The Intertidal Ecology of Taylor's Mistake, Banks Peninsula.

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Summary

A GENERAL description of the Taylor's Mistake area, Banks Peninsula, is given with a discussion of the climatic and tidal data for the region. The method of investigation is outlined and a list of 13 plants and 21 animals selected for special study is given.

The zonation and distribution of each of the species is described with reference to the physiographical features of the habitat, tidal flow and ebb and exposure to wave action.

The vertical zonations of the species in relation to tidal level are summarized and a comparison of the zonation of some of the species is made with that of the same species at Stanmore Bay, Piha and Narrow Neck, in the Auckland region.

The relation of the plants and animals to exposure and submergence is discussed and "critical levels" for species studied at Taylor's Mistake have been recognized. Comparisons are made with the results of similar surveys carried out in New Zealand and Great Britain, and it is concluded that the following regions, as determined by Evans (1947b), are the most critical for intertidal organisms: (1) between M.L.W.N. and M.L.W.S.; (2) in the vicinity of M.L.W.N.; (3) between M.H.W.S. and E.H.W.N. The least critical level on the shore is in the vicinity of M.T.L.

The general distribution of the species studied is discussed in relation to the factors controlling the vertical zonation and horizontal distribution of intertidal plants and animals. The primary causal factors are: (1) the existence of an interface between air and water, which plus wave action, produces the three primary zones, supralittoral, littoral and infralittoral; (2) tidal factors which are responsible for the often sharp upper and lower limits found within the littoral zone. Eight principal factors determining the horizontal and vertical distribution of intertidal organisms are recognized, namely, submergence and exposure; wave action; tidal flow and ebb; type of substrate; topography, including aspect and angle of slope; proximity of sand; climatic factors such as temperature, amount of sunshine, rainfall and wind; competition. It is shown that these factors act in varying combinations and proportions in different localities, for different species and for the upper and lower limits of the same species. Combinations of the primary factors result in secondary limiting factors such as desiccation. The influence of desiccation on intertidal organisms is described and is followed by a discussion of the effects of the primary limiting factors, particularly wave action, as presence or absence factors in the horizontal distribution and as modifying factors in the vertical zonations of the species studied.

CONTENTS

Introduction.

Apart from the general survey of the littoral plant and animal communities of New Zealand by Oliver (1923), there have been no ecological studies of the rocky shores of the South Island. In the North Island Cranwell and Moore (1928) have carried out a survey of the Poor Knights Islands and the first three papers of a series, dealing primarily with the algal zonation of the Auckland Province, have recently been published (Chapman, 1950; Beveridge and Chapman, 1950; Dellow, 1950).

In the present investigation a number of the more common and ecologically important species of plants and animals of the rocky shore are studied with reference to the physiographical features of the habitat, tidal flow and ebb and exposure to wave action. The vertical zonation of the species studied is described in relation to exposure to air and " critical levels " on the shore are recognized.

Although this investigation is concerned with a restricted strip of coast a survey of the rocky shores of the South Island and Stewart Island has been under way since 1948. The Banks Peninsula area as a whole has received special attention, and the general zonation of this area will be the subject of the first of a series of papers on the intertidal zonation of the New Zealand rocky coasts.

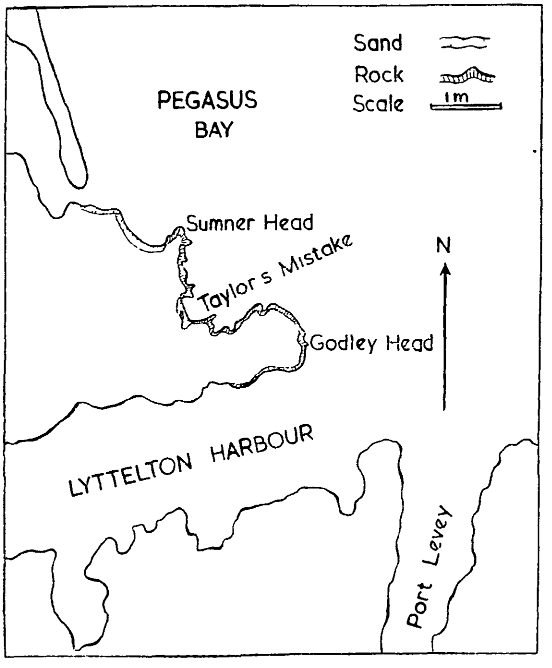


Fig. 1.—Map showing the location of the area studied.

GEOGRAPHY AND GEOLOGY

The region chosen for intensive study was Taylor's Mistake, a small bay on the northern side of Banks Peninsula to the west of the entrance to Lyttelton Harbour (Fig 1) In the centre of the bay, which faces north-east, there is a sandy beach about 250 yards long On either side there is a rocky shore of varied nature with bands of smooth, black basalt alternating with very pitted, vesicular, feldspar basalts. In restricted localities there are bands of reddish weathered scoria.

The different types and layers of rocks at Taylor's Mistake have weathered differentially into jagged reefs and ledges. The angle of slope varies from the horizontal to the vertical. In some areas the intertidal zone is covered by rocks and boulders of varying size. On either side and in the centre of the bay the rock merges into sand at low water; but further out there are steep cliffs descending into the infralittoral

CLIMATIC AND TIDAL DATA

Tidal Data The tides are diurnal, with a range of about 9·5 feet at extreme springs and about 4 feet at extreme neaps. The corresponding times of high and low water are on an average 24 hours 40 minutes later each succeeding solar day. Day and night tides differ slightly in amplitude.

Since there is considerable variation between the predicted heights and recorded levels, tidal levels were calculated from the marigrams obtained by the Lyttelton Harbour tide gauge during 1949. Observations made at Taylor's Mistake showed that there was no significant difference in the tidal ranges. The various levels worked out are shown in the following table. All heights are referred to the Chart Datum for Lyttelton Harbour

TIDAL SCALE FOR TAYLOR'S MISTAKE

	Ft. above or below C.D. (Chart Datum)
E. H. W. S.	8.0
M. H. W. S	7.3
M. H. W. N.	5.7
E. (lowest) H. W. N.	5.1
M. T. L.	3.3
E. (highest) L. W. N.	1.5
M. L. W. N.	0.7
M. L. W. S.	–0.4
E. L. W. S.	–1.5

Tidal Levels and Exposure to Air. The importance of exposure to air as a causal factor in the vertical zonation of plants and animals has been discussed by Chapman (1943), Doty (1946) and Evans (1947a, 1947b). A method of assessing percentage exposure per year at each level has been described by Colman (1933), and this method has been used here.

Four fortnights were chosen in 1949, including two high springs and two high neaps—i.e :

(1) January 2nd to 16th (Mid-summer).

(2) March 16th to 30th (Autumn Equinox)

(3) May 25th to June 9th (Mid-winter).

(4) September 15th to 29th (Vernal Equinox).

For each period the marigrams from the Lyttelton Harbour tide gauge were redrawn on squared graph paper. From each graph the hours of exposure at each level for the fortnight were calculated, and by multiplying by the requisite number of days the total exposure for the year at each level was worked out. These figures were divided by 8,760 (= number of hours per year) and a percentage figure was obtained. The above figures are shown graphically in Fig. 2.

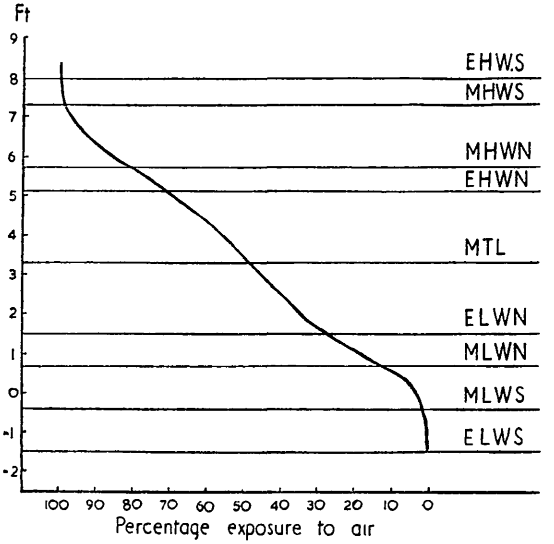


FIG. 2.—Percentage exposure to air at different levels.

This graph shows the same general form as those of Colman (1933, Fig. 10, p. 459) and Evans (1947, Fig. 7, p. 281). Chapman (1943) points out that the difference in the rate of change of percentage air exposure, from level to level, is most marked in the neighbourhood of E.H.W.N. and E.L.W.N. At Taylor's Mistake the rate of change is greatest between M.L.W.N and M.L.W.S and between M.H.W.S. and M.H.W.N.

Wind. The prevailing winds are north-east and south-west. Practically 90% of the winds blow from these directions in approximately equal amounts. Winds are generally of a strength 1 to 3 on the Beaufort Scale. On 97 days out of 365, winds of a strength 4 to 7 are experienced. Gales are not frequent.

Wave Action. This varies from day to day and locally with the degree of shelter afforded by reefs, headlands, etc. Taylor's Mistake faces north-east, and consequently is exposed to the prevailing easterly winds. It is, however, sheltered from the southerly winds, which are generally stronger than the easterly. The action of the surf is at its maximum on exposed rocks facing north-west. On the west side of the bay the area near the beach is sheltered from direct wave action by a jutting headland. The slope of the shore also has an effect; where this is gentle surf action tends to be less violent

The coast of Banks Peninsula is subject at times to considerable ocean swell, especially when the wind is from the easterly quarter. On the outer coasts this swell is seen to sweep along the shore instead of curving in and breaking on the rocks The absence of shelving floors at the foot of the cliffs prevents the refraction of the waves with the dissipation of their energy on shelving beaches.

Turbidity. The bottom deposits offshore consist of loess silt and sand. The former deposit is quickly stirred up by wave action, and consequently the water inshore is often laden with fine suspended material, which must have a considerable effect on light penetration. The sandy beach in the centre of the bay is subject to considerable alteration by tidal currents and wave action, the sand level on the inshore rocks varying up to two feet after a heavy sea. The covering of the lower levels of the rocks has a limiting effect on most of the attached organisms.

Rainfall. The average annual rainfall is 24 4 inches. It is fairly evenly distributed throughout the year, the period of maximum rainfall being May-July. The driest periods are February and September-October.

Sunshine. The average annual number of hours of sunshine is 2,002 hours. The sunniest period is November-January.

