of boundary lines between areas cleared at different times, this being more marked when the adjacent squares were of similar ages (Fig. 51).

Thus the following sequence of events occurred:

(i) settlement of *Xenostrobus pulex* and/or *Chamaesipho columna*;

(ii) growth of *Ulva* sp., *Petalonia fascia*, and *Porphyra columbina*;

(iii) *X. pulex* dominant.

A minor variation occurred on squares colonised by *Elminius plicatus*. These settled on squares up to at least 3 months after clearance but with a preference for newly cleared squares. Settlement also occurred on naturally cleared rock surfaces adjacent to the experimental area. The presence of *E. plicatus* had no lasting effect on the sequence of colonisation, since few survived more than 8 months after settlement.

Figs. 49, 52 show the sequence of events on an area cleared in August 1962. Each diagram is a generalised representation of an area 17 by 24 cm and has been drawn from the records of temporal changes on the shore. The size of the circles representing *Elminius plicatus* is approximately equal to their basal size, irrespective of the amount of the barnacle actually visible. In the accompanying photograph (Fig. 53), taken in March 1963, of a comparable stage to Fig. 52d the position of the barnacles in relation to the *Xenostrobus pulex* is clearly visible.

In previous seasons this area had been completely covered by *Perna canaliculus* but at the time of the study they were found mainly lower on the shore, and even here constant picking had kept their size below 80 mm in length. Over most of this area the mussel cover is patchy. Indiscriminate picking removes many small mussels needed to repopulate the beds. Several years of reduced spawning coupled with a high removal rate may be responsible for the reduction in size and density of these beds. If so, several seasons of heavy settlement, especially if accompanied by a reduction in picking, may well repopulate all the lower area occupied by *Xenostrobus pulex* as well as that covered sparsely by *P. canaliculus*.

Fig. 51 An area at the lower experimental level at Piha showing the mosaic of patches of *Xenostrobus pulex* of different ages which has developed six months after clearance. Calipers set at 5 cm.

Fig. 52 *(opposite)*. Succession at the lower experimental level at Piha where *Elminius plicatus* settled. Area cleared in August 1962; diagrams drawn from observations made in September 1962 (a), November 1962 (b), January 1963 (c), and March 1963 (d). Initial settlement of *Chamaesipho columna* and *Elminius plicatus*, with *Xenostrobus pulex* settling in increasing numbers from November, together with transient plants of *Ulva* sp. and *Petalonia fascia*. (*see* Fig. 49 for key)

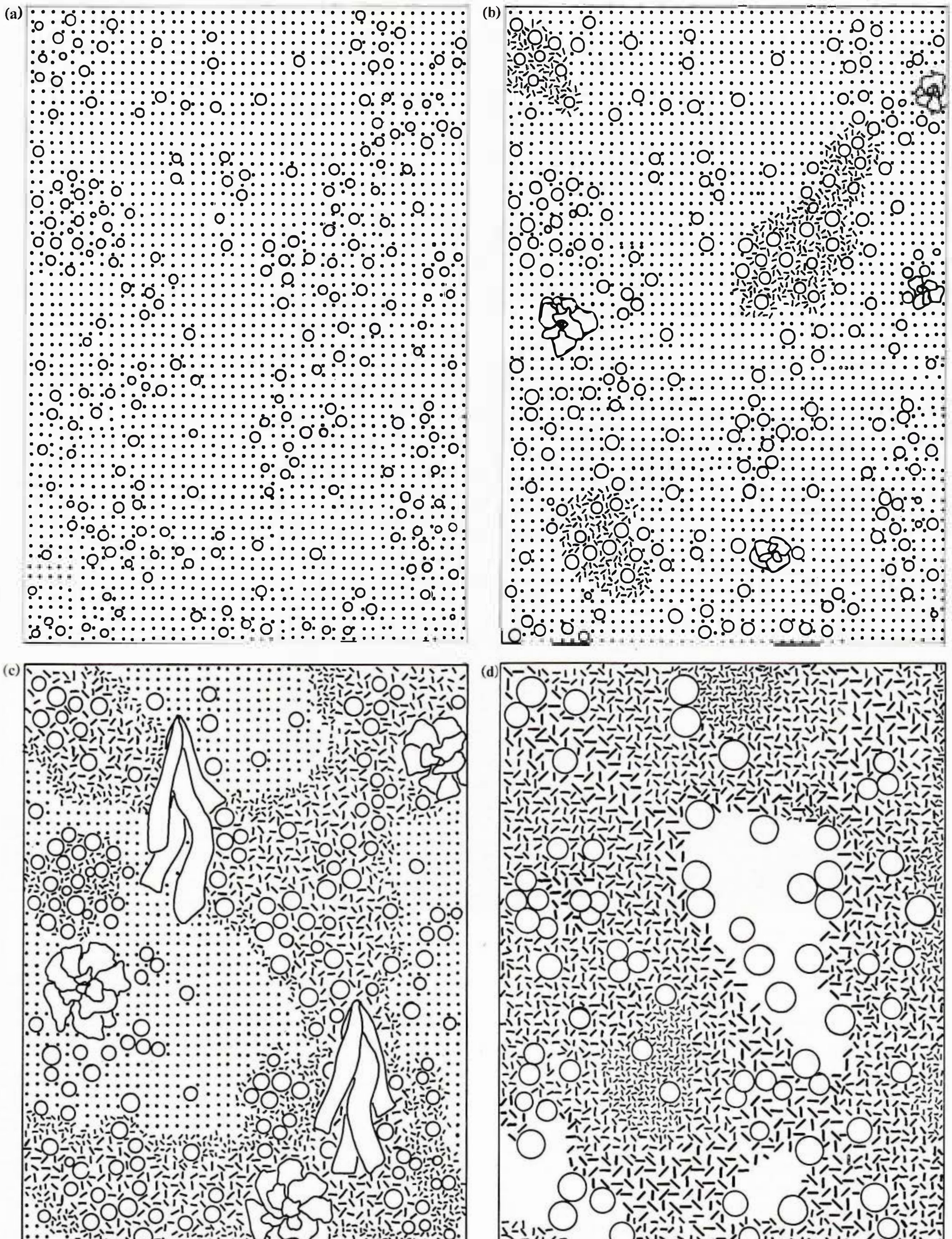

(a)
(b)
(c)
(d)

Fig. 53 The area from which the diagrams in Fig. 52 were drawn, photographed in March 1963. The dead shells of *Chamaesipho columna* smothered by the *Xenostrobus pulex* are visible on the bare patches where the *X. pulex* has itself been washed away. Calipers set at 5 cm.

(c) Upper experimental level

The pattern of temporal change here is related to that at the lower level but with several differences. At this higher level, grazing animals, including *Littorina antipoda*, *Cellana ornata*, and acmaeid limpets, were more abundant especially during the earliest stages of colonisation. Small specimens of *C. ornata* less than 1 cm long, occurred at densities of up to 20 per dm^2, and the *L. antipoda* occurred at densities of up to 10 per cm^2. Grazing animals were usually the first animals to appear in the cleared areas, followed closely in every month except January and February by *Chamaesipho columna*.

Compared with the lower levels, *Xenostrobus pulex* was slow to colonise these upper areas, but the time at which it settled appeared to depend on the amount of moisture available. This in turn depended on the time of the year, the position of the cleared area, and the organisms already present. Those cleared areas receiving seepage from adjacent regions were usually settled by *X. pulex* earlier than raised portions of the reef. The presence of small pools increased the algal growth, and this in turn encouraged *X. pulex* settlement. Once *X. pulex* had settled, the area became damper, as water was retained between the animals and in the accumulated silt, thus encouraging algal growth.

