Ecology of Southern New Zealand Exposed Rocky Shore at Little Papanui, Otago Peninsula

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At Little Papanui Beach there are 4 to 5 tiers of simultaneously breaking waves during calm weather, more during rough.

The region is cold temperate, inshore surface sea temperatures nearly always lying between 8° C. and 16° C.

The rocky shore supralittorally shows abundant *Melarhaphe cincta,* scattered *M. oliveri*

Midlittorally, the balanoids *Chamaesipho columna* and *Elminius plicatus* and the mussels *Modiolus neozelanicus* and *Mytilus planulatus* variously dominate; except on south-facing surge-exposed cliffs, where the covering is of encrusting coralline alga. *Bostrychia arbuscula* is abundant on S-facing, strongly wave-exposed rocks.

Sublittorally, usually the giant fucoid kelps *Durvillea antarctica* and *D. willana* co-dominate with *Mytilus canaliculus.* Where topography prevents full wave exposure, *Durvillea* is replaced by *Xiphophora* and *Lessonia.*

As compared with a sheltered harbour shore nearby, vertical ranges of most commoner species are greatly increased on this continuously wave-exposed shore.

Introduction

A study of the ecology of a harbour rocky shore near the Portobello Marine Station (Batham, in press) made desirable a comparative study of a continuously wave-exposed shore at the same latitude. The region selected was Little Papanui, on the outermost tip of Otago Peninsula.

Little Papanui was visited approximately monthly, at spring tides, for a year from 3.8.53; and thereafter at less regular intervals. During this period, various other N.Z. rocky shores have been examined as opportunity offered.

The beach at Little Papanui is an attractive one for the biologist. It lacks road access and no one lives there, although Maori artefacts by the south stream indicate past habitation. Yellow-eyed penguins (*Megadyptes antipodes*) breed in scrub on slopes above the shore, and small colonies of seals live on the rocks.

Accounts have been published by other N.Z workers of various North Island shores (e g, Cranwell and Moore, 1938; Chapman, 1950; Carnehan, 1952; Trevarthen. 1954; Dellow, 1955) and of that at Taylor's Mistake, near Christchurch (Knox, 1952). Prior to this was Oliver's more general account, in which some references to Little Papanui (which he calls Maori Papanui Beach) are given (Oliver, 1923).

In the present paper, nomenclature of molluscs follows Powell (1946); of seaweeds, Navlor (1954); of sessile barnacles, Moore (1944); of anemones, Parry (1951 and 1952).

Acknowledgments

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Systematic workers to whom the writer is indebted for identifications include Miss B. I. Brewin (ascidians), Dr. D. A Brown (Bryozoa), Mr R. Dell (molluscs),

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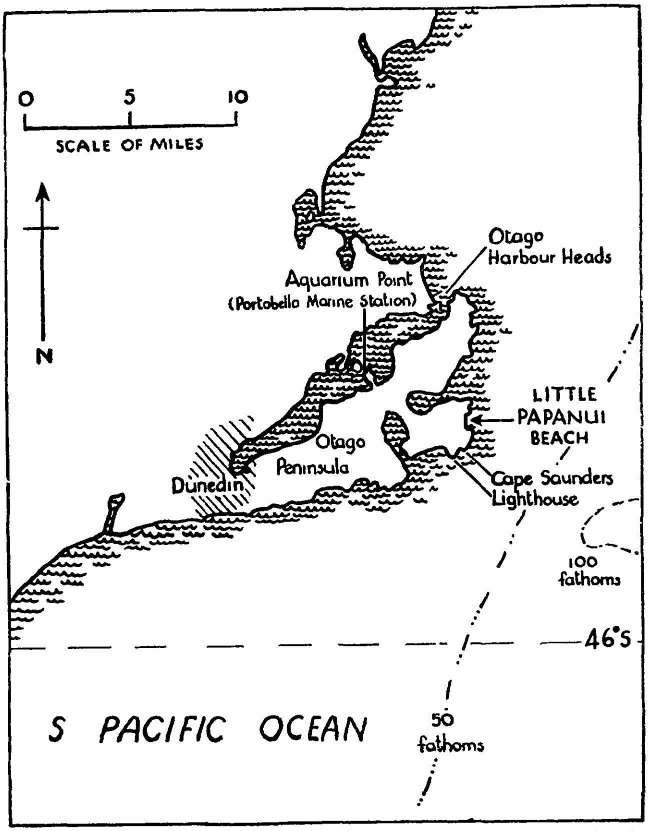


TEXT-FIG 1—Map of E Otago coast in vicinity of Otago Peninsula, showing position of Little Papanui Beach and other localities mentioned.

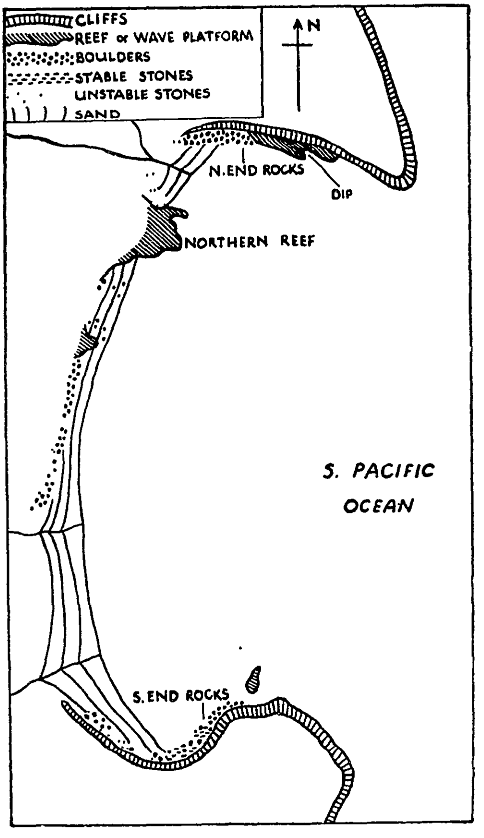
Dr. H B Fell (echinoderms), Mr. G A. Knox (polychaets), Dr M Naylor (seaweeds), and Miss P. M. Ralph (hydroids) Helpful discussion has been enjoyed with others interested in N.Z. shore ecology, especially Mr. G. A. Knox, Miss L. M. Moore, and Mr. C. B. Trevarthen.