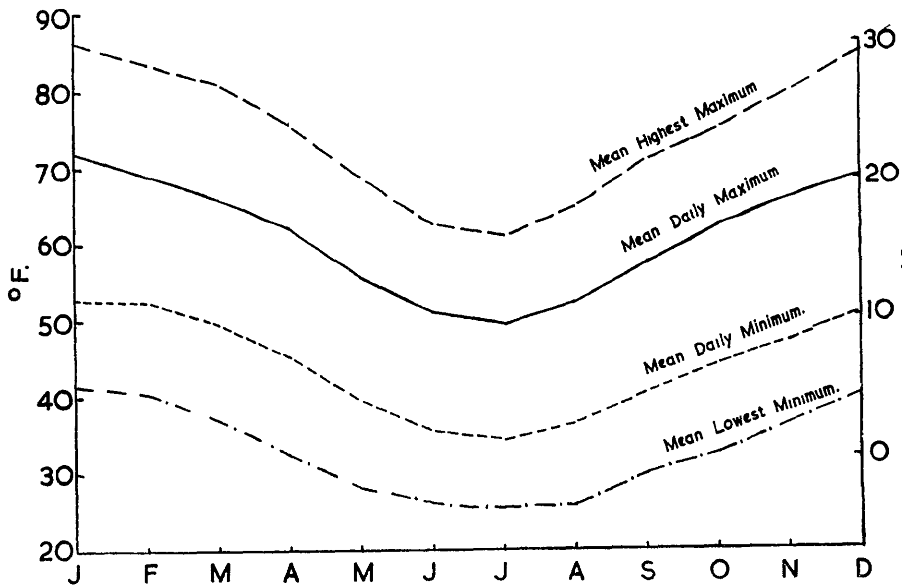


FIG 3.—Mean monthly air temperatures for Christchurch, 1864-80, 1905-45

Air Temperature. In Fig. 3, the graphs of the monthly means, mean daily maximum and minimum, mean lowest minimum and mean highest maximum, for Christchurch from 1864–80 and 1905–45 are shown. The mean annual range of 16·8° F. (9·0° C.) is not very great. However, from the point of view of the distribution of intertidal organisms the extremes of temperature are important. The difference between the highest, 95·7° F. (35·5° C.) and the lowest, 19·3° F. (–7 1° C.), temperatures recorded is 74·6° F. (41·5° C.). Variations in a single day range from 37° F. (20 5° C.) to 4° F. (2·2° C.). Local variation of temperature with the amount of shade, angle of slope and aspect is important. Temperatures on the rock surface may reach a higher temperature than the surrounding air temperature; the maximum temperature recorded on the rock surface was 84·5° F. (29·0° C), the temperature of the air several feet away being 5·0° F. lower.

Fig. 4.—Monthly mean sea temperatures as recorded near the entrance to Lyttelton Harbour

Sea Temperature. Fig. 4 graphs the monthly mean sea temperatures as recorded near the entrance to Lyttelton Harbour (latitude 43° S.) by the Government motor vessel " Maui Pomare," during the period 1929–40. The annual variation of the mean temperature is 12·5° F. (6 9° C.). Records of the sea temperature near the shore were made during the period of the investigation The lowest temperature recorded was 48 2° F. (9 0° C.), in July and the highest 68·0° F. (20·0° C.) in January. This gives an annual range of 19 8° F. (11 0° C.). The highest diurnal variation recorded was 9·0° F (5 0° C).

Method of Investigation

The area under investigation was visited at least twice a month for a period of 18 months. On several occasions visits on consecutive days were made over periods of up to one week. This enabled observations to be made in all types of weather and under varying tidal conditions. The relation of the organisms selected to tidal levels was studied by the method used by Evans (1947) This method involves the direct observation of tidal heights, the results obtained by Evans showing a high degree of accuracy, providing the observations are made on a calm day and the levels checked on different days and at different states of the tide (springs and neaps).

Starting from the high water mark, the area studied was traversed horizontally, along the water line, every half-hour during the first and last 90 minutes, and every quarter hour during the middle of the ebb tide. Notes as to the presence and absence, abundance and distribution of the various species were made during each traverse. The tidal data were obtained from records of the Lyttelton Harbour tide gauge, and the height of each traverse was calculated from the " New Zealand Nautical Almanac " (p. 110). Actual measurements were also made on vertical faces.

The following species were selected for special study with reference to tidal level, exposure and submergence, exposure to wave action, rock configuration and relationship to other organisms.

CHLOROPHYCEAE
Codium adhaerens (Cabr.) Ag. var. *convolutum* (Dellow).

PHAEOPHYCEAE
Cystophora scalaris J. Ag.
Colpomenia sinuosa (Roth.) Derb et Sol.
Carpophyllum maschalocarpum (Turn.) Grev.
Durvillea willana Lindauer.
Macrocystis pyrifera (L.) C. Ag.
Ralfsia verrucosa Aresch.
Scytothamnus australis H. et H.
Splachnidium rugosum (L.) Grev.

RHODOPHYCEAE
Bostrychia arbuscula H. et H.
Corallina officinalis L.
Laurencia heteroclada Harv.
Polysiphonia implexa H. et H.

ANIMALS

CRUSTACEA
Chamaesipho columna Spengler
Elminius modestus Darwin
Elminius plicatus Gray

POLYCHAETA
Pomatoceros coeruleus (Schmarda)

MOLLUSCA
Aulacomya maoriana (Iredale)
Buccinulum strebeli (Suter)
Cellana ornata (Dillwyn)
Cellana radians (Gmelin)
Lepsia haustrum (Martyn)
Lepsiella scobina albomarginata (Deshayes)
Melagraphia aethiops (Gmelin)
Melaraphe cincta (Quoy and Gaimard)
Melaraphe oliveri Finlay
Modiolus neozelanicus (Iredale)
Mytilus canaliculus Martyn
Mytilus planulatus Lamarck
Notoacmea parviconoidea (Suter)
Patelloida corticata (Hutton)
Rizellopsis varia (Hutton)
Sypharochiton pelliserpentis (Quoy and Gaimard)

TUNICATA
Pyura pachydermatina (Herdman)

DISTRIBUTION OF THE SPECIES STUDIED

The following terms referring to the degree of exposure to wave action are used in the discussion below:—Very exposed, exposed, semi-exposed, sheltered, very sheltered.

Flora

Cystophora scalaris. Range: E.L.W.N to below E.L.W.S.; 25% to 0·0% exposure.

This species is characteristic of the infralittoral fringe in sheltered to semi-exposed situations. Where wave action is strong it is absent. It is also absent on the rocky shore adjacent the sandy beach where there is considerable scour. Its upper limit is rather well defined, an occasional plant only being found above E.L.W.N. Above this level, however, it colonizes rock pools, especially on level platforms sheltered from direct wave action. Here, mixed with *Carpophyllum maschalocarpum,* it forms a dense fringe round the edge of the pools.

Carpophyllum maschalocarpum. Range: E.L.W.N. to below E.L.W.S.; 25% to 0·0% exposure.

The distribution of this species is very similar to that of *C. scalaris,* the two species being generally found together with *C. maschalocarpum* numerically more important. It is somewhat more tolerant of exposure to surf than *C. scalaris,* and is found on very exposed coasts where the main force of the waves is broken by rocks and ledges The presence of a stony beach, subject to movement, in many localities prevents the development of both species.

Where the *Carpophyllum* zone is well developed the upper limit is rather sharply defined at E.L.W.N., with an occasional plant higher up. On outer coasts, sheltered from direct wave action, but subject to a strong surge, the upper limit of the zone may be elevated several feet. The lower limit lies below E.L.W.S., never reaching more than two feet below.

Macrocystis pyrifera. Range. M.L.W N. to below E.L.W S.; 10% to 0 0% exposure.

The presence of this brown kelp is a characteristic feature of the stretch of coast studied. A *Macrocystis* zone is usually well developed except, (a) on outer very exposed coasts, (b) on vertical more or less wave beaten faces and (c) where the rock is replaced by sand near the low water mark. Relatively deep water is required for the development of the species, the holdfasts occurring up to 50 feet below E.L.W.S. The floating fronds form a conspicuous band stretching up to 250 feet out from the low water mark Its upper limit is well marked at M.L.W.N. and the best development occurs from M.L.W.S down. Unlike the other local kelps (*Cystophora, Carpophyllum, Durvillea willana* and *D. antarctica*) *Macrocystis* is tolerant of a wide range of conditions of exposure to wave action, being common in the most sheltered situations where the water is deep enough. Under such conditions, where there is very little swell, the upper limit does not extend above M L.W.S.

Durvillea willana and *Durvillea antarctica.* Range: M.L.W.N. –0 5ft. to below E.L.W.S.; 15 0% to 0 0% exposure

On the outer exposed coast these are the best developed of the kelps, being indicators of localities subject to strong wave action. In such localities there is usually a band of *Durvillea* from M L W.N. down, unless the rocks end in steep plunging cliffs Thick growths occur where the rock surface is sloped, the plants being absent from level platforms. Optimum development is found on the rocky broken points of exposed headlands. Fairly deep water immediately offshore is necessary for the growth of *Durvillea* as it is absent where there is sand near the low water mark.

The upper limit of the *Durvillea* zone is generally clearly defined at M.L.W.N. In situations where there is a strong surge the upper limit may extend up to 1·5 feet above this level. The lower limit is also clearly defined, lying just below E.L.W.S. Where *Durvillea* is growing on smooth, steep slopes it is often the single dominant species with a poor underflora consisting almost entirely of " Lithothamnion ". In semi-exposed situations the " Lithothamnion " is replaced by species of *Corallina, Gigartina,* other red algae and *Halopteris.* Where the rock is rough and broken *Durvillea* is co-dominant with *Mytilus canaliculus,* with which it competes for space, the spaces between the holdfasts having a dense carpet of mussels.

Both species of *Durvillea* may occur together or one species may be locally dominant. *D. antarctica* appears to be somewhat more tolerant of wave action than *D. willana.* The type of substrata also has an effect on the development of these species, *D. willana* being absent from steep, smooth faces where *D. antarctica* occurs in abundance. Where the species occur together they may be mixed throughout their vertical range, or *D. willana* may form a band on the seaward side of *D. antarctica.* This separation of the two species into two distinct sub-zones is particularly noticeable where flat rocks occur in the region of M.L.W.S.

Codium adhaerens var. *convolutum.* Range: E.H.W.N. –1 0ft. to M.L.W.N. –0·3ft.; 60% to 10% exposure.