Settlement and growth of *Xenostrobus pulex* resulted in the smothering of the earlier settled *Chamaesipho columna*, and prevented settlement of *Elminius plicatus*. However, barnacle settlement occurred rapidly when any *X. pulex* were removed by wave action. *X. pulex* provides a quickly growing cover which is easily removed when it becomes large, thus providing fresh settlement surfaces. Because of the time lag between clearance and *X. pulex* settlement on many of the upper areas, smothering of *E. plicatus* was delayed. Thus the relative positions of the two species on a square at the upper level, settled by *E. plicatus* 12 months earlier, was similar to the situation reached in only 6 months on an equivalent square at the lower experimental level.

The long survival time of *Elminius plicatus* together with the slower rate of smothering, enables it to become the animal occupying most of the rock surface at the higher level. The likelihood of *Xenostrobus pulex* being removed in the winter storms increases the chance of *E. plicatus* settlement in late winter and early spring. However, at the end of the experimental period *E. plicatus* had not become established on all the squares at this level, since some were already dominated by *X. pulex* at the time of *E. plicatus* settlement.

On some of the cleared areas *Chamaesipho columna* settlement was followed by a dense growth of species of *Ulva* and *Enteromorpha*. *Xenostrobus pulex* settled beneath the algae and smothered the barnacles.

The sequence of events at the upper level (Figs 49, 54) when *Elminius plicatus* did not settle was:

(i) an algal film with grazing animals,
(ii) *Chamaesipho columna* together with grazing animals,
(iii) *C. columna* with *Xenostrobus pulex* and algae,
(iv) *X. pulex*.

The sequence of events at the upper level when *Elminius plicatus* did settle (Figs 55, 56) was:

(i) an algal film with grazing animals,
(ii) *Chamaesipho columna* and *Elminius plicatus* with grazing animals,
(iii) *E. plicatus* and *Xenostrobus pulex*.

On squares where either *Xenostrobus pulex* or *Elminius plicatus* was dominant, algae such as *Porphyra columbina*, *Ulva* sp., and *Enteromorpha* sp. were found at irregular intervals throughout the experimental period.

WEST TAMAKI HEAD

(a) The upper platform

During most of the year *Elminius modestus* was the dominant sessile animal present. In late winter and spring of both years *Xenostrobus pulex* settled among the barnacles, and by December most of the barnacles were dead beneath the *X. pulex*. However, since *X. pulex* was almost entirely absent from the upper platform between February and July, it did not form a climax community. Removal of the *X. pulex* and dead *E. modestus* left a bare rock surface which was settled by *E. modestus* together with scattered *Balanus amphitrite*. Where the barnacles were removed together with any *X. pulex* in the spring, gaps were found in the *X. pulex* carpet in December, but light settlement of *X. pulex* together with the expansion of the surrounding *X. pulex* carpet later filled up these gaps entirely.

During the year, and particularly in the spring before *Xenostrobus pulex* became dominant, small *Ulva* sp. and *Enteromorpha* sp. were common, forming a green carpet over the barnacles.

Where *Elminius modestus* was absent *Xenostrobus pulex* did not settle readily, being limited to small crevices and surface irregularities; gaps in the cover of *X. pulex* were filled by growth from adjacent areas and by later settlement between older *X. pulex*.

(b) The lower platform

On the rock surface, *Elminius modestus* settled during almost all of the year, and was the dominant animal. In autumn and winter the brown algae *Petalonia fascia* and *Scytosiphon lomentaria* grew on and close to the cleared areas, and in summer *Xenostrobus pulex* settled among the barnacles and *Hydroides norvegica* on newly cleared areas, but otherwise *E. modestus* was the most conspicuous sessile organism. After the initial settlement, the barnacles grew, forming hummocks where they had settled densely, and then died where dislodged or were eaten by *Lepsiella scobina*. Further settlement of cyprids took place on the bare rock, and the cycle continued (Barnes & Powell 1950).

(c) The *Corallina* zone

Two patches of gently sloping rock were cleared during March 1962. For the first 2–4 months after clearance the rock was covered with silt containing algae. Later, *Elminius modestus* settled together with some *Corallina officinalis*, *Colpomenia sinuosa*, and *Hormosira banksii*. By November 1963, 20 months after clearance, there were still some barnacles, but most of the surface was covered by *Corallina officinalis* turf or paint, with *Colpomenia sinuosa* and *H. banksii* (Fig. 57).

(d) The western face

After the initial clearance in February 1962 and the reclearance of one strip in May 1962, this area was not touched. Instead, a record was kept of the numbers of the gastropods *Lepsiella scobina*, *Lunella smaragda*, and the chiton *Sypharochiton pelliserpentis* on the area (Figs 58, 59). The numbers of both *L. scobina* and *L. smaragda* fluctuated greatly but in a similar manner,

(a) (b) (c) (d)