Thanks are also expressed to the staff of the Cape Saunders Lighthouse, who have kindly recorded sea temperatures approximately weekly for two years.

INORGANIC ENVIRONMENT

Little Papanui is placed on the tip of Otago Peninsula, jutting out towards the nearby continental shelf and into the South Pacific Ocean (Text-fig 1). It is thus well exposed to continuous wave action, whether wind is blowing or not. The continuously surging and breaking Pacific rollers are the chief ecological feature whereby this shore differs from the harbour shore previously considered

In climatic features the two regions, only five miles apart, probably differ but slightly. In a general way, the sunshine and rainfall data given in the previous paper may be applied here; i.e., hours of sunshine per month would probably usually lie between 80 and 200, and rainfall would average about 30in a year, fairly evenly distributed through the months. Total wind experienced at any given part of Little Papanui per year is probably less than at the tip of Aquarium Point by the marine station; for the latter is exposed to both southerlies and northerlies. At Little Papanui, on the other hand, cliffs cause local protection



Text-fig. 2—Map of Little Papanui Beach.

Southerly winds are more often of gale force than northerlies, so that on the whole the north end of the beach is exposed to greater wave action

Little Papanui itself consists of a half-mile stretch of sandy beach bounded by high cliffs at each end The cliffs at the north end (Fig 2), about 80ft in height, have large boulders at their base intertidally nearest the beach, a sloping wave-cut platform east of this and further seawards drop vertically into the water. The height and aspect of the cliffs keeps the shore below in continuous shade during the winter months, and shaded till middle day in summer. Fresh water seepage occurs at several points.

The south end cliffs (Fig 1, Text-fig 2) are sun-facing, and jut out to shelter rocks below from southerly storms A tiny offshore islet further helps break wave force. Hence the boulders and rocks intertidally here are not exposed to nearly such strong wave action as at the north end of the beach.

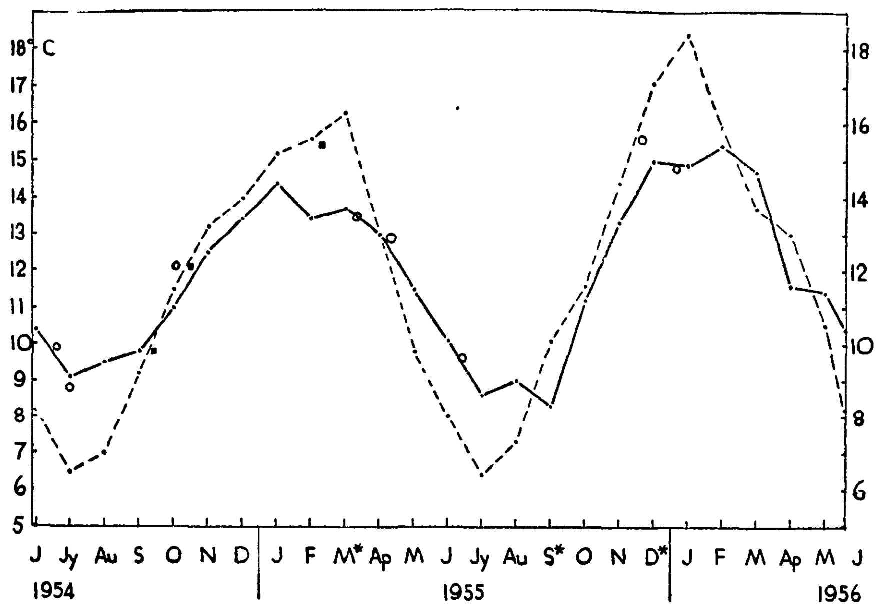
For the rest, a rocky reef (the Northern Reef) runs out to below low tide near the north end of the beach, South of this, rocks are exposed along much of the beach during periods of sand depletion (Fig 1), but at other times the sandy beach is continuous except for a cluster of boulders above half tide Areas of unstable stones occur by these boulders, adjacent to the Northern Reef, and at the inner corner of the south end (Text-fig. 2, small dots). The relatively lifeless habitats of unstable stones and unstable sand are not considered in this paper

The rock of the rocky shore is predominantly coarse basalt, hard and of dark colour.

The region lies in the cold temperate zone, nearly always south of the subtropical convergence. Ice does not occur in open sea here. There are probably occasional frosts intertidally, although none were observed during visits.

Inshore surface sea temperatures have been recorded approximately weekly from the cliffs below Cape Saunders Lighthouse, about two miles south of Little Papanui. Monthly averages of these are plotted in Text-fig. 3, continuous line; while the broken line shows sea temperatures at Aquarium Point, averaged for the same dates. As might be expected, the outer coast sea temperatures neither rise as high in summer nor fall as low in winter as those of shallow, land-locked Otago Harbour. Of individual sea readings from Cape Saunders, the minimum in 1954 was 8 4° C. on 10.7.54, in 1955 was 7·9° C. on 16.7.55; the maximum in the summer of 1954–5 was 14.9° C. on 22.1.55, and the following year was 16.2° C. on 27.1.56. Scattered inshore sea temperature readings were taken at Little Papanui during field work. These, shown as squares and circles on Text-fig. 3, are in fairly close agreement with the more regular Cape Saunders readings Of 95 Cape Saunders readings nearly weekly over two years, 93 lay between 8·0° C. and 16·0° C. The high sea and harbour temperatures of early 1956 were associated with a heat wave, of air temperatures exceptional for the region.