The distribution of this species is rather scattered, being determined by the amount of shade and the degree of exposure to wave action. It does not grow on faces exposed to direct sunlight, being well developed on the west shaded side of the bay. On faces that do not receive any direct sunlight the upper limit of the species is elevated to M.H.W.N. *C. adhaerens* does not tolerate strong wave action, being confined mainly to sheltered situations, with local occurrence in regions of moderate exposure. The flattened, fleshy growths of this species are best developed on more or less vertical faces and grow well on smooth surfaces. Where the patches of *Codium* spread over the rock surface all other plants and animals are excluded, apart from epiphytic algae such as *Colpomenia* and the herbivorous gastropods, *Onchidella patelloides, Lunella smaragada, Rizellopsis varia* and *Siphonaria australis.* Often a bare area of rock surrounds the radiating growths of this species. Dellow (1950) states that at Narrow Neck *Codium* grows over the sandy Sabellid and calcareous *Pomatoceros* tubes. At Taylor's Mistake no such growth has been observed on the *Pomatoceros* tubes.

Bostrychia arbuscula. Range: M.H.W.S. to M.H.W.N.; 98% to 82% exposure.

This is another shade loving species attaining its best development on the west shaded side of the bay, where it forms a conspicuous band above the main barnacle growth. In moist shaded crevices the upper limit may extend up to 1·5 feet above M.H.W.S. The lower limit appears to be relatively constant, occurring above the " Barnacle-line ", where the main growth of *Chamaesipho columna* ends. Scattered specimens of barnacles may occur in the *Bostrychia* band. This alga does not tolerate direct wave action, being found only in sheltered and semi-sheltered situations. It is tolerant of freshwater seepage from above.

Corallina officinalis. Range: M.H.W.N. –0·3ft. to below E.L.W.S.; of 75% to 0 0% exposure

This cosmopolitan species is extremely tolerant with regard to intensity of surf action and the nature of the substratum. It occurs in pools at all levels up to E.H.W.S., forming a dense fringe round the edges of the deep pools on the lower half of the shore and covering the bottoms of the shallower ones. The upper limit of the species is rather variable, depending on the degree of exposure to wave action and the type of substrate. In sheltered areas it may extend up to E.H.W.N., growing on the barnacle encrusted rock; but on the open shore, as found by Evans (1947a), it is more characteristic of the levels below M. T. L. At Taylor's Mistake, as at Cardigan Bay, Wales, it is one of the most tolerant of the littoral algae with regard to wave action. On steep, exposed, vertical faces it may often be the only alga present, forming a turf of short plants from the lower limit of the barnacles down to E.L.W.S., and extending into the infra-littoral.

On the open coast *Corallina* may also form the main species of the underflora of the *Durvillea* zone, extending as a thick carpet on the rock surface below *Cystophora* and *Carpophyllum* in the less exposed areas. It is also present in the most sheltered situations and extends to the rocks near the sandy beach, being tolerant of periodic coverage by sand. It grows equally well on all types of substrate, including soft red scoria on which other species are absent. Where patches of this rock occur the upper limit of *Corallina* zone may be several feet higher than on the adjacent basalt rocks.

FAUNA

Barnacles. Three species of barnacle, *Chamaesipho columna*, *Elminius plicatus* and *Elminius modestus* occur abundantly in the region studied. Of these *C. columna* and *E. plicatus* are ecologically the most important, being the dominant animals of the midlittoral region, except in sheltered areas.

Chamaesipho columna. Range: M.H.W.S. -0·5ft. to M.L.W.N.; 90% to 10% exposure

Elminius plicatus. Range: Between M.H W.N. and E.H.W.N. to M.L.W.N.; 75% to 10% exposure.

The development of the barnacle zone depends on the degree of exposure to direct wave action and on the configuration of the rock surface. On very exposed rocks, especially on vertical faces, the midlittoral zone, from M.H.W.S. down to M.L.W.N., is populated almost exclusively by *C. columna,* which forms a close mat with the individuals touching each other on all sides. In localities subject to less intense wave action, in exposed to sheltered situations, *E. plicatus* is found competing with the former species for space.

C. columna is typically dominant on the upper shore, having a higher upper limit than *E. plicatus.* Usually the upper limit of the latter species does not extend above M.H.W.N. On the shaded west side of the bay where the rock face receives direct sunlight only in the early morning, the upper limit of *E. plicatus* extends up into the zone occupied by *Bostrychia arbuscula,* as far as E.H.W.S., with a few isolated individuals up to 18 inches above this level. The distribution of *E. plicatus* in this upper region is more scattered than in the lower, individuals occurring singly or in small clumps, never forming mats. It is also noticeable that the individual barnacles are considerably smaller than those lower down on the shone. The height reached by *C. columna* is more variable than that of *Elminius* and may extend up to six feet above the upper limit reached by the latter species.

The upper limit of the barnacles in quantity, the "*Chamaesipho*-line," is best seen on steep, exposed faces, where it is sharply defined, the thick barnacle cover ending abruptly. The level of the "*Chamaesipho*-line" varies in height in relation to the intensity of surf experienced, as noted by Evans (1947b) for the "*Chthamalus*-line" on the English shore. In sheltered localities the upper limit lies in the region of M.H.W.S., while on steep, semi-exposed faces it reaches up to E.H.W.S. Where the rocks are exposed to strong wave action the effect of the surf is to raise the upper limit considerably. This is particularly evident on sloping rock faces where the waves run up the shore as they break. Here the upper limit of the barnacles may extend up to several feet above E.H.W.S. On one shaded, exposed, sloping face, on the west side of the bay, with an angle of about 45° the upper limit reached by the barnacles is 20 feet above M.L.W.N. The lower limit of the barnacle zone is also frequently marked by a barnacle line on exposed vertical faces. This line is, however, not as clearly marked as the upper one, and varies with the amount of exposure to direct wave action. On very exposed faces the barnacle zone extends down to the upper limit of *Durvillea* at about M.L.W.N. In some localities, however, there is a band of pink "*Lithothamnion*" extending up to 18 inches above the upper limit of the bull kelp; in others there is a similar band of *Corallina*. The presence of these calcareous algae appears to limit the downward extension of the barnacles. With increase in shelter the upper limit of the algal zone of the infralittoral fringe is raised and the lower limit of barnacles in quantity ends at E.L.W.N., with scattered individuals extending down to M.L.W.S. Evans (1947a) and Moore (1935) both note the effect of surf in lowering the lower limit of *Balanus*, the English equivalent of the local species. The same effect is noted for *C. columna* and *E. plicatus*. This may be partly due to competition with algae and mussels with increasing shelter or, as Moore (1935) suggests, to the increased aeration of the water that occurs where surf action is strong.

The nature of the rock surface bears a direct relationship to the density of the barnacle cover; smooth, polished rocks may be completely bare, while adjacent rough rock may have a dense population. Movable material has an adverse effect on the development of both *Chamaesipho* and *Elminius*, barnacles being absent or sparsely represented on the boulder beaches, where the abrasive action of the shifting rocks destroys the newly settled larvae.

The negative correlation between barnacle and brown algal distribution noted by British workers (Moore, 1935; Evans, 1947b) does not occur in the areas studied. The main species of algae in the barnacle zone, *Scytothamnus, Adenocystis, Colpomenia, Ulva* and *Porphyra* are of seasonal occurrence, and the year round breeding season enables the barnacle larvae to become established in the absence of the algae. However, as mentioned above, there is a negative correlation between barnacle development and the growths of *Codium adhaerens*. This latter species occurs only locally in the lower half of the barnacle zone.

Elminius modestus. Range: M.T.L –1 0ft. to below E.L.W.S.; 55% to 0 0% exposure.

This species, although common throughout the area studied, does not form a dense cover except under special circumstances It is not tolerant of strong wave action, being absent in semi-exposed and exposed situations, but characteristic of the more sheltered regions. As mentioned by Moore (1944) and Dellow

(1950) its most striking ecological attribute is its ability to withstand brackish and very muddy water. Thus it is found high on the shore, often above the upper limit of the other species, where fresh or brackish water seeps over the rock surface. The upper limit of *E. modestus* normally lies about a foot above M.T.L., while its lower limit, unlike that of the other species of barnacle, extends down below E.L.W.S. It also differs from the other species in that it can tolerate shade to a much greater extent, being found on the under sides of fixed boulders. When the lower parts of stones are buried in the sand or mud there is usually a thick fringe of *E. modestus* around the embedded edge. This ability to tolerate coverage by sand and mud is another characteristic of this species, enabling it to colonize substrata, such as level platforms, that may be covered by fine sand or silt. *E. modestus* is also a characteristic species of the mussel beds of the lower portion of the midlittoral zone and the infralittoral fringe, often forming a dense cover on the shells of *M. planulatus* and *M. canaliculus.* In some localities few specimens of the mussels are without a few attached *Elminius.*

Melaraphe oliveri. Range: E.H.W.S. + to about M.T.L.; 100% to 50% exposure.

The habits and habitat of this species are very similar to those of the British species *Littorina neritoides.* The supralittoral zone above E.H.W.S. is populated almost exclusively by *M. oliveri,* in addition to *M. cincta* in some localities. It is absent where the upper parts of the beach are covered with movable boulders; but abundant on rock masses, headlands and cliffs, especially on steep, rough, exposed faces. The species occurs in decreasing numbers from semi-exposed to sheltered situations, being scarce or absent under conditions of extreme shelter. It is also absent where the water is normally laden with muddy sediment as in the upper reaches of Lyttelton Harbour. Shade favours the development of a *M. oliveri* zone, the upper limit extending up considerably higher on rock faces that are normally shaded. On faces exposed to direct sunlight the snails are restricted to cracks and crevices.

The upper limit of distribution is extremely variable, depending on the amount of shade and the degree of exposure to wave action. On one very exposed, shaded, steep stretch of coast, where there is considerable splash, keeping the cliff face constantly moist, specimens have been found up to 48 feet above C.D. (i.e., E.H.W.S. + 40ft.). On sunny faces, however, the upper limit extends about 10 feet above E.H.W.S. The optimum lower limit lies at about M.T.L. + 1·0ft. Below this point scattered individuals are found, especially where there is a good cover of barnacles.

Melaraphe cincta. Range: E.H.W.S. + to E.H.W.N.; 100% to 75% exposure.

The vertical range of this species is more restricted than that of *M. oliveri.* The lower limit is relatively constant at E.H.W.N., while under sheltered shaded conditions its upper limit is a little lower than that of *M. oliveri.* This snail prefers rather more sheltered conditions than *M. oliveri,* and is best developed on irregular broken rock with plenty of cracks and crevices. It is also more tolerant of water laden with fine sediment, being found further up Lyttelton Harbour than *M. oliveri.*

Melagraphia aethiops. Range: E.H.W.N. –0·5ft. to M.L.W.S.; 60% to 0·0% exposure.