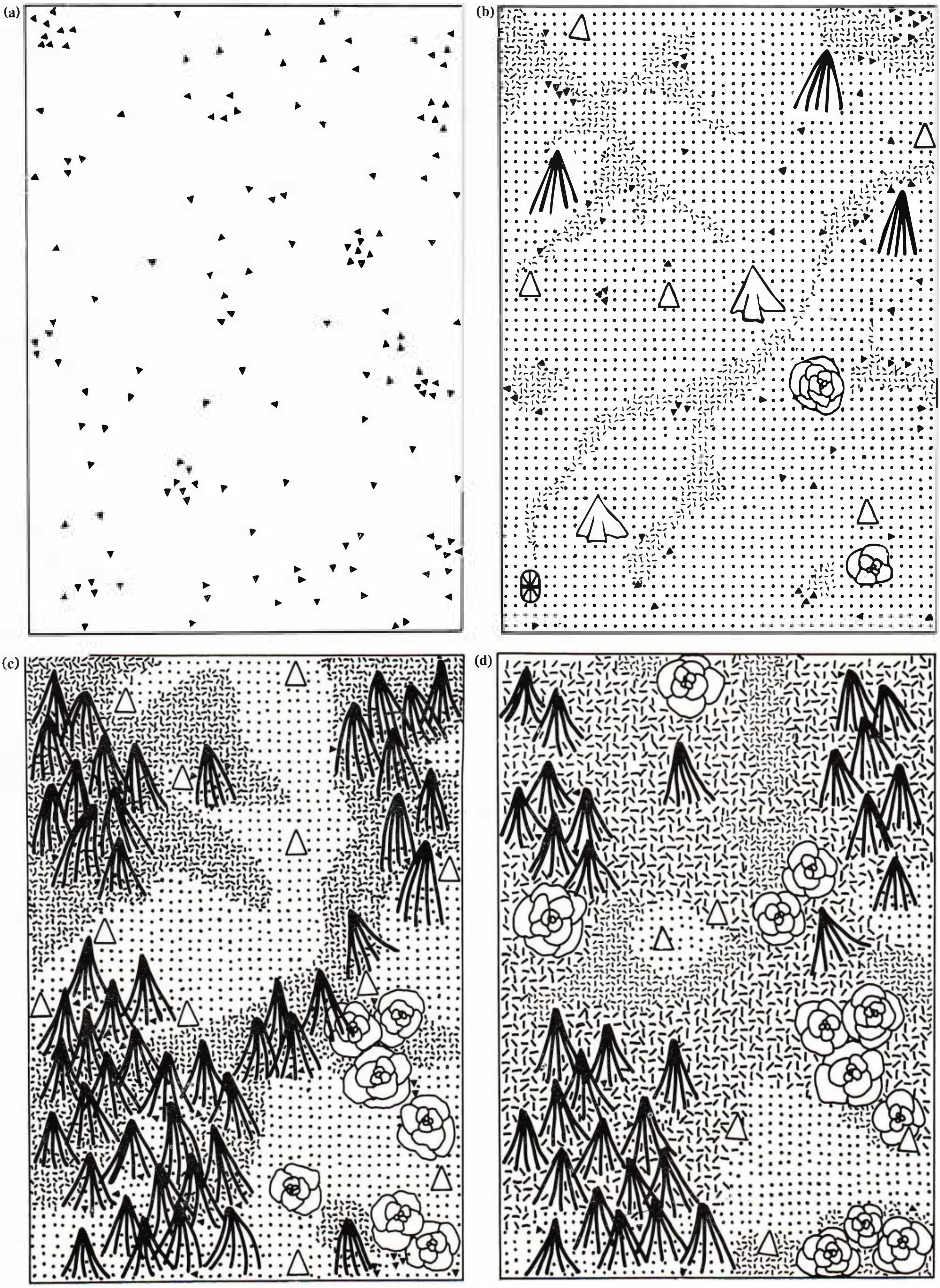


Fig. 54 *(opposite)* Succession at the upper experimental level at Piha on an area cleared in January 1962. Diagrams drawn from observations made and photographs taken in February (a), April (b), May (c), and July 1962 (d). By the end of the first month *Littorina antipoda* had moved on to the cleared area but no settlement had occurred. Three months after clearance most of the rock surface was covered by *Chamaesipho columna* with *Xenostrobus pulex* in the crevices, and a scattering of *Ulva* sp., *Porphyra columbina*, and *Enteromorpha* sp. plants. Some *L. antipoda* were still present together with the limpet *Cellana ornata* and the whelk *Lepsiella scobina*. As this was a poorly drained area there were further settlements of *X. pulex* and algae. *Chamaesipho columna* cover was reduced and *Elminius plicatus* did not settle. (*see* Fig. 49 for key)

Fig. 55 A well-drained cleared area at the upper experimental level at Piha settled by *Chamaesipho columna* and *Elminius plicatus*. *Porphyra columbina* has settled on the barnacles and *Xenostrobus pulex* among the barnacles. Calipers set at 5 cm.

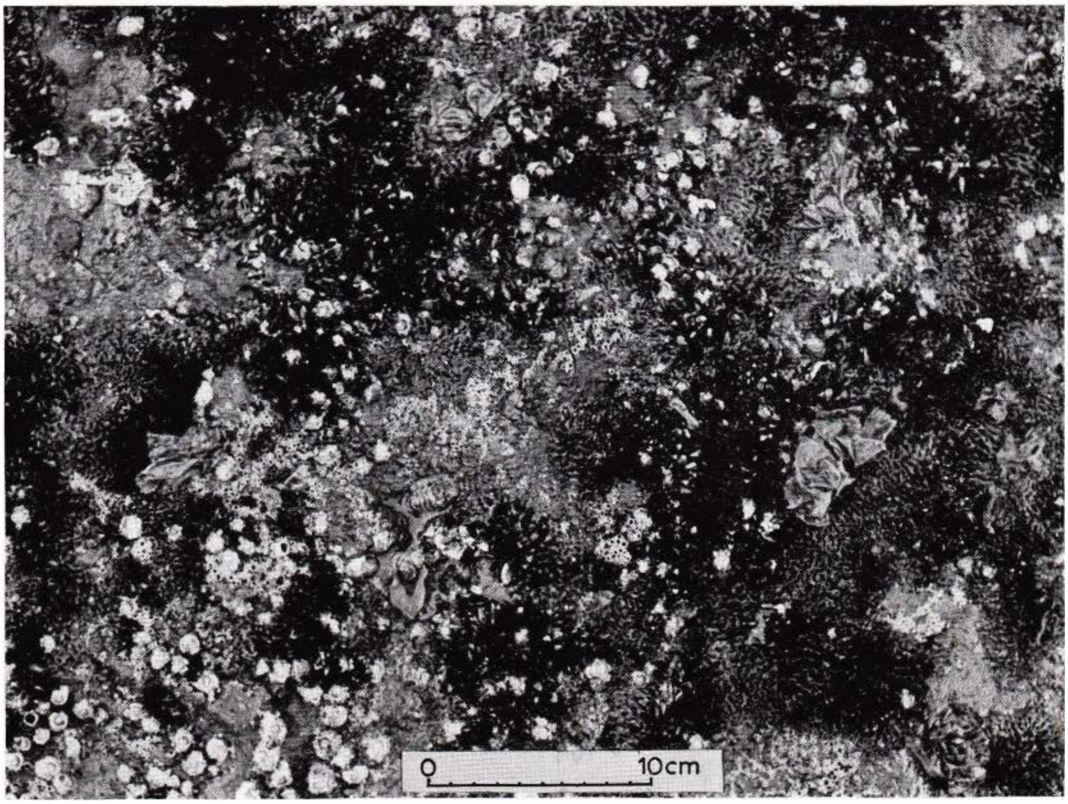


Fig. 56 An area at the upper experimental level at Piha similar to that of Fig. 55 taken one year later showing the *Xenostrobus pulex* smothering the barnacles, particularly the smaller *Chamaesipho columna*.