Tides are semi-diurnal, low spring tides occurring about 1¼ hours earlier than predicted for the Port of Dunedin. Tidal range was measured, as closely as was practicable, by a temporary scale on a calm day at the less wave-exposed south end of the beach. On 5.9.56, with a predicted low spring tide for Dunedin of minus 0 3ft (the lowest predicted for 1956) and barometer at 30 2ins, high tide level



Text-fig. 3.—Surface tea temperatures Heavy line, monthly averages of approx. weekly 9 a m. readings taken below Cape Saunders Lighthouse, near Little Papanui Broken line, monthly averages of 9 a.m. temperatures on same dates taken from end of main wharf at Portobello Marine Station Months during which points based on fewer than 3 readings marked with asterisk. Scattered individual low tide sea readings during field work at Little Papanui marked as squares (1953 and early 1954) or circles (mid-1954 to 1956).

was between 7½ft and 8ft above low tide level, as marked on Text-fig. 4. In general, on most of this shore where Pacific rollers continuously break, precise tidal levels are not easily defined. In practice, low spring tide level is regarded as the level readily accessible on a low spring tide, and other levels are gauged upwards from this and from coverage at different times of tide.

BIOLOGICAL

This wave-exposed rocky shore shows a dense assortment of organisms, both intertidally and sublittorally. These will first, for convenience, be divided according to their major zones from above downwards. In actuality, however, zoning is not sharp, and the effect of continuous wave action on vertical ranges of common species will be considered in a later section

Supralittoral Fringe

The two New Zealand littorinids both abound here *Melarhaphe cincta* is extremely abundant and shows a wide vertical range. The blue-banded *M. oliveri* is locally abundant, and vertically more strictly confined to the splash zone around and above high tide level. Lichen blackening is patchily dense, chiefly on south faces of rock. The green, high tide limpet *Notoacmea pileopsis sturnus* is moderately abundant, more especially in crevices (e.g., 81 specimens counted on one large boulder). Dying plants of *Durvillea,* cast up among high tide boulders, are usually being devoured by hundreds of the purple periwinkle *Zediloma digna. Bostrychia arbuscula* from tigh tide neap extends far into the supralittoral where shade and splash predominate.

Midlittoral Zone

Wave-pounded rock of the midlittoral usually carries a dense covering of compact organisms. Dominants competing for substratum in most of this area are the barnacles *Chamaesipho columna* (wall valves fused, typical basal length 5 mm) and *Elminius plicatus* (valves often yellowish, typical basal length 15 mm) and the mussels *Modiolus neozelanicus* (tiny, shells black or mauve) and *Mytilus planulatus* (medium, shells usually navy)

Several factors appear involved in the relative abundance of these four dominants. For instance, *aspect* often markedly affects the barnacle distribution, north (sun-facing) rocks chiefly carrying *Chamaesipho,* whereas *Elminius plicatus* dominates on south-facing (shaded) rocks (Plate 49, fig. 6). Surf pounding is best tolerated by *Chamaesipho.* Flatter surfaces likewise suit *Chamaesipho,* whereas mussels or *Elminius* are usually denser on vertical faces. Crevices favour both mussels, especially *M. planulatus.* Sand-scour appears most readily tolerated by *Modiolus.*

Whereas for most of this rocky shore these balanoids and mussels variously dominate the midlittoral, two regions appear (from a distance) an exception. These are the south face of the offshore south end islet and the south-facing cliffs furthest seaward at the north end. Both, above the dark *Durvillea* fringe, show not the dirty yellowish-white of a balanoid zone, but the dull pink of encrusting coralline algae (Plate 47, fig. 2, C).

Various other species characterise the midlittoral. Molluscs frequent throughout it are *Lepsiella scobina albomarginata, Sypharochiton pelliserpentis, Cellana ornata, Cellana redimiculum* (commoner higher), and *C. radians* (commoner lower) *Ulva* and *Enteromorpha* at upper levels are usually in pools; or, with the latter genus, where fresh water seepage occurs.

Chiefly above half tide, *Bostrychia arbuscula* abounds, in fact often dominating on shaded south faces. *Apophloea lyallii* shows scattered tufts on exposed rock faces *Porphyra ? columbina* girdles boulders. *Scytothamnus fascicularis* and the high tide form of *Scytosiphon lomentaria* are seasonably dense. *Pollicipes spinosus* clusters in crevices, *Actinia tenebrosa* in crevices and pools. Exposed rock masses carry *Benhamina obliquata.* Another pulmonate limpet, *Gadinalia nivea,* clusters among north end rocks. During winter shade it may here even occur on upper rock faces at high spring tide level, with *Tetraclita purpurascens, Spirorbis* and *Cnemidocarpa bicornuata.*

In the *lower midlittoral, Mytilus planulatus* commonly carries *Conacmea parviconoidea* and *Chamaesipho columna. Scytothamnus australis* is on and amongst *M. planulatus; Aulocomya maoriana* amongst it. *Splachnidium rugosum* is especially common round pool margins. Browns seasonably here in evidence are *Adenocystis utricularis, Scytosiphon lomentaria* (low tide form), *Colpomenia sinuosa* and *Leathesia difformis. Pachymenia lusoria* forms a broken band just above *Durvillea,* is scattered higher. Other frequent lower midlittoral animals include *Patelloidea corticata, Anthopleura aureoradiata* carpeting shallow pools, *Oulactis muscosa* in crevices and pools, and *Pyura suteri* on shaded rock faces

Pools of the midlittoral are best developed in the Northern Reef. *Cheilosporium elegans* and other corallines line some, *Enteromorpha* others A large pool here at low neap tide level shows constantly *Cystophora scalaris, Halopteris* sp, *Codium fragile, Curdiaea coriacea, Ulva* sp., corallines and some filamentous reds, and seasonally *Laurentia thyrsifera* and *L. virgata, Adenocystis utricularis, Glossophora kunthii, Scytosiphon lomentaria* and *Desmarestia firma;* also occasional young plants of *Durvillea* and *Macrocystis* which do not long survive. Of animals, mussels (*Mytilus canaliculus* and *M. planulatus, Aulocomya maoriana*) and the anemones *Actinia tenebrosa* and *Anthopleura aureoradiata* are the only species playing a conspicuous part in such a pool.