Melagraphia is intolerant of exposure to surf, and is found on the open rock surface only in sheltered situations. On broken surfaces it may be found in crevices and on the landward side of projecting rocks and ledges, where there is a degree of local protection from surf action. The favourite habitats of the species are boulder banks, where it is often the most abundant species in the spaces between the stones, areas of flat rock near M.T.L. and among the brown algae between E.L.W.N. and M.L.W.S. In the range of habitats *M. aethiops* resembled the European species *Gibbula umbilicus,* which prefers stony gullies, boulder areas and flat rocks (Evans, 1947). The vertical ranges of the two species are also similar, that given by Evans for *Gibbula* being from E.H.W.N. to M.L.W.S.

The upper limit of *M. aethiops* generally lies below E.H.W.N., although in rock pools it may be found as high as M.H.W.S. It is generally most abundant between M.T.L. and E L.W.N. The lower limit is rather variable, depending on the type of cover. It is absent from areas covered by *Corallina* and among the mussel beds, but plentiful among the brown weeds, *Carpophyllum* and *Cystophora,* down to E.L.W.S.

Lepsiella scobina albomarginata. Range: M.H.W N. + 0 5ft. to midway between M.T.L. and E.L.W.N.; 85% to 40% exposure.

Throughout the midlittoral zone this is the most abundant gastropod, occurring in large numbers throughout the upper barnacle zone. Barnacles appear to form its main article of diet and there is a definite correlation between the distribution of *Lepsiella* and that of the barnacles, especially *C. columna,* the snail being more abundant on growths of the small *Chamaesipho* than on the larger *Elminius plicatus.* The small black bivalve *Modiolus neozelanicus* also forms part of the diet of *Lepsiella,* which occurs throughout the zone occupied by *Modiolus,* although not as abundantly as on barnacle covered rocks.

Lepsiella resembles the species *Nucella lapillus,* which occupies a similar ecological niche on the British coast, in that while it is more tolerant of waves and surf than the Trochidae, it still requires a certain amount of local shelter in barnacle areas (Evans, 1947a). Where the wave action is strong *Lepsiella* is absent from vertical exposed faces, but is present in large numbers in crevices and on the landward sides of rocks and boulders.

The upper limit of the species generally lies midway between M.H.W.S. and M.H.W.N., although in situations where the height of the barnacle zone is extended upwards by wave action the upper limit may be raised considerably. The lower limit is rather more variable. In the area studied the lower limit of *Lepsiella* in quantity lies about halfway between M.T.L and E.L.W.N., although occasional specimens are found down to the lower limit of the barnacles at M.L.W.N. On other parts of the coast of Banks Peninsula the lower limit may extend down to M.L.W.N.

Sporadically throughout the region studied there occurs a colour variety of the species with a reddish orange interior to the shell opening. This is regarded as a sub-species *Lepsiella scobina rutila;* but appears to be simply a colour variety of the sub-species *albomarginata,* as the two occur on the same rock surface, with the variety *rutila* much less numerous.

Sypharochiton pelliserpentis. M.H.W.S. to E.L.W.S. -0 5ft.; 95% to 0·0% exposure.

This is one of the most ubiquitous animals on the shore, ranging from conditions of extreme exposure to those of extreme shelter. It extends practically throughout the inter-tidal zone, and is tolerant of a wide range of substrates and conditions of shade. In habits and habitat this species resembles the limpets *Cellana radians* and *C. ornata,* occupying a similar ecological niche.

The upper limit of the species generally lies at M.H.W.S., although occasional individuals may be found above this point, especially on well shaded faces. Exposure to wave action, with consequent increase in the amount and height of splash, raises the upper limit several feet, coinciding with that of the barnacles From M.H.W.S. down to the upper edge of the kelp zone of the infralittoral fringe, *Sypharochiton* is evenly distributed, except where *Pomatoceros* encrustations and dense mats of *Modiolus* occur. It is common among the mussel beds of both the lower midlittoral and the infralittoral fringe; but is rare where there is a thick covering of algae, except in the holdfasts of *Durvillea.* The lower limit lies a few inches below E.L.W.S.

Throughout the barnacle zone this species competes with the barnacles for space, and where dense growths of the latter occur it is often confined to cracks and crevices. Its articulating shell enables it to cling to very irregular surfaces that are not suitable for the attachment of limpets. With regard to slope and type of substrate *S. pelliserpentis* is extremely tolerant; it occurs on all types of surface, from very rough pitted rock to smooth polished surfaces; is common on all angles of slope, even under overhangs, and is plentiful on the undersides of boulders.

The shells of specimens on the lower region of the shore are often encrusted with "*Lithothamnia,*" while those of the upper regions are usually deeply eroded. *Sypharochiton* is also a common inhabitant of rock pools, especially those high on the shore, being found in lithothamnia-encrusted pools above E.H.W.S.

Limpets. Three species of *Cellana, C. radians, C. ornata* and *C. redimiculum,* occur within the region, the latter having a restricted local distribution. Other common species of limpets are *Patelloida corticata, Notoacmea pileopsis, Notoacmea parviconoidea, Notoacmea daedala* and *Atalacmea fragilis.* In addition there occur four species of the limpet-like Siphonariidae, *Siphonaria australis, Siphonaria zelandica, Siphonaria cookiana* and *Benhamina obliquata.* As it is planned to deal with the distribution and ecology of these species in a subsequent work, the zonation of a few selected species will be briefly summarized.

Cellana ornata. Between E.H.W.S. and M.H.W.S. to E.H.W.N. –; 95% to 60% exposure.

This species is characteristic of the upper region of the midlittoral zone. Its upper limit generally lies below E.H.W.S.; but where conditions of shade and moisture are suitable it may be, with the exception of the Littorinids, one of the highest animals on the shore. It is found from sheltered to exposed situations, being highly characteristic of the latter, and typically prefers rough rock surfaces. The lower limit in quantity lies between E.H.W.N. and M.T.L., although individuals may be found below these levels.

Cellana radians. Range: M.H.W.N. to E.L.W.S.; 80% to 0 0% exposure.

This limpet is less tolerant of exposure than *C. ornata,* being more characteristic of situations where there is local shelter from direct wave action. It also differs in that it is common on the undersides of boulders and on smooth polished surfaces. Its zone of abundance begins where *C. ornata* decreases in numbers and is common right down to E.L.W.S., except where there is a thick covering of algae. *C. radians* is also common in rock pools up to above E.H.W.S.

Notoacmea parviconoidea. Range: M.H.W.S. to E.L.W.S.; 95% to 0 0% exposure.

Notoacmea occurs throughout the inter-tidal zone in situations ranging from extreme shelter to extreme exposure. The upper limit is variable, depending on the amount of shade and splash. Where conditions are suitable the species may be found up to several feet above E.H.W.S.

Patelloida corticata. Range: E.L.W.N. + 1 0ft. to E.L.W.S.; 40% to 0 0% exposure.

Patelloida is characteristic of exposed situations, especially on vertical rock faces above the upper limit of the infralittoral fringe. Here there is often a band of " Lithothamnion " about 18 inches wide between the upper limit of the algae and the lower limit of the barnacles. Large numbers of *Patelloida* with lithothamnion-encrusted shells are found in this zone.

Mytilus canaliculus. Range: E.H.W.N. -1 0ft. to below E.L.W.S.; 60% to 0 0% exposure.

M. canaliculus, the green mussel, can be regarded as an indicator species of localities subject to strong wave action, being characteristic of the infralittoral fringe of the outer exposed headlands. With increase in shelter the species is less frequent and is replaced by *M. planulatus* and species of red and brown algae.

Although isolated specimens and small clumps may be found up to a foot above M.T.L. the optimum upper limit of the species in quantity lies at about E.L.W.N., just above the upper limit of the brown kelps. Where *M. canaliculus* and *M. planulatus* overlap the former species is dominant in the lower part of the " mussel zone " from M.L.W.N. down, while the latter is dominant in the upper part between E.H.W.N. and M.L.W.N. Although scattered individuals of one species may be found in the band occupied by the other, the transition between the *M. canaliculus* and *M. planulatus* zones is usually sharply defined. The development of both species is favoured by surf as noted by Fischer (1929) and Newcombe (1935) for *Mytilus edulus* and by Guiler (1950) for *M. planulatus.* Dense beds of *M. canaliculus* are also only found where the water is comparatively clean, being replaced by beds of *M. planulatus* where the water is muddy.

Beveridge and Chapman (1950) recognize a *Durvillea-Mytilus* association at Piha, occurring in the form of two separate consociations dominated either by *Durvillea* or *Mytilus,* the two species appearing to be antagonistic to each other. This antagonism has not been observed at Taylor's Mistake, *Durvillea* and *Mytilus* usually occurring together. Where one of these species occurs alone the angle of rock slope and the type of substrate is generally responsible for the absence of the other. On broken, exposed headlands, where a good growth of *Durvillea* is usually found, the spaces between the holdfasts are covered with densely packed mussels often several layers deep. The older mussels often have deeply eroded shells and bear encrusting coralline algae. The densest beds are found where there are platforms and projecting broken rock below M.L.W.N.

M. canaliculus is absent on smooth, vertical, exposed faces, being replaced by " Lithothamnia " and other species of red algae. The species is also found well into the infra-littoral, growing abundantly in several fathoms of water.

Mytilus planulatus. Range: E.H.W.N. + to M.L.W.S. + 0·5ft.; 75% to 10% exposure.

This species is more characteristic of the midlittoral zone and of regions of moderate exposure to wave action. It is also much more tolerant of shelter than *M. canaliculus.* Optimum development in the form of extensive beds, from E.H.W.N. down to just above M.L.W.N. is seen on semi-exposed faces and platforms where there is a considerable amount of wave movement. Under such conditions *M. planulatus* competes with barnacles for space and mussel beds are absent on steep, smooth faces, which are colonized almost exclusively by barnacles, but are well developed on broken or fissured rock where the dense growth of mussels prevents the barnacles from colonizing the rock surface. Barnacles, however, are abundant on the shells of the mussels, *E. modestus* being characteristic of the lower part of the *M. planulatus* zone and *E. plicatus* of the upper part.