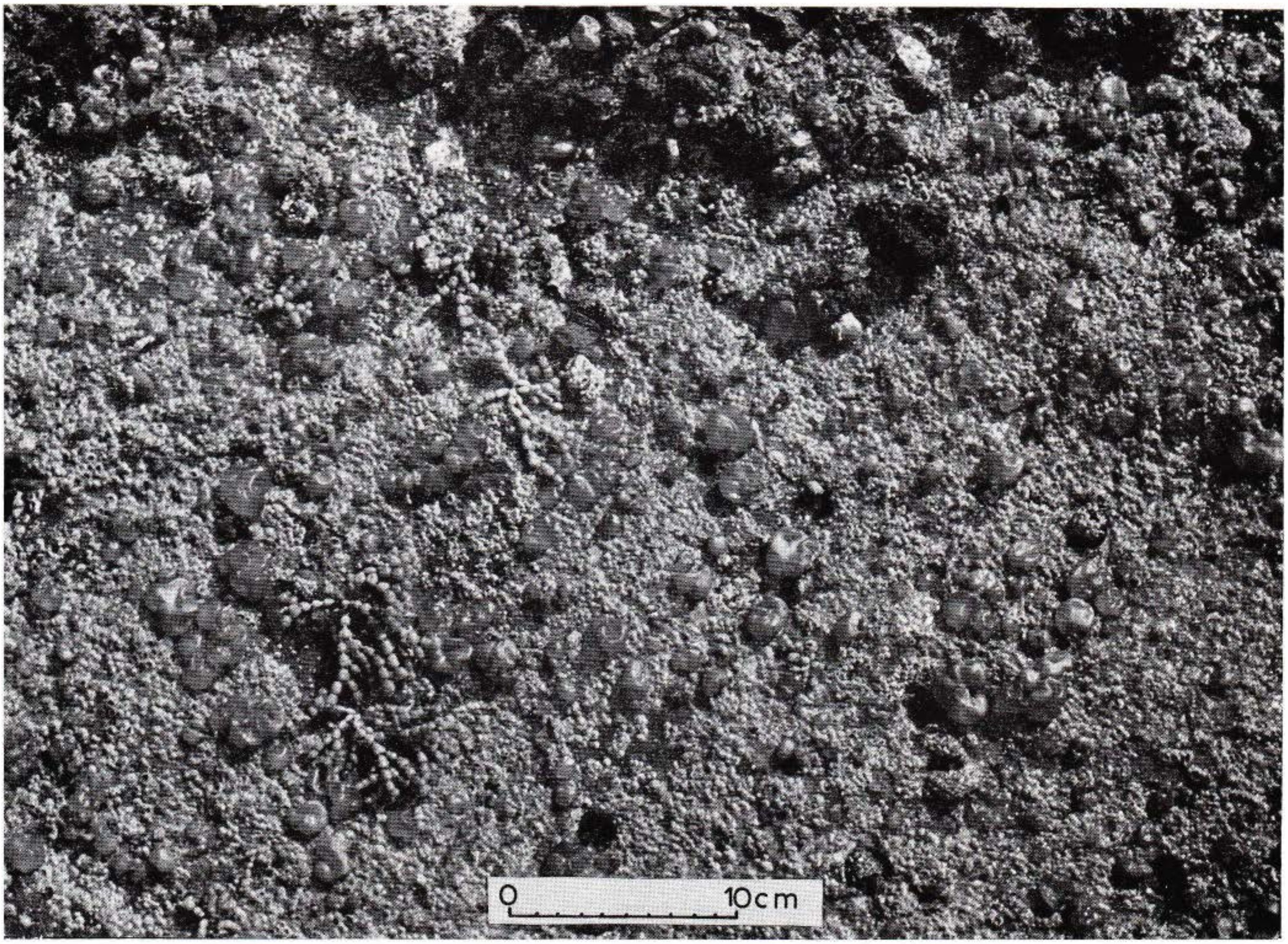


Fig. 57 The sloping area in the *Corallina officinalis* zone at West Tamaki Head cleared in March 1962 and photographed in November 1963. Some *Elminius modestus* are still present, but most of the surface is covered by *C. officinalis* turf and paint, together with *Colpomenia sinuosa* and *Hormosira banksii*.

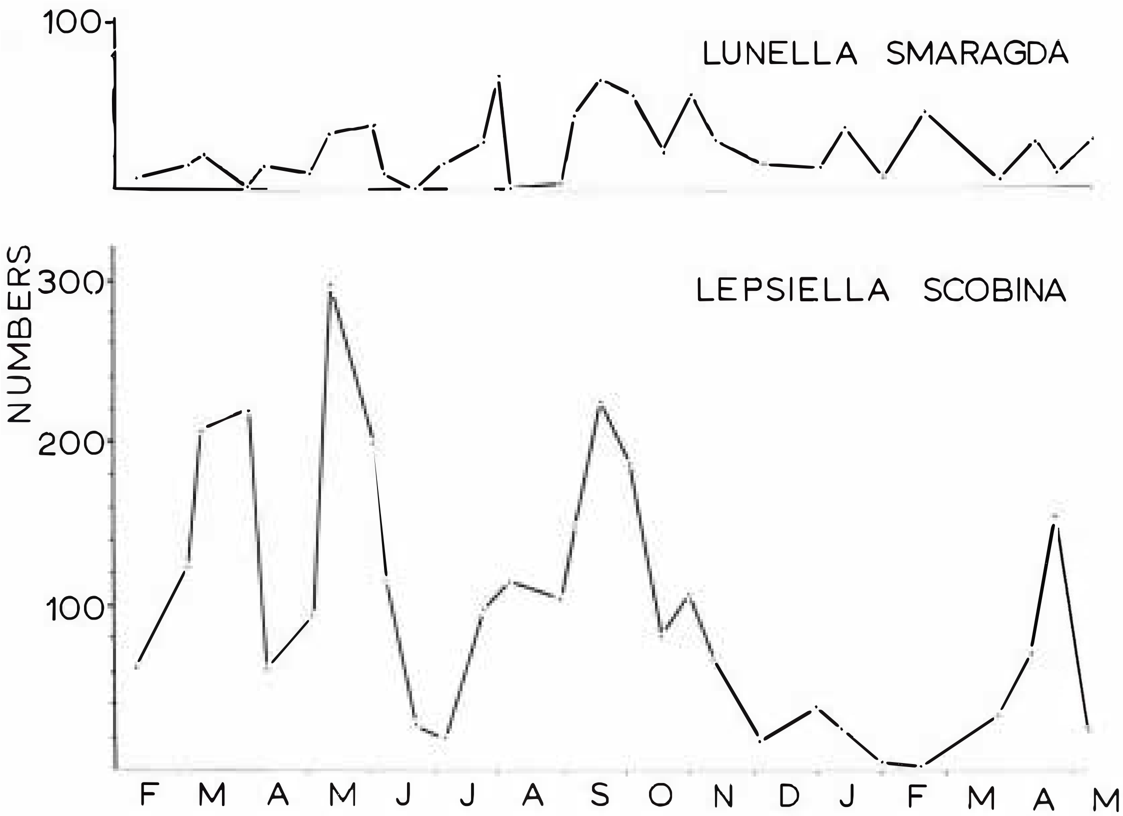
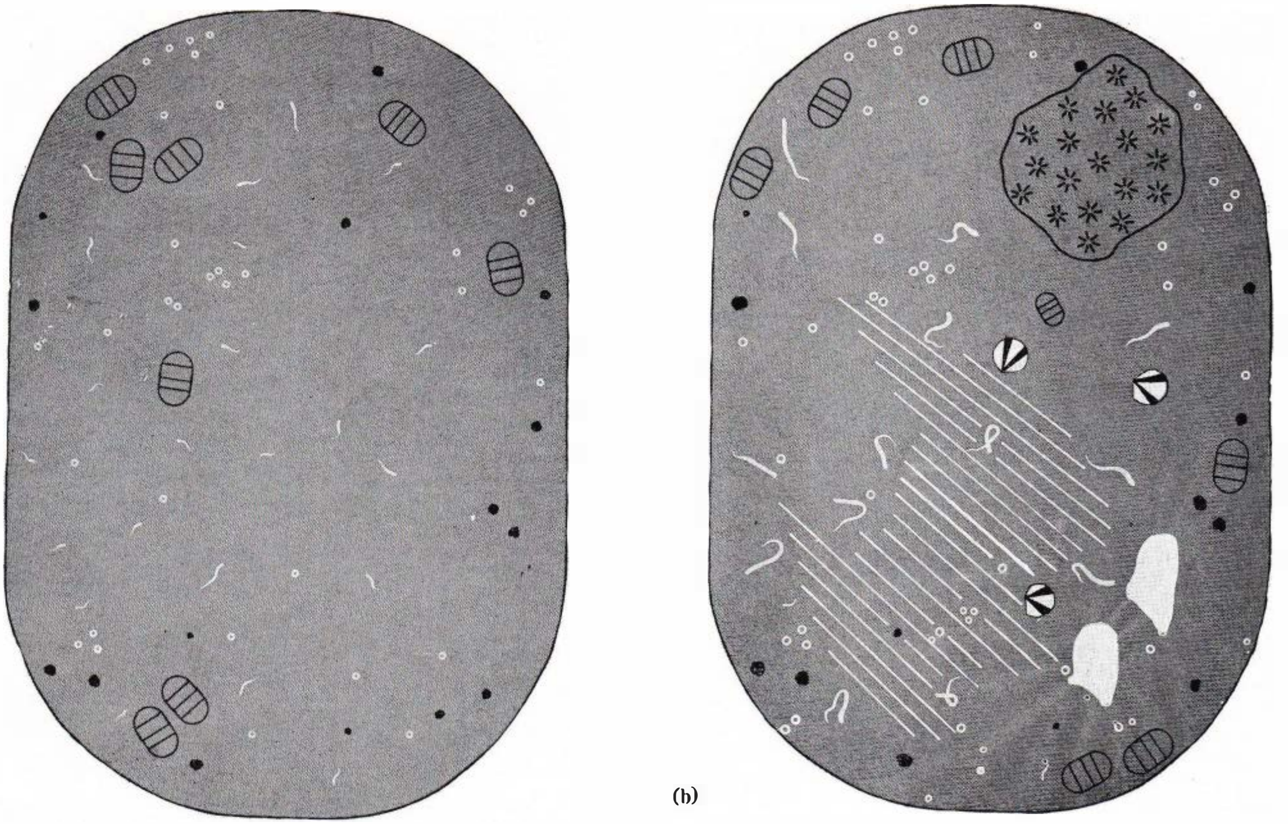


Fig. 58 The numbers of *Lepsiella scobina* and *Lunella smaragda* found on the western face at West Tamaki Head from February 1962 until May 1963.