Under stone life was chiefly examined at the south end; as at the more exposed north end stones small enough to turn over were unstable, and hence an almost lifeless habitat. Abundant under and among south end lower intertidal rocks are: *Actinothoe albocincta; Galeolaria hystrix, Spirorbis* and other polychaets; *Hippothoa distans, Hippadenella margaritifera* and other encrusting bryozoans; *Sypharochiton pelliserpentis, Terenochiton otagoensis, Acanthochiton zealandicus,* and less commonly *Amaurochiton glaucus* and *Cryptoconchus porosus; Atalacmea fragilis, Cellana radians, Buccinulum littorinoides; Corella eumyota* and other ascidians; *Ophionereis fasciata;* and *Diplocrepis puniceus.* Commonly under stones on sand are: *Anthopleura rosea, Audouinia filigera, Eulalia,* pink nemertines, sipunculids (probably *Physcosoma scolepsannulata* Hutton), *Protothaca crassicosta* and *Trochodota dunedinensis. Petrolisthes elongatus* is very abundant under stones from low tide to high tide spring (there sometimes sharing stones with *Cyclograpsus chavauxi*); *Hemigrapsus edwardsi* occurs sparsely at half tide level

Kelp Zone or Infralittoral Fringe

At low tide on the wave-exposed periphery of Northern Reef and north end rocks, *Durvillea* co-dominates with the large, green-shelled mussel *Mytilus canaliculus* *Durvillea antarctica,* its yellow-brown thongs bouyed by air tissue, fringes at low tide neap. Darker, branched *D. willana* replaces it at low tide spring and a little below (Plate 48, fig. 3). Abundant *Porphyra subtumens* and scattered *Hapalospongidion durvillei* grow on *Durvillea* fronds, but larger epifauna is absent.

Competition for substratum appears strong. Young *Durvillea* plants often grow on the posterior ends of mussels. Abundant among the mussels are encrusting pink corallines, *Codium adherens, Chaetomorpha darwini,* various sponges, ascidians, bryozoans, and *Petrolisthes elongatus.* Species macroscopically in evidence on the mussels include *Sertularia bispinosa, Anthopleura aureoradiata, Diadumene zelandica, Hippadenella margaritifera, Balanus decorus, Tetraclitas purpurascens* and *Molgula sluiteri.*

Flatter or less wave-exposed rocks at low tide carry, not *Durvillea* and green mussels, but dense beds of red algae. These are chiefly small sturdy species, such as *Heterosiphonea coccinea, Gymnogrongus ? vermicularis, Plocamium* sp., *Ballia* *scoparia,* various *Polysiphonia* species, and *Lenormandia oblongifolia.* Small specimens of *Pyura pachydermatina* are scattered. *Elzerina blainvilli* is locally dense on rock races.

Behind the shelter of the offshore islet at the south end of the beach, *Durvillea* gives way to a dense covering of *Xiphophora chondrophylla* var. *maxima* and *Lessonia variegata* (Plate 47, fig. 4, and left column of Text-fig. 4). These co-dominate at low spring tide, *Lessonia* dropping out just above this. Both *Xiphophora* and *Cystophora scalaris* here carry the well-camouflaged anemone *Cricophorus nutrix.*

As well as green mussels, larger animals in evidence at low tide include: *Isocradactis magna, Oulactis muscosa, Guildingia obtecta, Vaferochiton biramosa, Scutus breviculus, Haliotis iris, Lepsithais lacunosa, Lunella smaragda, Venustas punctulata urbanior, Calantica villosa, Asterina regularis, Calvasterias suteri* (wave-swept crevices), and *Pseudechinus novaezelandiae*

Seasonal Changes

Several species show marked seasonal fluctuations

Tubularia colonies, fringing boulders standing in pools at low tide, show dense winter outbursts (June–August). While scattered *Benhamina obliquata* can be found throughout the year, larger numbers appear in November, their characteristic egg-coils being observed from October till March.

Algae abundant at some seasons, macroscopically absent at others, include: A species of *Enteromorpha* that fringes high tide boulders in late winter; *Scytothamnus fascicularis* (summer months); *Scytosiphon lomentaria* (November–January); *Desmarestia firma* (September-December); *Adenocystis utricularis* (e.g., 24.10.53 to 5.4.54). Common algae showing some seasonal variation include *Ulva* sp., *Bryopsis vestitum, Leathesia difformis, Splachnidium rugosum, Scytothamnus australis* and *Porphyra ? columbina.*

Of interest is the difference in seasonal fluctuations of some of these species at Little Papanui as compared with Aquarium Point. *Benhamina* and *Porphyra,* both moderately abundant (though fluctuating) throughout the year at Papanui, are much more strictly seasonal at Aquarium Point. *Adenocystis, Scytothamnus fascicularis* and *Scytosiphon* all regularly show much later outbursts on the outer coast than at Aquarium Point.