M. planulatus is more tolerant of shade than *M. canaliculus,* growing well under overhangs. It can also tolerate muddy water and sediment to a much greater extent, penetrating considerably further up Lyttelton Harbour. In sheltered situations, where the *Pomatoceros* encrustations are developed, *M. planulatus* is restricted to a narrow band, a foot to eighteen inches in vertical height, above the upper limit of the *Pomatoceros* zone.

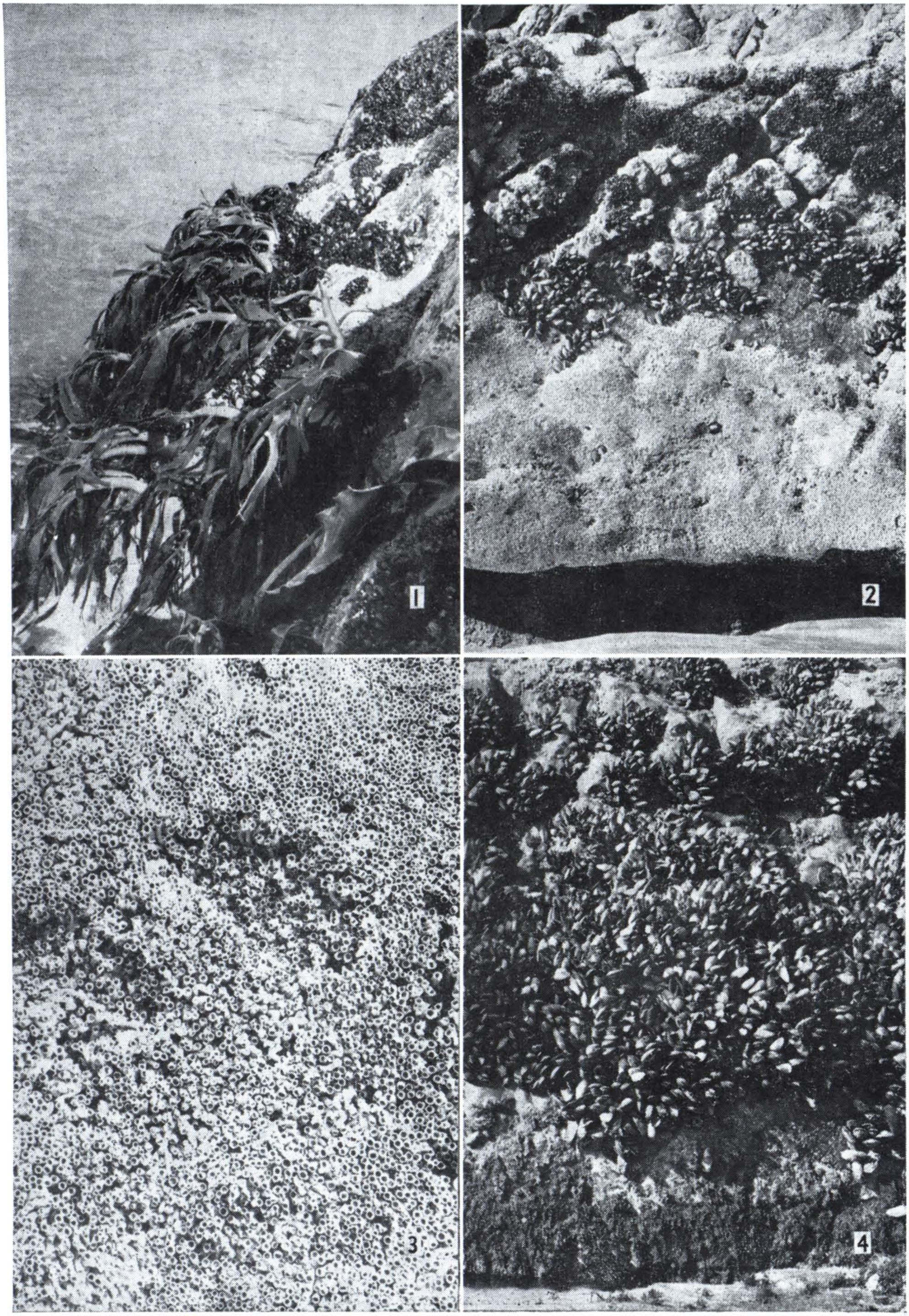
The lower limit of the *M. planulatus* zone is usually well defined, lying about half way between M.L.W.N. and M.L.W.S.; below it is replaced by thick growths of algae, or by *M. canaliculus.*

Aulacomya maoriana. Range: E.H.W.N. - 1·0ft. to below E.L.W.S.; 60% to 0·0% exposure.

This species, the ribbed mussel, has a much more scattered distribution than the previous mussel species. It is found singly or in scattered clumps throughout the lower midlittoral zone and the infralittoral fringe, never forming a closed community as to *M. canaliculus* and *M. planulatus. Aulacomya* grows well on a wide range of substrates, from smooth rock faces to stable boulder banks, and is tolerant of varied conditions of exposure, being found on very exposed headlands and in sheltered muddy situations. It also differs from *M. canaliculus* and *M. planulatus* in that it is common on the undersides of boulders.

Modiolus neozelanicus. Range: M.H.W.N. + to E.L.W.N. - 1·0ft.; 85% to 40% exposure.

This species is extremely tolerant of a wide range of environmental conditions, occurring on all types of substrate in situations of extreme exposure to those of extreme shelter. It resembles *E. modestus* in that one of its most striking ecological attributes is its ability to withstand brackish and muddy water. It penetrates right to the upper end of Lyttelton Harbour, where it is found on level platforms that are covered by a layer of silt and mud. *M. neozelanicus* can also tolerate coverage by sand to a much greater extent than any of the other dominant sessile animals of the littoral zone. Thus *Modiolus* is able to colonize rock surfaces, between M.H.W.N. and M.L.W.N. that subject to periodic coverage by shifting sand, and is often the only species in such situations. On isolated rocks projecting from the sand in the centre of the bay *Modiolus* is well developed on the sides and forms a compact mat on the flattened tops where sand accumulates.



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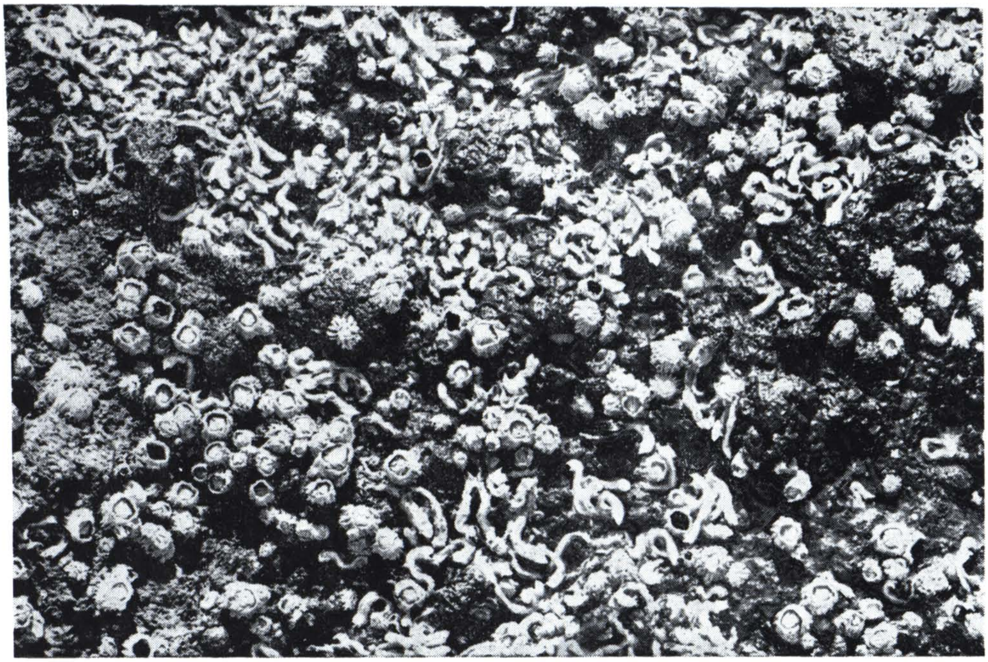

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The development of a *Modiolus* zone depends largely on the degree of exposure to wave action. In exposed situations the species competes with *C. columna, E. plicatus* and *M. planulatus* both for space and for food, while in sheltered regions it competes with *Pomatoceros coeruleus.* On sheltered faces where *Pomatoceros* encrustations are developed the vertical range of *Modiolus* is very much restricted, forming a vertical band, about 2 feet wide, from between M.H.W.S. and M.H.W.N. down to E.H.W.N. On the open exposed coast, on the other hand, the lower limit lies well below E.L.W.N. and the upper limit varies considerably with the degree of wave action.

On steep, vertical, exposed faces *Modiolus* forms a band, about 6 feet wide, commencing about 3·5 feet above the upper limit of the infralittoral algae. Throughout this band *Modiolus* is mixed with *C. columna,* the greatest density of the former occurring in a band about 2 feet wide, between 4·5 and 6·5 feet above the upper limit of the algae. Surf has the same effect on the upper limit of this bivalve as on that of the barnacles. On the sloping exposed face on the west side of the bay, mentioned above in connection with the distribution of *C. columna,* the upper limit of *Modiolus* lies about 18 feet above the upper limit of the infralittoral fringe, to within 3 feet of the upper limit of the barnacles.

On smooth vertical faces in situations of extreme exposure *Modiolus* is usually absent; but is well developed in crevices and on platforms and ledges between M.H.W.S. and M.L.W.N.

Pomatoceros coeruleus. Range: M.H.W.N. to M.L.W.N.; 75% to 10% exposure.

The calcareous tubes of this species may be found singly or in small groups at almost any level of the midlittoral zone, except on exposed vertical faces. Where the surface is broken it occurs in cracks and crevices and on ledges where there is a degree of local shelter from direct wave action. However, in sheltered areas *Pomatoceros* occurs as an encrusting mass of tubes, closely packed and intertwined, completely covering the rock surface. These encrustations may reach a thickness of eighteen inches, the bulk of the mass consisting of empty tubes packed with sand, pieces of shell and other debris. The worms occupy the outer ends of the tubes, which grow out more or less at right angles to the rock surface and are so closely packed that when they are covered by water the protruding gill filaments form a dense blue carpet.

These encrustations are particularly well developed on vertical faces at right angles to the wave front, and on exposed shores similar growths are found on the sheltered landward sides of fixed boulders, projecting rocks and ledges. In its inability to tolerate strong wave action *Pomatoceros* shows a marked resemblance to the common Australian, intertidal Serpulid, *Galeolaria caespitosa* (Dakin, et. al., 1948; Guiler, 1950), which forms similar encrustations under sheltered conditions.