Fig. 59 The western face at West Tamaki Head. Many *Lunella smaragda* can be seen on the lower part of the face and on the irregular ledge below. Most of the smaller *Lepsiella scobina* are on the *Elminius modestus* at the top of the face. The oyster *Crassostrea glomerata* is found across the centre of the face, particularly on the right half. To the left, slates and a glass plate have been attached to the rock with stainless steel screws and Rawlplugs. The glass plate attached on top of one of the slates is three inches square.



(a) (b)

These fluctuations were caused by a combination of several factors including the amount of food available and the weather. After a storm few animals would be found on the face as they had been swept on to the ledge below. On hot dry afternoons with low spring tides many would be found either low on the shore or against the slates and plates attached beside the cleared area. The numbers of *L. scobina* were a reflection of the size and abundance of *Elminius modestus*, since when most of the barnacles were small, or dead, there was little food for *L. scobina*. At certain times of the year there was a heavy growth of microscopic green algae on the barnacles and the rocks, and many *L. smaragda* gathered to graze on this.

At the end of 1963 *Corallina officinalis* turf had grown on the ledge below the face and on the lower parts of the face itself. Above this, *Elminius modestus* continued to the top of the rock. On the lower half, scattered rock oysters (*Crassostrea glomerata*) were interspersed with the barnacles, and higher up the red alga *Gelidium* sp. had started to form a clearly defined band.

(e) Rocks placed in the pools

Initial settlement on the rocks was a reflection of the larvae available and varied greatly throughout the year (Table 3). Many organisms were smothered either by the settlement and growth of later organisms, or by egg capsules or eggs laid by molluscs and fishes.

Table 3 Organisms found on rocks immersed in pools in the *Corallina* zone for one month or less at West Tamaki Head.

Species found	Month of immersion											
	J	F	M	A	M	J	J	A	S	O	N	D
Enteromorpha sp.		X	X	X		X		X				
Colpomenia sinuosa			X				X					
Ecklonia radiata					X	X	X					
Scytosiphon lomentaria						X						
Gelidium sp.				X	X							
Corallina officinalis			X			X						
Sagartia sp.			X	X		X	X					
Plumularia sp.							X	X	X	X		
Thecate hydroids						X	X	X	X	X	X	
Hydroides norvegica	X	X	X	X	X	X	X					
Spirorbis sp.			X									
Pomatoceros cariniferus	X	X										
Bugula neritina			X									
Watersipora cucullata	X	X	X	X	X	X						
Elminius modestus	X	X	X	X	X	X	X	X	X	X	X	X
Balanus amphitrite			X									
Ostrea lutaria			X	X								
Anomia trigonopsis			X							X		
Chlamys zelandiae									X			
Xenostrobus pulex								X	X	X	X	X
Cominella virgata (egg capsules)								X	X	X		
C. maculosa (egg capsules)										X	X	
Notoacmaea daedala									X	X		
Anisodiloma lugubris									X	X		

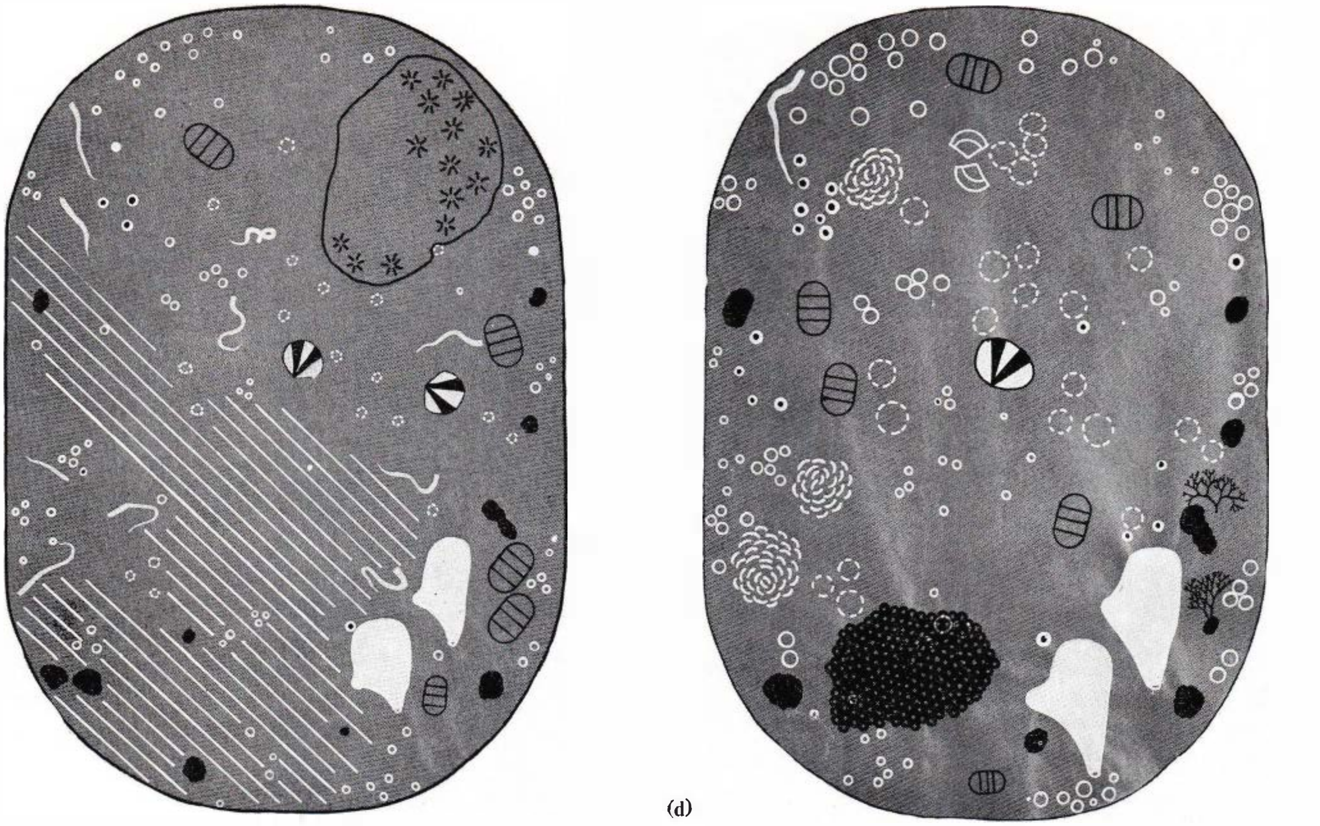


Fig. 60 a–d Diagrams of the animals found on a rock immersed in a pool at West Tamaki Head on 5 April 1962. Diagrams drawn from observations made and photographs taken in May (a), June (b), July (c), and October (d).

KEY

The final assortment of organisms was usually very mixed and included, on the lower surface, *Elminius modestus*, polyzoans, sponges, ascidians, and hydroids, whereas the upper surface usually became covered with *Corallina officinalis* turf, preceded by *E. modestus*.