INTERTIDAL ZONATION AND EFFECT OF WAVES ON VERTICAL DISTRIBUTION

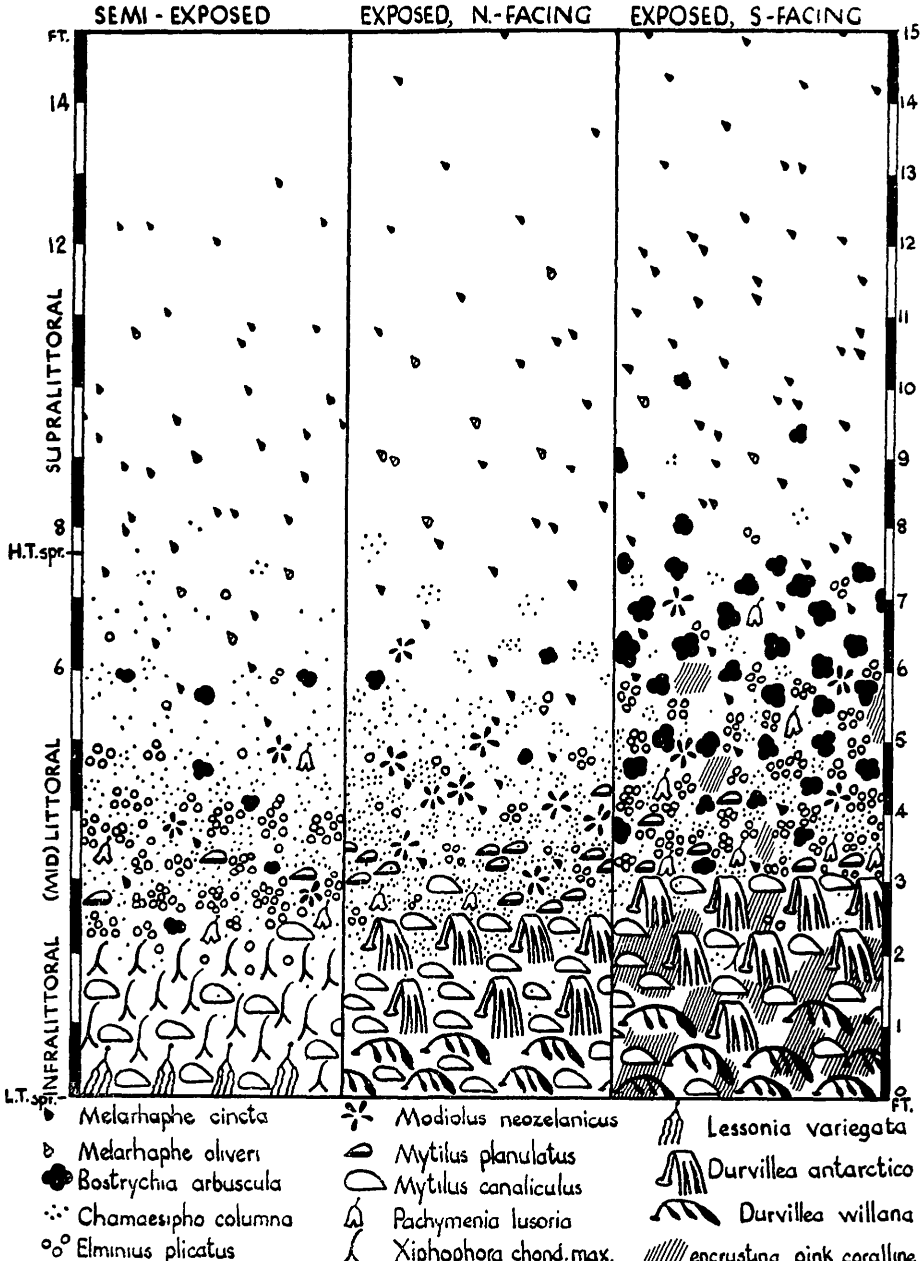
Text-fig. 4 shows zonation diagrams for more important species for typical portions of Little Papanui rocky shore. These appear confused, for the simple reason that zoning is not sharply shown on this shore. There would seem three main reasons for this.

Firstly, most of the midlittoral dominants occurring here thrive from low tide to high tide—e.g., *Elminius plicatus, Chamaesipho columna, Modiolus neozelanicus.*

Secondly, various belt-forming species important on other N.Z. shores are absent here for geographic and/or ecological reasons. For instance, *Chamaesipho brunnea, Carpophyllum maschalocarpum, C. plumosum, C. elongatum* and belt-forming *Sabellariid* tubeworms do not come as far south as this; *Pomatoceros (coeruleus) cariniferus,* near its southern limit, cannot here tolerate such wave exposure. Wave exposure also appears too great for *Ostrea hefferdi* and *Hormosira banksii,* both in places dense in Otago Harbour.

The third reason for obscurity in zoning lies in the greatly increased vertical range shown by many species where wave exposure is strong.

The most extreme case of this seen at Little Papanui is at the dip in the wave platform beyond the north end rocks. This dip causes great upsurging of waves. At the top of the cliffs here (Fig. 2, X), about 70ft above sea level, the soil is bare



TEXT-FIG 4.—Zonation diagrams for three examples of rocky shore at Little Papanui Left, semi-exposed south end rocks Centre, north-facing portion of Northern Reef. Right, south-facing north end rocks. Where surge is locally greater, upper *Durvillea* level is higher than in this diagram, and vertical range of species increased.

FIG. 1.—View of Little Papanui Beach, looking towards south end. On second of two successive calm days there are 4–5 tiers of simultaneously breaking waves.

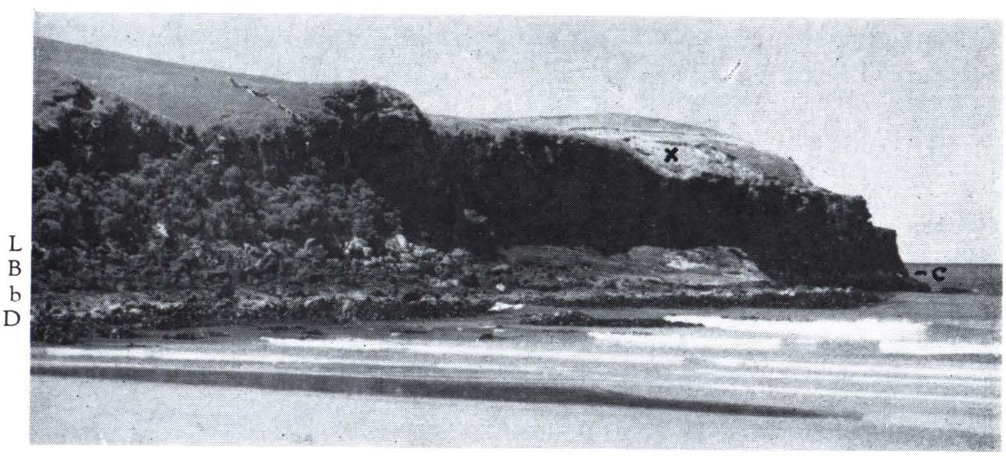


FIG. 2.—North end rocks, Little Papanui, calm summer afternoon, low spring tide. X, area at top of cliff bare of halophytic turf, presumably due to excessive seawater. L, broken white lichen zone. B, darker *Bostrychia* zone, chiefly upper midlittoral and above. b, yellowish-white balanoid zone. D, dark *Durvillea* fringe. c (at right), pale band of pink coralline alga, here the midlittoral dominant above *Durvillea*.