The lower limit of the *Pomatoceros* zone is sharply marked at about M.L.W.N., the region below being occupied by *M. planulatus, M. canaliculus* and the algae of the infralittoral fringe. On vertical sheltered faces the zone extends up about 4 feet from this level to E.H.W.N. with scattered individuals up to M.H.W.N. In semi-exposed areas, although *Pomatoceros* occurs only as isolated tubes and in the form of small patches of tubes attached lengthwise to the substratum, the limits are approximately the same.

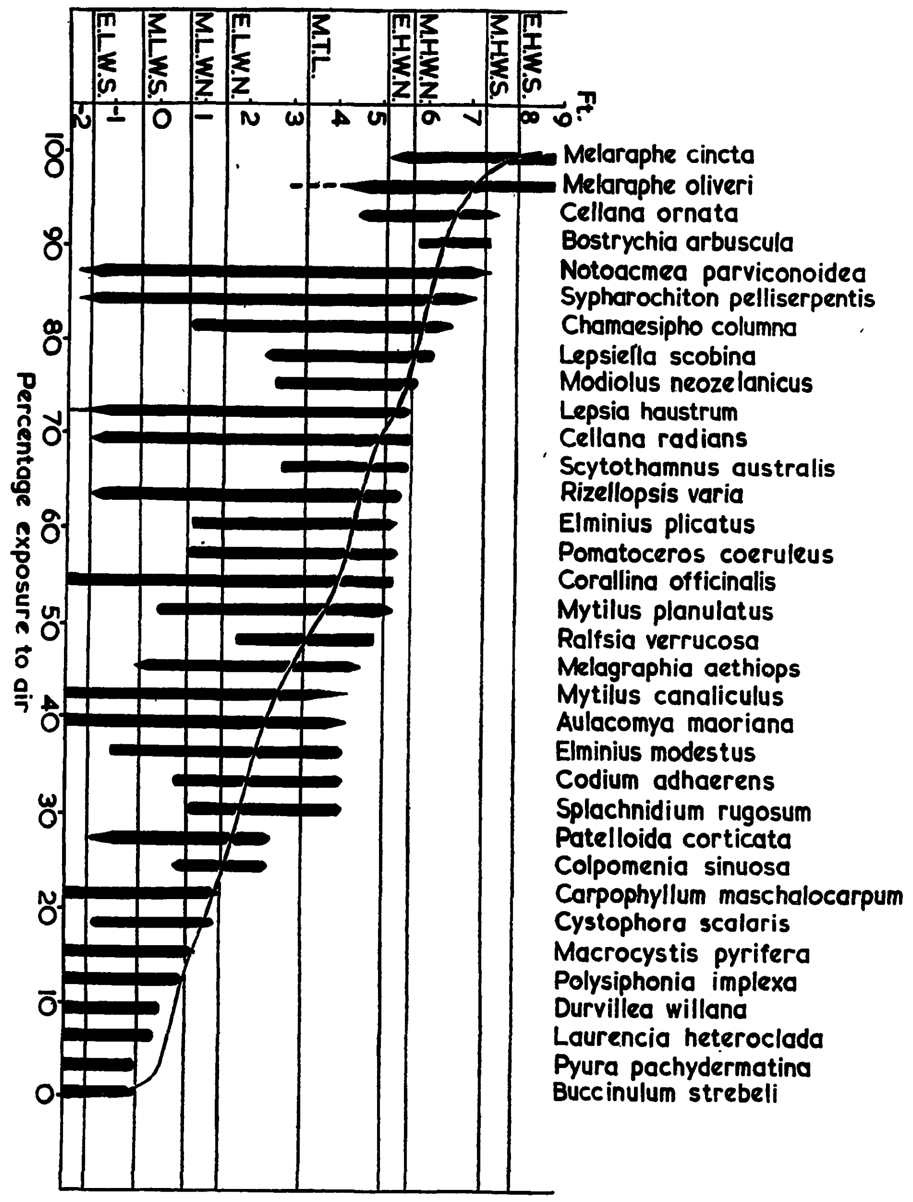

FIG. 5.—Vertical zonation of the species studied at Taylor's Mistake. The curve representing the percentage exposure to air at the different levels is superimposed.

RELATION OF THE SPECIES TO TIDAL FACTORS

Tidal Levels.

The vertical zonations of the species studied are summarized in Fig. 5. This represents the basic pattern of zonation as found in a fairly sheltered situation. In determining the upper and lower limits an attempt has been made to eliminate as far as possible the effect of wave action. The effect of the breaking of the waves is to form a " wash zone " (Bokenham, Neugebauer and Stephenson, 1938), which raises the tide marks above the levels predicted in tide tables or recorded by tide gauges. The height of this " wash zone " is extremely variable, depending on the amount of shelter, the state of the weather, and the configuration of the rock. The influence of exposure on the vertical zonation will be discussed later.

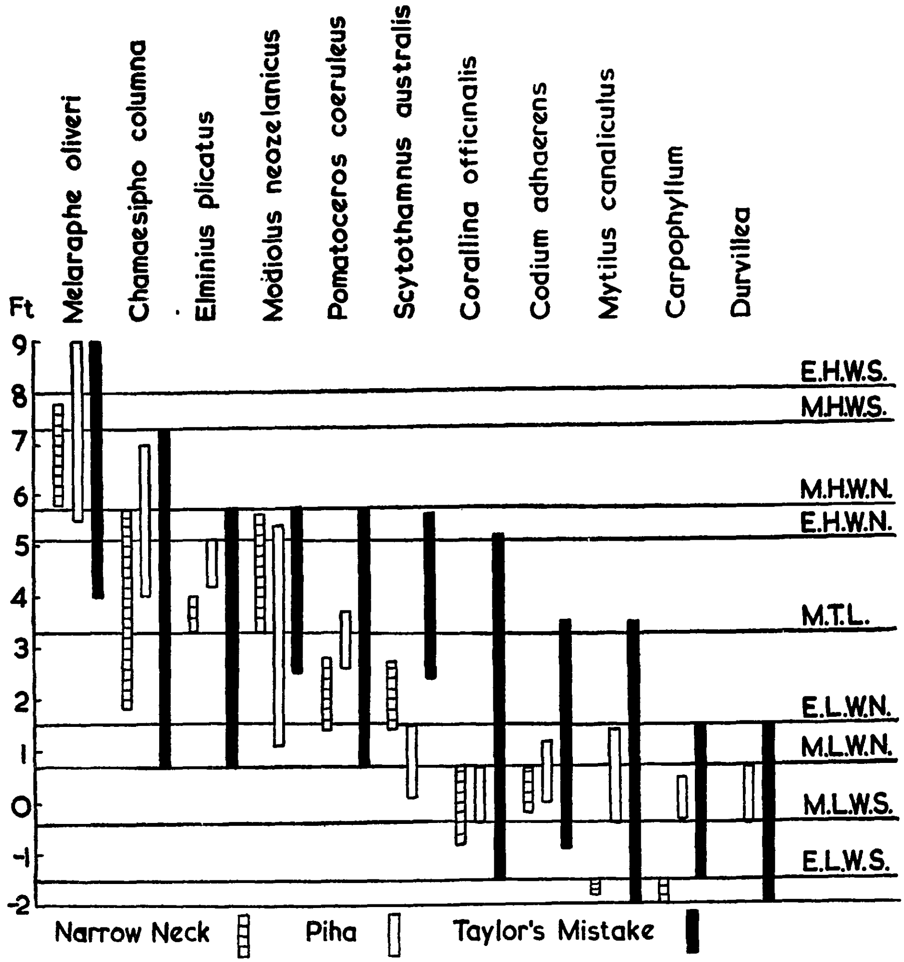

FIG. 6.—Comparison of the vertical zonation of the same species at Narrow Neck, Piha and Taylor's Mistake. The vertical ranges of the species at the latter localities are reduced to the Taylor's Mistake tidal scale.

A comparison of the vertical zonation of some of the species at Taylor's Mistake with that of the same species at Stanmore Bay (Chapman, 1950), Piha (Beveridge and Chapman, 1950), and Narrow Neck (Dellow, 1950), near Auckland, has been made. Fig. 6 compares the zonation at Taylor's Mistake with that of Piha and Narrow Neck, the levels at the latter localities being reduced to the Taylor's Mistake tidal scale. The following table compares the vertical heights of the zones occupied by the same species in the three localities. (The vertical heights of the zones are given in feet.)

	Narrow Neck	Stanmore Bay	Piha	Taylor's Mistake	Taylor's Mistake corrected to tidal range of 10ft.
Tidal Range M.H.W.S.–M.L.W.S. ..	10.3	10.3	10.3	7.7	10.0
Bostrychia arbuscula			1.5	1.8	2.3
Carpophyllum maschalocarpum ..	0.0		1.0	3.5	4.6
Scytothamnus australis	1.4		1.3	2.8	3.7
Durvillea			2.0	2.0	2.7
Corallina	2.4		2.0	6.4	8 3
Codium adhaerens	1.6		0.8	3.8	5.0
Modiolus neozelanicus	3.8	3.0	5.5	3.1	4.0
Mytilus canaliculus	0.0		3.0	6.0	7.8
Chamaesipho columna	5.3	4.0	2.7	6.0	7.8
Elminius plicatus	1.0		1.4	4.8	6.5
Pomatoceros coeruleus	1.7	1.0	0.7	4.8	6.5

From the figure and the table the following points are worth noting:—

(1) In nearly all cases the vertical height of the zones occupied are much greater at Taylor's Mistake, although the tidal range is considerably less. The single exception is *Modiolus neozelanicus,* and an explanation for this discrepancy is offered below.

(2) The upper limit of the majority of the species is higher at Taylor's Mistake, and generally, the lower the relative position an organism occupies in the intertidal zone the greater the elevation.

(3) The lower limits of the majority of the species are lower at Taylor's Mistake, in some cases the difference being very marked. One notable exception is *Modiolus neozelanicus.* Under the conditions of exposures where the zonation was determined, the lower limit of this species is fixed by the presence of the encrusting growth of *Pomatoceros coeruleus,* which prevents the downward extension of the *Modiolus* zone. Where the encrustations are absent *Modiolus* extends down to M.L.W.N., having a vertical range of 6·0 feet.