The temporal changes occurring on rocks immersed on 5 April 1962 are shown in Fig. 60. The drawings represent a generalised picture built up from records taken from the three rocks immersed on this date. The organisms present on the lower surface of one of the rocks in August 1963 are shown in Fig. 61.

The changes occurring on the lower side of a rock immersed in a pool on 27 March 1963 and subsequently photographed in April, June, August, and October 1963 are shown in Fig. 62 a–d.

Fig. 61 The underside of a rock from West Tamaki Head settled by *Elminius modestus*, *Watersipora cucullata*, *Rhynchozoon bispinosa*, *Lichenopora novaezelandiae*, and *Hydroides norvegica* showing successive settlements and the interactions and overgrowths of the various species.

NARROW NECK

(a) *Corallina* zone – vertical surfaces

Several squares were cleared on the reef mainly during the summer of 1962. At the end of the first month after clearance the organisms present were *Elminius modestus*, *Spirorbis* sp., *Hydroides norvegica*, and *Corallina officinalis* paint, with some *Lunella smaragda* and *Sypharochiton pelliserpentis*. Neither the *Spirorbis* sp. nor the *H. norvegica* survived much longer than a month. During the second month *Colpomenia sinuosa* settled. As the *C. officinalis* paint grew, it spread out over both the rock surface and the barnacles, and by the end of the third month upright portions were beginning to appear from it. A few *E. modestus* were still present at the end of the seventh month, although they were covered with a thin film of green algae. *Enteromorpha* sp. was also present on the *C. officinalis* turf which covered most of the area and was still extending both outwards and upwards. During the entire period *L. smaragda* were present feeding on the *C. officinalis*. Even at the end of the first year the *C. officinalis* turf was not as long as that on adjacent areas which had not been cleared.

The sequence of temporal succession was:

(i) *E. modestus*, *Spirorbis* sp., *H. norvegica*, and *C. officinalis* paint;

(ii) *E. modestus*, *C. officinalis* paint, and *C. sinuosa;*

(iii) *E. modestus*, *C. officinalis* paint, and *C. officinalis* turf;

(iv) *C. officinalis* turf, with its associated animals, and algae.

(b) *Corallina* zone – horizontal surface

The pattern of colonisation and temporal succession was closely related to that on the vertical surfaces except that *Spirorbis* sp. did not settle on the horizontal surface.

The sequence of temporal succession was:

(i) *Elminius modestus*, *Hydroides norvegica*, and *Corallina officinalis* paint;

(ii) *E. modestus*, *C. officinalis* paint, and *Colpomenia sinuosa;*

(iii) *E. modestus*, *C. officinalis* paint, and *C. officinalis* turf;

(iv) *C. officinalis* turf, with its associated animals, and algae.

The results from the horizontal and vertical squares show clearly the temporal changes from a cover of short-lived species, in this case *E. modestus*, *H. norvegica*, and *Spirorbis* sp., to a cover of the long-lived perennial species, *C. officinalis*. These squares were cleared in the summer. Squares cleared at other seasons were settled initially by other species but the final domination of *C. officinalis* occurred invariably (Table 4).

Table 4 Monthly sequence of colonisation of rock surfaces in the *Corallina* zone cleared 6 February 1962, at Narrow Neck.

Species found	Months after clearance									
	1	2	3	4	5	6	7	8	9	10
(a) VERTICAL SURFACES:										
**Lunella smaragda*	X	X	X	X	X	X	X	X	X	X
**Sypharochiton pelliserpentis*	X	X	X	X	X	X	X			
Elminius modestus	X	X	X	X	X					
Hydroides norvegica	X									
Spirorbis sp.	X								X	
Corallina officinalis paint	X	X	X	X	X	X				
Corallina officinalis turf			X	X	X	X	X	X	X	X
Colpomenia sinuosa		X								X
Enteromorpha sp.					X		X			
(b) HORIZONTAL SURFACES:										
**Lunella smaragda*	X	X	X	X	X	X	X	X	X	X
Sypharochiton pelliserpentis	X		X	X	X					
Elminius modestus	X	X	X	X	X	X	X			
Hydroides norvegica	X									
Corallina officinalis paint	X	X	X	X	X	X				
Corallina officinalis turf				X	X	X	X	X	X	X
Carpophyllum maschalocarpum							X	X	X	X
Colpomenia sinuosa		X	X	X	X					X

*mobile grazing species invading from surrounding areas.

(c) The rock slopes cleared by Dellow

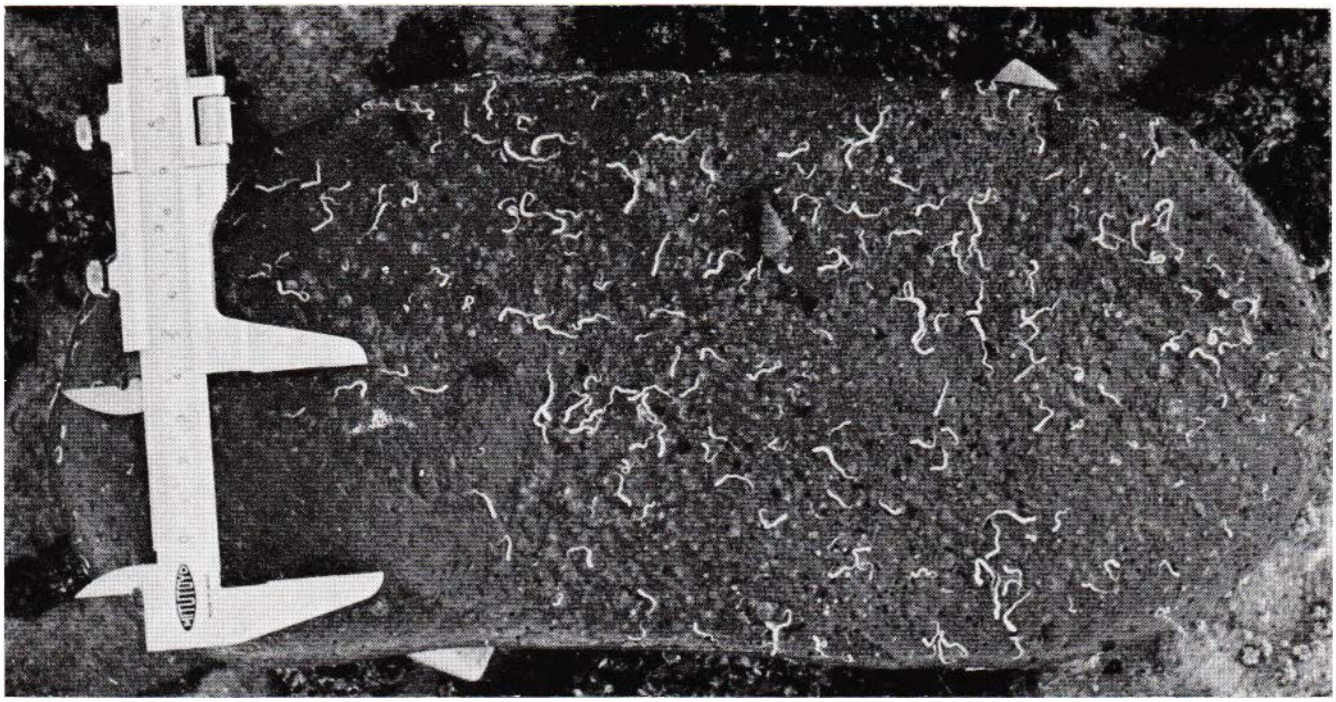
The results obtained here resembled those obtained by Dellow (1948), most differences being related to the time at which the rocks were cleared, namely February 1962, rather than June 1947.