FIG. 3.—*Durvillea* dominant on north end rocks exposed to strong waves. Left, at low tide neap, *D. antarctica* with unbranched stipes. Right, at lower tide level, *D. willana* with side branches.

FIG. 4.—Semi-exposed south end rocks at lowest spring tide level. *Lessonia variegata* (centre) and *Xiphophora chondrophylla* var. *maxima* (above and below) here replace *Durvillea*.

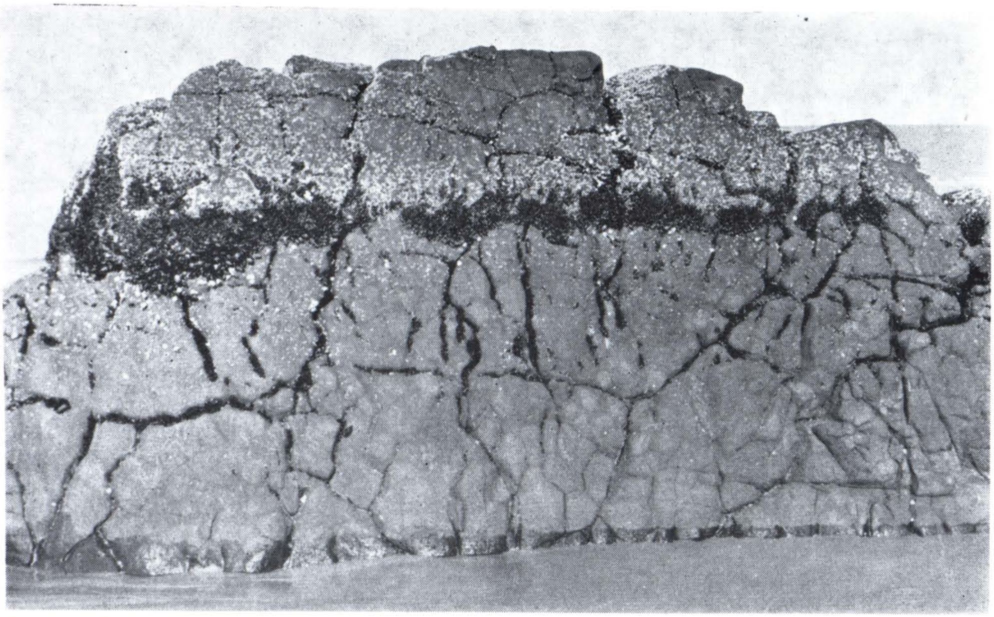


FIG. 5.—Sand-Zonation. Rock mass in sand, which several weeks before was two-thirds covering it. Recently sand-covered region largely bare; above, dark zone of sand-tolerant *Modiolus neozelanicus*; above that, sprinkling of *Chamaesipho columna*.

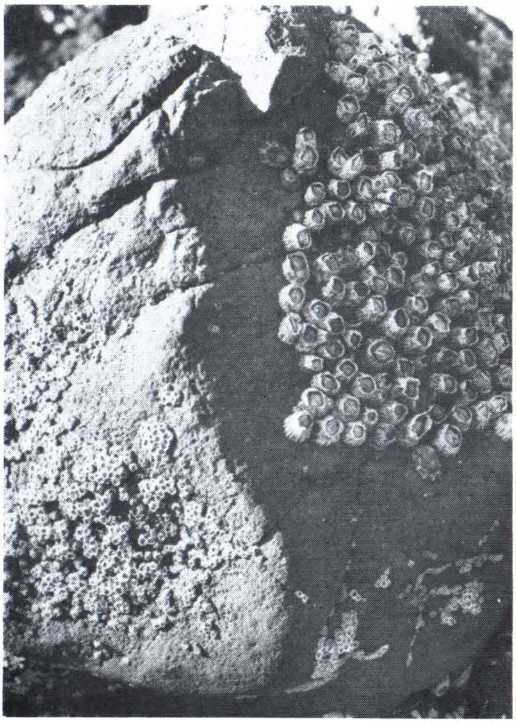


FIG. 6.—Boulder photographed from above. Left (north or sun-facing aspect), *Chamaesipho columna*. Right (shaded) face, chiefly *Elminius plicatus*.

FIG. 7.—Face of boulder, lower mid-littoral, north end rocks. Strong wave exposure, much shade. *Bostrychia arbuscula* (right), usually a high neap tide species, dense alongside *Pachymenia lusoria* (left).

of the usual halophytic turf, presumably owing to excessive sea water. *Durvillea antartica* holdfasts, in the dip, tier upwards for about 10ft. Whereas the main barnacle belt stops 3–4 feet above this, *Chamaesipho* are still sprinkled 15 feet above the uppermost *Durvillea*. *Bostrychia arbuscula, Notoacmea pileopsis sturnus* and lichen blackening occur 40 feet above the *Durvillea*, just meeting the lower limit of the halophytes *Scirpus cernuum* and *Tillea moschata*. *Melarhaphe cincta* is large and abundant at this level and extends up another 10 feet—in all some 50 feet above the uppermost *Durvillea* holdfasts.

While this upsurging dip is an extreme case, the north end rocks as a whole show considerable splaying of the vertical range of species (Text-fig 4, right column).

Bostrychia arbuscula and *Melarhaphe cincta* both extend down to the uppermost *Durvillea* holdfasts in the lower midlittoral.

Pachymenia lusoria, dense at that level, is scattered up to high spring tide. Hence in the lower midlittoral is seen the unusual feature of *Pachymenia* and *Bostrychia* thriving side by side (Fig. 7). Such instances contrast markedly with Aquarium Point, where *Melarhaphe cincta* is confined to a high spring tide zone 18 inches deep, and the *Bostrychia* zone at high neap tide is almost as narrow. Even at the semi-exposed south end of Little Papanui, an under-stone species such as *Petrolisthes elongatus* shows an appreciably greater vertical range than at Aquarium Point.