The narrow band occupied by *Pomatoceros coeruleus* at Auckland is very interesting. The lower limit appears to be determined by the presence of a Sabellid, *Sabellaria* occurring immediately below; Dellow states that *Vermilia* (*Pomatoceros*) nearly always occurs above *Hermella* (*Sabellaria*), although the two species occasionally inter-mix. However, the combined vertical range is less than three feet; whereas the vertical height of the *Pomatoceros* zone at Taylor's Mistake is nearly five feet. Chapman and Beveridge state that at Piha the *Hermella-Vermilia* (*Sabellaria-Pomatoceros*) association is characterized by a distinctly restricted vertical range (about 18 inches). *Elminius plicatus* has a similarly restricted vertical range, Dellow stating that this species is locally dominant just above Mean Sea Level, where it may form a closed community, usually not exceeding one foot in vertical extent. At Taylor's Mistake the same species has a vertical range of five feet.

The elevation of the upper limits of the species at Taylor's Mistake when compared with the Auckland localities could be explained on the basis of temperature differences between the two regions. Gislén (1944) in an investigation of the littoral region of the Pacific coast of North America, found a depression of the levels of the communities when proceeding from a northern latitude to a southern one; this would correspond to an elevation when proceeding from north to south in the Southern Hemisphere. The depression of the lower limits of the dominant sessile animals, *Chamaesipho, Elminius* and *Pomatoceros,* at Taylor's Mistake is more difficult to explain on the basis of temperature differences. It appears that in Auckland region the lower half of the midlittoral zone is occupied by algae to the exclusion of the fixed animal species. Dellow states that below the level of low water neap tides there is an abrupt change in the type of community; animals become of secondary ecological importance, and algae of one kind or another are physiognomic No such marked change occurs at Taylor's Mistake, although *Codium* and *Corallina* may have a restricted local dominance. The lower half of the midlittoral zone down to the upper limit of the brown kelp is occupied by barnacles, mussels and *Pomatoceros*. The variations in the levels of the same species at the four localities serves to emphasise the complexity of the factors that control the zonation of intertidal organisms.

Exposure and Submergence.

The primary causal factor of intertidal zonation is the effect of the tide on the periods of exposure and submergence to which the plants and animals are subjected. As shown in the graph of percentage annual exposure to air (Fig. 2) marked changes in the amount of exposure occur between M H W.S. and M.H.W.N. and between M L.W.N. and M.L.W.S All levels between E.H W.N and E L.W.N are submerged and exposed twice daily, and as pointed out below this is the least critical region of the shore for intertidal organisms Levels above E H W.N. are subject to periods of continuous exposure—i.e., periods of more than 12 hours when no tide covers the area; while levels below E L W.N. are subject to periods of continuous submergence.

The percentage of monthly submergences and exposures at each level are shown in Fig. 7. There is a significant change in the percentage of submergences between 5 feet and 6 feet C D—i e, between M.H.W N and E.H.W.N. From Fig. 5 it can be seen that a number of species have their upper limits between these levels. From the 5ft. level up the plants and animals are subject to increasing periods of continuous exposure. Above this level, therefore, the upper limits of the animals and particularly of the plants will be determined by the degree of desiccation they can tolerate. For the filter feeders a limiting factor is also the availability of food, which depends on the amount of submergence. The majority of suspension feeders, barnacles, bivalves and *Pomatoceros* have their upper limits between 6ft. and 5ft. C.D.—i.e, between M.H.W.N. and E.H.W.N.

A significant change in the percentage of exposures occurs between 0·5ft. and –0·5ft. C.D.—i.e., between M L.W.N. and M.L.W.S. From M.L.W.N. down the plants and animals are subject to increasing periods of continuous submergence, and it is significant that a large number reach their upper limits between M L.W.N. and M.L.W.S.

The exposure factor is of great importance during the critical settling period of the life history of the plants and animals. As shown in Fig. 7, the percentage of monthly submergences shows a marked decrease from the 5·5ft. level up during August-October, the levels from 6ft. up being rarely covered. Periods of continuous exposure above this level must result in the death of newly settled larvae and sporelings. The percentage of monthly exposures also shows a marked

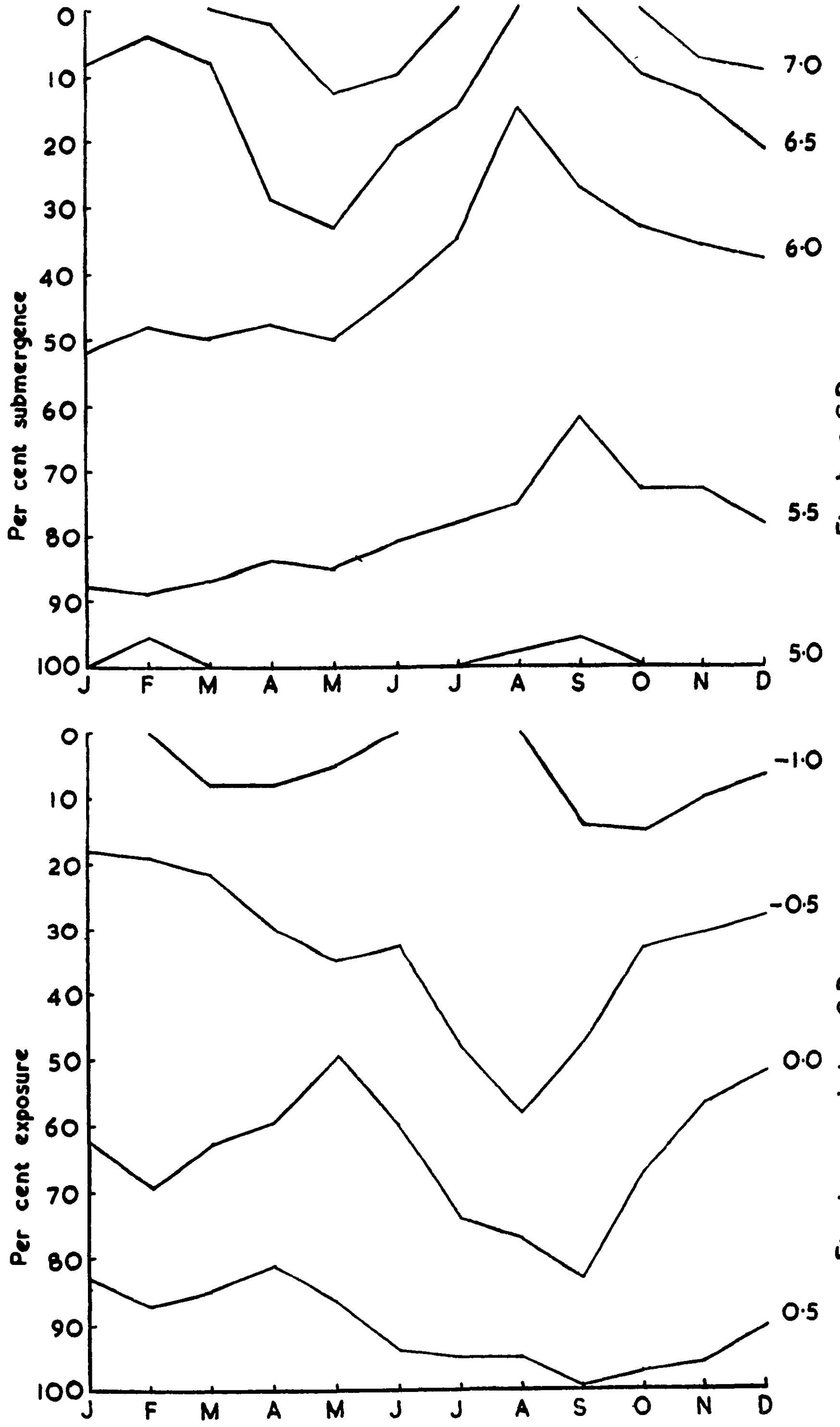

FIG. 7.—Upper: Percentage monthly submergence at high tides. Lower: Percentage monthly exposures at low tides.

increase from the -0·5ft. level down during the same period. The lowest spring tides of the year are recorded during September and October, the times of the low tides occurring between 10 a.m. and 4 p.m. These low tides may also result in the death of the sporelings of the young plants of the brown kelps.

Critical Levels.

Colman (1933), Chapman (1941), Evans (1947a, 1947b), Beveridge and Chapman (1950) and Dellow (1950) have discussed the significance of critical levels on the shore and the possible factors that may account for them. Such levels have been recognised in the present survey, and a comparison of the results obtained with those of the above workers has proved most interesting.

From Fig. 5 the number of upper and lower limits and the total number of species occurring between -2·0ft. and -0·5ft., -1·5ft. and 0·0ft. etc., can be obtained as Colman (1933, p. 463) has described. These are shown graphically in Fig. 8.

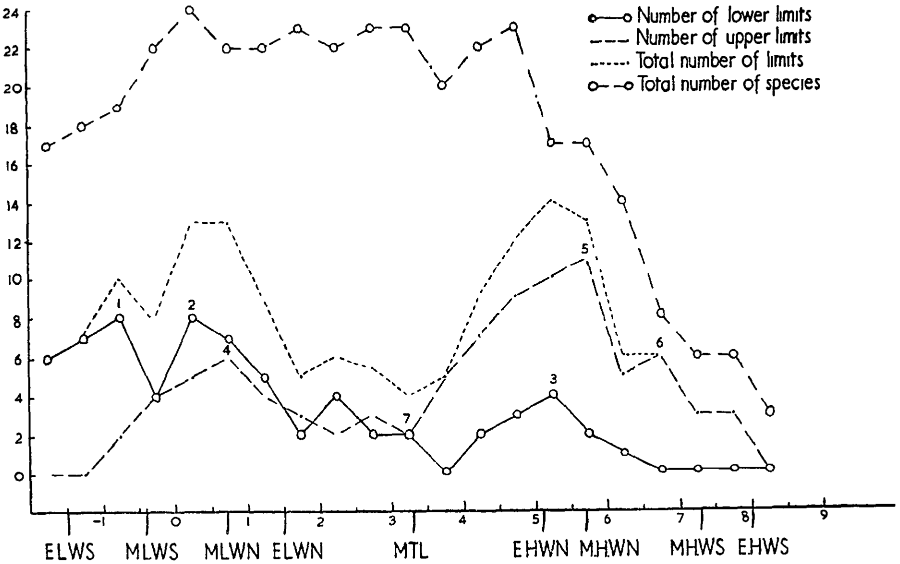

FIG. 8.—Number of upper and lower limits, total number of limits and total number of species present at different shore levels.