Consequently although Dellow recorded the barnacles *Elminius modestus* and *Chamaesipho columna*, and the algae *Carpophyllum maschalocarpum*, *Colpomenia sinuosa*, *Laurencia thyrsifera*, *Scytothamnus australis*, *Gelidium caulacantheum*, and *Ecklonia radiata* as settling in the first 6 months after clearance, the earliest settlement in the present study consisted of *E. modestus*, *Watersipora cucullata*, *Hydroides norvegica*, *Spirorbis* sp., and *Corallina officinalis*. The two opposing faces slope north and south and algae found on both slopes were at higher levels on the south-facing slope. *Codium adherens* (Chlorophyceae) and *Chamaesipho columna* were found only on the south-facing slope, but *Crassostrea glomerata* although present at the top of both slopes was much more numerous on the north-facing one.

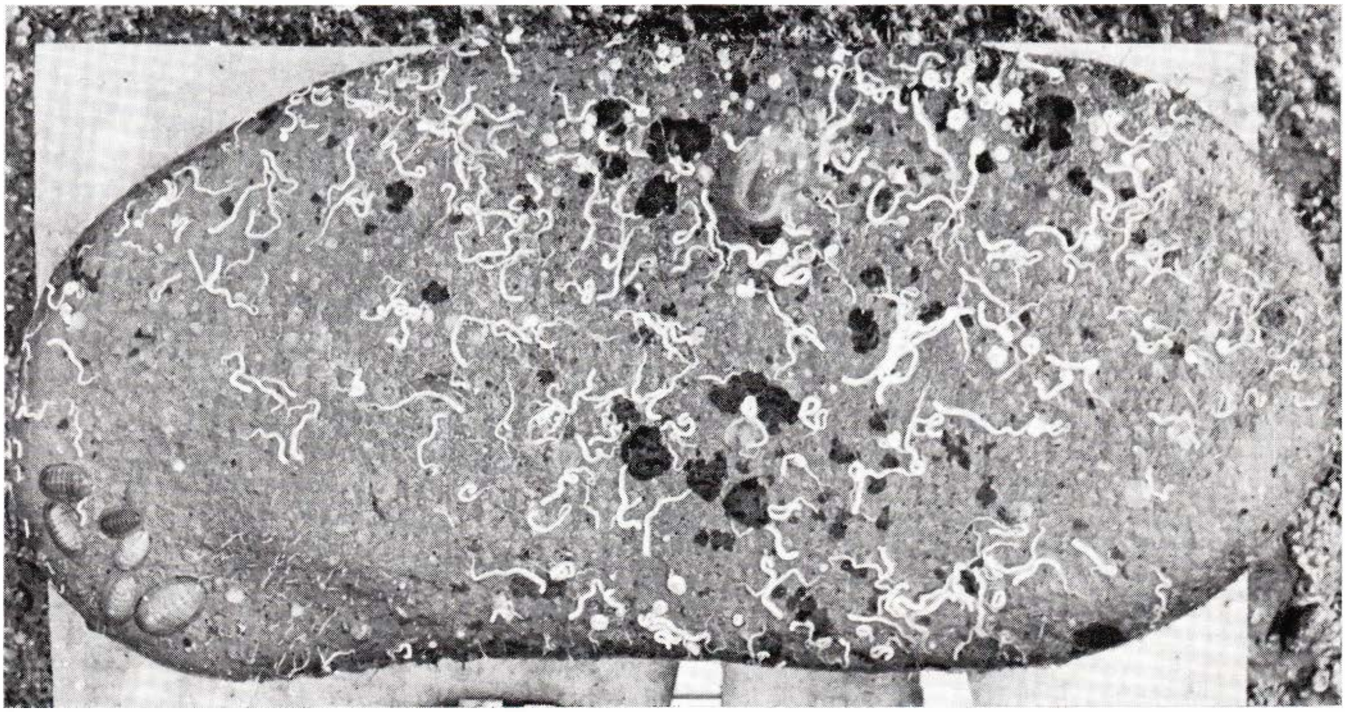
Dellow did not record settlement of *Watersipora cucullata* in 1947 and it is probable that, at that time, it had not reached Narrow Neck reef in its spread from the Port of Auckland (Skerman 1960).

(d) The rocks placed at E.L.W.S.

Succession on the rocks at Narrow Neck was very similar to that at West Tamaki Head. The number of species settling was greater than at West Tamaki Head but the final cover on the rocks was a mixture of polyzoans, sponges, and ascidians, with settlements of other animals as bare areas occurred.



(a)



(b)

Fig. 62 a–d The underside of one rock immersed in a pool at West Tamaki Head on 27 March 1963 and photographed in April 1963 (a), June 1963 (b), August 1963 (c), and January 1964 (d). Settlement in April consisted mainly of *Hydroides norvegica* and small but numerous colonies of *Watersipora cucullata*. Calipers set at 5 cm. By June the previously settled species have grown considerably and been joined by *Elminius modestus*, *Corella eumyota*, hydroids, and *Amaurochiton glaucus*. In August *Lichenopora novaezelandiae* and *Rhynchozoon bispinosa* had settled but the latter species is much more evident in (d). Three large *Sagartia* sp. can be seen in the bottom right corner with another specimen towards the centre.


(c)

(d)

TEMPORAL SUCCESSION

As a general principle during the repopulation of intertidal rocky shores "one phase . . . does commonly affect later ones" (Bokenham & Stephenson 1938). There the questions "Are any of the earlier animals essential to the seating of the later ones?" and "Do forms drop out as the community progresses?" (Shelford 1930) are clearly answered in the affirmative. Shelford concluded "that succession does occur in the intertidal zone, and the communities which were becoming established at the end of the period of observation may perhaps be regarded as climaxes or subclimaxes".

However, in the present study the answers to these two questions are answered in the negative for most of the areas studied.

In areas such as the *Corallina officinalis* zone at Narrow Neck the earliest macroscopic settler is commonly the barnacle *Elminius modestus*. This is soon smothered by the enlarging patches of *C. officinalis* paint, so that *E. modestus* may be said to have "dropped out" but the earlier presence of the *E. modestus* is in no way "essential to the seating of" the *C. officinalis*.

In many of the barnacle-dominated areas a barnacle species may be one of the first to occupy cleared rock surfaces, but it is then smothered or overgrown by other organisms, only to settle again on these smothering species. Some of the areas cleared in the *Perna canaliculus* zone at Piha were settled by *Chamaesipho columna*, to be succeeded by *Xenostrobus pulex* and/or *P. canaliculus* which then form a suitable substrate for later settlements of barnacles such as *C. columna*, *Elminius modestus*, *E. plicatus*, and *Balanus* spp. Thus forms come in rather than "drop out" as time elapses after clearance. The presence of algae and hydroids facilitates the settlement of *P. canaliculus* by providing a broken, fibrous surface, although it is not "essential".

Similarly, at the lower experimental level at Piha *Chamaesipho columna* often settled before *Xenostrobus pulex*, but their settlement was not a prerequisite for *X. pulex* settlement, providing there were crevices or pits in the rock surface; higher on the shore the presence of *X. pulex* or algae increased the dampness of the area and encouraged further *X. pulex* settlement. In the absence of other *X. pulex* or algae, *X. pulex* still settled in any small cracks and crevices. Thus both at Piha and West Tamaki Head the *X. pulex* were able to settle and grow on the bare rock, but the presence of other organisms, either algae, barnacles, or mussels increased the settlement of *X. pulex* by increasing the dampness of the area. Settlement of one organism sometimes influences the amount or the speed of subsequent colonisation, but does not alter the eventual assemblage of organisms. Species which are prominent on newly cleared rock surfaces may either reappear at a later date or fail to appear until a cleared rock surface is available again.