Lewis (1954–5, p. 722), studying a north Scotland shore, concluded that upward displacement of species and zones results from heavy surf action At Papanui, where wave exposure is much greater, such upward displacement is much more marked.

As a whole, then, it will be seen that intertidal zonation is not well shown at Little Papanui. The only abrupt change of zone is between *Durvillea* and balanoids (Fig. 2, D and b) That this is controlled by the upper level *Durvillea* can reach rather than the lower balanoid level is indicated by odd washed up *Durvillea* holdfasts, studded with *Chamaesipho*

Sand-scour zonation. Some rocky faces on the beach show a marked vertical banding within the midlittoral zone. Fig. 5 is an example, with largely bare rock below, standing in sand; a dark *Modiolus* band next, and *Chamaesipho* pale above it. When visited several weeks earlier, most of this rock was buried in sand A more constant example is the south face of the Northern Reef, which rises vertically from sandy beach and runs seawards at right angles to the waves. Here, encrusting pink corallines are lowermost, a mussel band (*Modiolus* with scattered *Mytilus planatulus*) comes next, with a balanoid band (both species) above it Banding of this sort is lacking from rocky shores not rising from sand. Hence it would seem to be not intertidal zonation in the usually accepted sense of degree of tolerance to air exposure. Instead it appears controlled by the degree to which dominants can tolerate sand scour, where every breaking wave swirls clouds of sand grains.

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The rocky shore at Little Papanui is being considered as an example of *wave-exposed* shore in *Southern* New Zealand. The material described will now be discussed from these angles.

Wave Exposure

In considering New Zealand shore habitats, the distinction is seldom made between shores *continuously* wave-exposed and shores exposed to waves only during winds. Accepting that this distinction is not absolute, it is nevertheless felt that it is a useful one ecologically. Certain species occur exclusively in one or other of these conditions; other species predominantly so.

Degree of wave exposure is difficult to measure or define in a manner convenient for ecologists. Moore (1935) attempted this on a basis of "the number of days per hundred days in which any wind blows into the aperture in question". This is impracticable around Otago Peninsula. Aquarium Point in the harbour, exposed to most prevailing winds, also has many calm periods because of its landlocked site. But Little Papanui, less wind-exposed, is continuously wave-pounded because it is directly open to a great ocean mass. Evans (1947) arranges 37 S. England stations in 5 groups from "very exposed" to "very sheltered". From my experience of Plymouth and Otago, I gauge that his "very exposed" regions are about comparable with the south end rocks at Little Papanui, which I am calling "semi-exposed". The Northern Reef and north end rocks at Little Papanui are very much more wave-exposed.

A simple scheme I have been following in field-work is to record the number of tiers of simultaneously breaking waves on a shore during calm weather. This gives a figure of 0 for Otago Harbour and other land-locked water masses, thereby classified as "sheltered"; for Taylor's Mistake, on the north of Bank's Peninsula, about 2; for Long Beach, in the northerly lea of Otago Peninsula, 1–2: for Little Papanui 4–5, except at the south end, where it is 2–3 (Plate 47, Fig. 2). In general the number of tiers of breaking waves on a beach during calm weather (e g., on the second of two predominantly calm days) would seem a useful comparative indicator of degree of wave exposure. One inconvenient aspect is the consideration of surge-exposed cliffs where there is no beach nearby. Here the height of surge during calm weather would be a measure probably able to be correlated with the last. Such measures are minimal ones of wave-exposure in a given locality. I suspect that the strength of wave action during heavy winds is less critical for many species than the continuous presence of water movement in all weathers.

In general, most of Little Papanui rocky shore, by standards of N Z. rocky shores usually examined by zoologists, is very wave-exposed.

Species Associated with Wave-Exposed Shore

Durvillea antarctica and *willana* are the most conspicuous species thus associated. They thrive where waves surge or break, dropping out just inside Otago Heads. Their holdfasts are strongly attached and cannot be dislodged by pulling, as can those of *Macrocystis. Pollicipes spinosus,* which does not rhythmically withdraw its cirri but depends on water movement to bring food, is another species obviously requiring continuous wave action. There are many other species which, so far as my field notes go, seem locally to belong to exposed coast and not harbour—e.g , *Isocradactis magna, Cricophorus nutrix, Sertularia bispinosa, Symplectoscyphus johnstoni, Stereotheca elongata, Hippadenella margaritifera, Mytilus canaliculus, Modiolus neozelanicus, Guildingia obtecta, Cellana redimiculum, Zediloma atrovirens, Gadinalia nivea, Calvasterias suteri, Ophionereis fasciata, Molgula sluiteri, Berrillia boltenioides, Dumus areniferus* and *Diplocrepis puniceus.* Algae, as well as *Durvillea,* include *Chaetomorpha aerea, Codium adherens,* and *C. fragile, Microzonia velutina, Glossophora kunthii, Apophloea lyallii, Curdiaea coriacea, Gymnogongrus vermicularis, Ballia scoparia* and *Lessonia variegata.*

Then there are various species, relatively common on the outer coast, that occur only in limited parts of Otago Harbour, where water movement is considerable. Among animals are *Tubularia ? larynx, Oulactis muscosa* and *Actinia tenebrosa, Vaferochiton biramosa, Haliotis iris, Atalacmea fragilis* and *Notoacmea pileopsis sturnus.* Of plants, *Xiphophora, Splachnidium rugosum, Scytothamnus australis* and *Pachymenia lusoria* occur at limited parts of Quarantine Island in the harbour, but not at Aquarium Point.

Species Intolerant of Wave Exposure

Various species important at Aquarium Point and other harbour rocky shores appear absent or much less in evidence at Little Papanui.