Those organisms with a longer life span will usually become dominant on an area, but often the increased length of life is also associated with a capacity for smothering organisms already present. This "covering phenomenon" has already been noted by Hoshiai (1961). Some of the smothering organisms such as *Corallina officinalis*, *Botryllus schlosseri*, and *Rhynchozoon bispinosa* present a surface that is evidently unsuitable for the settlement of other species since little or no settlement of competing organisms occurred on them. *Rhynchozoon bispinosa* stops the advance of *B. schlosseri*, perhaps by secreting an inhibiting agent, and so is not smothered by the rapidly advancing *B. schlosseri* front.

Climax Populations

In some ways conditions of temporal succession on the shore parallel those on land. However, the time taken from clearance to reach a stable state is much less than in terrestrial examples. Usually on the shore a stable state is reached in less than 5 years, and often in less than 1 year, whereas on land the same process may take decades, or centuries in a community such as a hardwood forest.

SUMMARY

Areas of rock at certain levels on the shore were denuded at regular intervals at Piha, West Tamaki Head, and Narrow Neck, Auckland. The settlement and growth of organisms on these areas was recorded over 2 years. In addition, clean boulders were placed in pools (West Tamaki Head) or subtidally (Narrow Neck) and artificial settling surfaces attached intertidally (Piha and West Tamaki Head) to provide additional information.

Before clearance the dominant organisms were as follows:

(i) Piha
- (a) *Perna canaliculus*
- (b) *Xenostrobus pulex*
- (c) *Elminius plicatus* and *Chamaesipho columna*

(ii) West Tamaki Head
- (a) *Elminius modestus* and *Xenostrobus pulex*
- (b) *Corallina officinalis* turf

(iii) Narrow Neck
- (a) *Corallina officinalis* turf

Settlement of *Chamaesipho columna* and *Xenostrobus pulex* at Piha, and *Elminius modestus* at West Tamaki Head and Narrow Neck occurred in every month during 1962 and 1963. Algae were prominent in the cooler months on all three shores. Serpulids and *Watersipora cucullata* settled during the warmer months. On the east coast (West Tamaki Head and Narrow Neck) mussels settled during winter and spring, but oysters settled in summer and autumn.

Information on the settlement times, location, and density of more than 40 species has been tabulated.

Most of the organisms settled and grew on bare rock, either on newly cleared surfaces, or on bare areas on surfaces cleared up to 2 years previously. *Perna canaliculus* settled only where there was protection from desiccation. The time of settlement of one organism at different levels on the shore or on different shores was not necessarily the same. The general pattern of seasonal settlement was similar each year, but the actual time and amount of settlement of any organism varied from one year to the next.

The organisms which settled first on a cleared area could affect the time and rate at which later organisms settled, but none of them appeared to be essential to the settling of the later ones. One exception to this is that the presence of a primary algal film was considered necessary for barnacle settlement, but was not investigated further.

Many of the organisms which settled on a newly cleared area, or became dominant early, were later replaced by other species. The same species could be one of the early colonisers on one area, and the final dominant organism on another area.

Most of the organisms forming the final stable assemblage were those with a longer life span than many of the forms which they replaced. They also often possessed growth characteristics that smothered the earlier organisms. Many had a limited power of movement, but others had either "stems" which raised them above the general level, or had surfaces which were not readily colonised by other organisms. Certain polyzoans could stop the advance of *Botryllus schlosseri* and thus avoid being smothered by it.

Development of organisms on a cleared area may consist of a cyclical progression in which there is a mosaic of patches of different ages. At a certain point in the succession, the whole patch is removed leaving bare rock, and the cycle starts again. Such cyclical progression may be related to interference with the natural habitat.

Zonation appears to be the result of complex interactions of the organisms on the shore, both with each other and with physical and climatic conditions. The assemblages of animals and plants on the shore are relatively permanent and are thought to be climax or subclimax by some workers.

Under stable conditions aggregations of one or a few species are found, but where conditions are unstable there is often a complex of many species.

Progression from cleared rock to a stable assemblage of organisms occurs in a much shorter time than in most terrestrial communities.

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APPENDIX

Checklist of the species and genera mentioned in the text and tables.

For the purposes of this study, species as listed here were identified as accurately as possible in the field. See also p. 9.

Chlorophyceae	*Ulva* spp., *Letterstedtia* spp., *Enteromorpha* spp., *Codium adhaerens*.
Phaeophyceae	*Glossophora kunthii*, *Myriogloia lindaueri*, *Petalonia fascia*, *Scytosiphon lomentaria*, *Colpomenia sinuosa*, *Leathesia difformis*, *Ecklonia radiata*, *Durvillea antarctica*, *Carpophyllum maschalocarpum*, *Sargassum sinclairii*, *Hormosira banksii*, **Scytothamnus australis*, Chordariales.
Rhodophyceae	*Porphyra columbina*, *Corallina officinalis*, *Champia* spp., *Ceramium* spp., *Laurencia* spp., *Gelidium* spp.
Porifera	*Hymeniacidon perlevis*.
Coelenterata: Hydrozoa	*Sertularia bispinosa*, *Sertularella* spp., *Plumularia* spp.
Coelenterata: Anthozoa	*Sagartia* spp., *Anemonia olivacea*.
Ectoprocta	*Rhynchozoon bispinosa*, *Bugula neritina*, *Eurystomella foraminigera*, *Lichenopora novaezelandiae*, *Penetrantia irregularis*, *Watersipora cucullata*.
Polychaeta: Serpulidae	*Hydroides norvegica*, *Pomatoceros cariniferus*, *Spirorbis* sp., *Idianthyrsus quadricornis*, **Galeolaria hystrix*.
Crustacea: Cirripedia	*Elminius modestus*, ‡*Elminius plicatus*, *Chamaesipho brunnea*, *Chamaesipho columna*, *Balanus amphitrite*, *Cryptophialus melampygos*.
Insecta	Clunioninae.
Mollusca: Amphineura	*Sypharochiton pelliserpentis*, *Guildingia obtecta*, *Amaurochiton glaucus*.
Mollusca: Gastropoda	*Littorina antipoda*, *Littorina cincta*, *Risellopsis varia*, *Lepsiella scobina*, *Dicathais scalaris*, *Cellana ornata*, *Lunella smaragda*, *Taron dubius*, *Melagraphia aethiops*, *Zeacumantus subcarinatus*, *Eatoniella olivacea*, *Cominella virgata*, *Cominella maculosa*, *Notoacmaea daedala*, *Anisodiloma lugubris*, *Facelinella*.
Mollusca: Bivalvia	*Perna canaliculus*, *Xenostrobus pulex*, *Chlamys zelandiae*, *Anomia trigonopsis*, *Ostrea lutaria*, *Crassostrea glomerata*, *Anchomasa similis*, *Pholadidea spathulata*, **Mytilus* spp., *Chione stutchburyi*.
Ascidiacea	*Corella eumyota*, *Microcosmus kura*, *Botryllus schlosseri*.
Pisces	*Acanthoclinus quadridactylus*.

*Species mentioned in the discussion of similar work but not found on the experimental areas.

†Now known provisionally as *Dicathais orbita* (Phillips *et al*. 1973).

‡Now known as *Epopella plicata* (see note and references, p. 4).

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INDEX

All species and genera mentioned in text, figures, and tables are listed in the Appendix.

Page numbers of major references (Table 1) are in **bold** type; page numbers referring to figures are in *italic*.

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