Macrocystis pyrifera, dominant in the harbour where there are moderate currents, is practically absent at Little Papanui. In all, I have seen three young plants there, each under 1 metre long The species can tolerate mild wave exposure. For example, at Long Beach scattered long *Macrocystis* plants grow in proximity to *Durvillea,* but their fronds are tashed. On the outer coast, the typical *Macrocystis* habitats are offshore beds, especially in the northerly lea of headlands (e g., Karitane, Moeraki) and the entrances to inlets (e g , Papanui Inlet, Purukanui Inlet) where currents are strong. *Hormosira banksii,* which in Otago Harbour thrives optimally in less current-exposed sites than *Macrocystis,* again tolerates some wave exposure. Whereas scattered plants grow at St. Clair, I have met none attached to the more wave-exposed Little Papanui shore The barnacle *Elminius modestus* similarly thrives locally in harbours and mildly wave-exposed shores; but I have not found it at Little Papanui.

Other abundant Aquarium Point species not met at Little Papanui include *Parvacmea helmsi, Zeacumentus subcarinatus* and *Saccoglossus otagoensis.* Abundant Point species much sparser at Little Papanui include *Hypsistozoa fasmeriana, Melagraphia aethiops, Ostrea heffordi* and *Pyura pachydermatina.* Sponges and ascidians form much more of the total bulk of sublittoral life at Aquarium Point than at Little Papanui.

Southern N.Z. Features of Little Papanui

The great, thriving kelp beds of *Durvillea antarctica* and *willana* that encircle more surf-exposed rocks of Otago Peninsula are, within N Z., primarily a southern feature Scattered outposts of *D. antarctica* (and also *Lessonia variegata*) occur as far north as Auckland (Dellow, 1955, p. 61), whereas *D. willana* has a more restricted range. *Bostrychia arbuscula* similarly occurs as far north as Auckland (Dellow, 1955, p 60), but at Papanui shows an abundance and luxuriance of growth that is essentially southern *Apophloea lyallii* in southern N Z replaces *A sinclairii* of more northern shores The stouter *Xiphophora chondrophylla* var *maxima* in the South Island replaces *X chondrophylla* var *minus* of the North Island

Of molluscs ecologically in evidence at Little Papanui, *Benhamina obliquata, Mytilus planulatus* and *Aulocomya maoriana* are more abundant in the south, and *Cellana redimiculum* is a southern species (Powell, 1946). The starfish *Calvasterias suteri* has not been recorded north of Bank's Peninsula (Fell, H. B., spoken communication).

GENERAL N Z. FEATURES OF LITTLE PAPANUI

Little Papanui species important on rocky shores throughout New Zealand include *Melarhaphe cincta* and *M. oliveri*; *Elminius plicatus* and *Chamaesipho columna; Mytilus canaliculus* and *Modiolus neozelanicus*; *Splachnidium rugosum* and *Scytosiphon lomentaria*

* * * * *

These generalisations about species abundant or absent at Little Papanui endeavour to spotlight characteristics of a wave-exposed, southern New Zealand rocky shore Exhaustive fauna and flora lists have not been attempted, the emphasis being rather on species in evidence on this or other rocky shores in New Zealand. Wider field-work may modify the picture presented But more serious gaps in knowledge are apparent when we ask, why do certain species require continuous wave-exposure? What modifications enable them to cope with its mechanical force, which allied forms of sheltered shores lack? Favourable features of the wave-exposed habitat are greater oxygenation, more water movement (which may more effectively bring food, remove waste and prevent silting up), less range of temperatures than in land-locked water bodies, and sea water more chemically constant. To be able to participate in such advantages, an organism requires greater power to retain its hold in breaking waves, and sturdier structure, less liable to be torn. But until we have a fuller knowledge of the biology of many species, the relative importance of these or other features is largely conjectural.

Literature Cited

Batham, E. J, "Ecology of Southern New Zealand Sheltered Rocky Shore" *Trans. Roy. Soc. N Z.* (in press).

Carnahan, J A. 1952. "Inter-tidal Zonation at Rangitoto Island, New Zealand." Pacific Science, 6: 35–46.

Chapman, V. J., 1950. "The Marine Algal Communities of Stanmore Bay, New Zealand." Pacific Science, 4: 63–68.

Cranwell, L. M. and Moore, L. B., 1938. "Inter-tidal Communities of the Poor Knights Islands, New Zealand." *Trans. Roy. Soc. N.Z.*, 67: 375–407.

Dellow, V., 1955. "Marine Algal Ecology of the Hauraki Gulf, New Zealand." *Trans. Roy. Soc. N.Z.*, 83: 1–91.

Evans, R. G., 1947. "The inter-tidal Ecology of Selected Localities in the Plymouth Neighbourhood." *Jour. Mar. Biol. Ass.*, 27: 173–218.

Knox, G A., 1953. "The Inter-tidal Ecology of Taylor's Mistake, Banks Peninsula." *Trans. Roy. Soc N.Z.*, 81: 189–220.

Lewis, J. R., 1954–5. "The Ecology of Exposed Rocky Shores of Caithness." *Trans Roy. Soc. Edinburgh*, 62: 695–723.

Moore, H. B., 1935. "The Biology of *Balanus balanoides*. IV Relation to Environmental Factors" *Jour Mar Biol Ass.*, 20: 279–307.

Moore, L B., 1944 "Some Intertidal Sessile Barnacles of New Zealand." *Trans Roy. Soc. N.Z.* 73· 315–334.

Naylor, M, 1954. "A Check List of the Marine Algae of the Dunedin District." *Trans Roy Soc. N.Z* 82· 645–663.

Oliver, W. R. B., 1923. "Marine Littoral Plant and Animal Communities in New Zealand." *Trans N Z Inst*, 54: 496–545.

Parry, G, 1951–2 "The Actiniaria of New Zealand, I and II." *Proc. Cant. Mus.* 6: 83–119 and 121–141.

Powell, A. W. B., 1946. "*The Shellfish of New Zealand.*" Whitcombe and Tombs Ltd

——— 1947. "*Native Animals of New Zealand.*" Auckland Museum Handbook. Unity Press.

Trevarthen, C B, 1953–4. "Features of the Marine Ecology of Little Barrier, Mayor and Hen Islands." *Tane*, the journal of the Auckland University College Field Club, 6: 34–75.

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