From the graphs the following may be noted:—

(1) There is a maximum number of lower limits lying between 0 0ft. and -1·5ft., C.D.—i.e., between M.L.W.S. and E.L.W.S. This marks the lower limits of *Elminius modestus, Rizellopsis varia, Patelloida corticata* and *Cystophora scalaris.*

(2) Another maximum in the number of lower limits occurs between 1·0ft. and -0·5ft. C.D., or between M.L.W.N. and M.L.W.S. This level marks the lower limits of *Elminius plicatus, Chamaesipho columna, Pomatoceros coeruleus, Codium adhaerens, Colpomenia sinuosa* and *Mytilus planulatus.*

(3) There occurs another smaller, though well defined maximum of lower limits between 6·0ft. and 4·5ft., C.D.—i.e., between M.H.W.N. and

E.H.W.N. The lower limits of *Bostrychia arbuscula, Melaraphe cincta, Melaraphe oliveri* and *Cellana ornata* occur here.

(4) On the graph for upper limits there is a maximum marking the upper limit of the species of the infralittoral fringe between 1·5ft. and 0·0ft. C.D. or between E.L.W.N. and M.L.W.N. The brown kelps *Carpophyllum maschalocarpum, Cystophora scalaris* and *Durvillea willana* end here.

(5) Another very prominent maximum of upper limits occurs between 6·5ft. and 6·0ft. C.D.—i.e., at M.H.W.N. This marks the upper limits of the majority of filter feeders, the barnacles, bivalves and *Pomatoceros.*

(6) Between 7·5ft. and 6 0ft. C.D. there is a less well defined maximum of upper limits. This lies below M.H.W.S. and marks the upper limits of *Cellana ornata, Notoacmea parviconoidea, Sypharochiton pelliserpentis* and *Chamaesipho columna.*

(7) The minima of the graphs for both upper and lower limits occur at about 3·5ft., C.D., or approximately at M.T.L. This marks the least critical level on the shore for the species studied.

In the region studied then there appear to be six critical levels for the species under investigation. These are:—

1. Between M.L.W.S. and E.L.W.S.
2. Between M.L.W.N. and M.L.W.S.
3. Between M.H.W.N. and E.H.W.N.
4. Just above M.L.W.N.
5. At M.H.W.N.
6. Below M.H.W.S.

A comparison of the findings here with those of Coleman (1933), Evans (1947), Beveridge and Chapman (1950), and Dellow (1950) has yielded some interesting results. If the graphs in Fig. 7 are compared with those of Evans (Fig. 9, p. 303) a marked similarity in the general trend of the curves and the positions of the maxima are noted. Evans, however, did not find a marked maximum at the point numbered 3—i.e., between M.H.W.N. and E.H.W.N.

There appears to be a good deal of similarity between Taylor's Mistake and the locality Evans studied at Cardigan Bay, Wales. Evans summarizes the climatic conditions at the latter locality in the following words: "The climate is typically northern cold temperature then, and the intertidal region is not subject to great annual variation; generally speaking conditions may be described as mild." If the word northern were to be changed to southern the above description might well be a summary of the climate of the area studied in the present investigation. The mean annual range of sea temperature is about 20° F. in both localities, while the mean annual range of air temperature is 21° F. (11° C.) at Christchurch and 25° F. (14° C.) at Aberstyth, Wales. Also. the species studied by Evans, although in most cases belonging to different genera, are members of the same family or order. It would appear that under similar conditions these species have developed the same tolerances as regards exposure to air and wave action.

Beveridge and Chapman also recognise six critical levels for 36 species, of which 7 are animals and 29 are plants. Corresponding numbers for the present survey are 34 species, 21 animals and 13 plants, for that of Evans (1947) 28 species, 15 animals and 13 plants, and for that of Dellow (1950) 25 species, 8 animals and 17 plants. In view of the different proportions of animals and plants in the four surveys the correspondence in the relative positions of the critical levels as shown in the following table is very marked. As the critical levels given by Beveridge and Chapman (1950) were calculated by a different method to that outlined above, the date for Piha, as depicted by them (p. 200, Fig. 13), has been graphed and the critical levels determined as for the other surveys.

	Cardigan Bay	*Taylor's Mistake*	*Narrow Neck*	*Piha*
1.	M.L.W.S.–E.L.W.S.	M.L.W.S.–E.L.W.S.	Absent	M.L.W.S.–E.L.W.S.
2.	M.L.W.N.–M.L.W.S.	M.L.W.N.–M.L.W.S.	M.L.W.N.–M.L.W.S.	E.L.W.N.–M.L.W.N.
3.	E.H.W.N.	E.H.W.N.–0.5ft.	E.H.W.N.–	E.H.W.N.–0.5ft.
4.	M.L.W.N.–	M.L.W.N.	M.L.W.N.	M.L.W.N.–1 0ft.
5.	M.H.W.N.–	M.H.W.N.	M.H.W.N.	E.H.W.N.
6.	E.H.W.S.–M.H.W.S.	M.H.W.S.–	E.H.W.S.	M.H.W S –
7.	M.T.L.–1.0ft.	M.T.L.	M.T.L.	M.T L.

Comparing the critical levels at Taylor's Mistake with those at Piha, it will be seen that level (2) is lower with reference to the tidal levels at the former locality; while levels (4) and (5) are higher and levels (1), (3), (6) and (7) are the same. At Narrow Neck level (1) is absent and level (6) is higher than at Taylor's Mistake. At all four localities the least critical level on the shore is in the region of M.T.L.

Graphs of the total number of limits at each level on the shore were compared for the four localities. In all cases the graphs showed two pronounced maxima, one in the lower and one in the upper region of the intertidal zone. The positions of these maxima are shown below:

	Lower Maximum	*Upper Maximum*
Taylor's Mistake	Just below M.L.W.N.	Between M.H.W.N. and E.H.W.N.
Narrow Neck	Between M.L.W.N. and M.L.W.S.	Between M.H.W.S. and M.H.W.N.
Piha	Between M.L.W.N. and M.L.W.S.	M.H.W.S.
Cardigan Bay	Between M.L.W.N. and M.L.W.S.	Between M.H.W.N. and E.H.W.N.

In addition, at Cardigan Bay there was another lower maximum between M.L.W.S. and E.L.W.S. and a less pronounced second upper maximum of total limits between E.H.W.S. and M.H.W.S. However, when the varying proportions of plants and animals and the differences in the total number of species studied at the four localities are taken into consideration, the agreement in the relative positions of the principal critical levels is very marked. The results of all four investigations indicate that the two most critical regions which determine the vertical zonation of the plants and animals are between M.L.W.N. and M.L.W.S. and between M.H.W.S. and E.H.W.N. Between these levels there must occur a change in one or several of the factors that determine vertical zonation. The most obvious of these is the exposure factor. As pointed out above significant changes in the percentage of monthly submergences occurs between M.H.W.N. and E.H.W.N. and in the percentage of exposures between M.L.W.N. and M.L.W.S. The operation of this exposure factor is highly complex, depending on the nature of the tidal system. As Beveridge and Chapman (1950) point out, the tidal factor may be considered under three headings:

1. Hours of submergence and air exposure.
2. Periods of continuous air exposure or submergence.
3. Number of submergences and exposures.

The operation of these factors varies throughout the year, from month to month, as well as from week to week. Also they operate with different intensities at different stages in the life histories of the intertidal organisms. A period of continuous exposure that an adult plant or animal could easily tolerate might well be fatal to newly settled sporeling or larvae. More information on the tolerances of intertidal organisms at different periods of the life history is required.

As mentioned by Evans (1947b), the results obtained by any arbitrary method of graphing specific limits and deriving critical levels from the graphs will vary with the number and types of species studied, the degree of exposure to wave action, the presence of shading influences, rock slope, etc. In spite of these factors, the results of investigations on coasts in different parts of the world indicate that there are certain levels that can be regarded as being more critical than others in determining the vertical zonation of intertidal organisms. Results of the present survey support the following generalizations arrived at by Evans (1947b).

(1) The regions between M.L.W.N. and M.L.W.S. is critical in the sense that the majority of intertidal plants and animals reach their lower limits here.

(2) While certain sublittoral species penetrate into the littoral region, they generally extend only as high as the vicinity of M.L.W.N.

(3) The region between M.H.W.S. and E.H.W.N. is critical for a large number of species in that they reach their upper limit here.

(4) The least critical level on the shore is in the vicinity of M.T.L

The most critical regions lie between M.H.W.S. and E H.W.N. and between M.L.W.N. and M.L.W.S. It is in these regions that marked changes in the amounts of exposure and submergence occur.

Discussion

In the present state of knowledge concerning the zonation of marine intertidal organisms we are still very far from an understanding of the factors that control the upper limits of the plants and animals. Stephenson and Stephenson (1949) rightly emphasize that zones between the tide marks have no constant *depth* whatever, the upper and lower limits of the same species often differing considerably in places only a few yards apart. According to the above authors the primary cause of intertidal zonation is the existence of an interface between air and water, which plus wave action, is sufficient to produce the three primary zones supralittoral, littoral and infralittoral. The addition of tidal action serves to strengthen the zonation produced by the above factors.

Other workers, particularly Doty (1946), Doty and Garnic (1948), Doty and Archer (1950), hold that intertidal zonation is the result of tidal action. Doty attributes the sharp upward and downward limits of intertidal organisms to the existence of tidal factors, or peculiarities of tidal variation that, from one level to the next, may result in two or three fold increases or decreases in the time of exposure to submergence and submergence. The influence of exposure and submergence on the species studied at Taylor's Mistake has been discussed above. Doty has subjected his hypothesis to experimental test by exposing algae to adverse conditions such as exposure to air, increased temperature and 0·001 formaldehyde for varying periods of time and concludes:

" It seems that the marine algae used to have a physiology that would cause them to be limited in range sharply, through such sudden variations in the time of exposure as are provided by the tide factors The tide factors are considered to be the primary factors controlling abrupt variations in secondary factors that, in turn, have a physiological, or at times physical, vertical range limiting effect on intertidal organisms.''

The above two theories are not necessarily antagonistic, but rather complementary. Granted that the three primary zones are due to the existence of an interface between air and water plus the influence of wave action, there still exists within the intertidal zone the often sharp upper and lower limits of different species of plants and animals. As discussed above it appears from the results of the present work and that of Coleman (1933), Grubb (1936), Zanefeld (1937), Beveridge and Chapman (1950) and Dellow (1950) that the action of the tidal factor does cause abrupt variations in environmental factors, and that the levels where these changes occur are related to the upper and lower limits of intertidal organisms. These tidal factors, as pointed out by Doty and Archer (1950), result in a large number of secondary factors that act on intertidal organisms with varying intensities and in differing combinations. The action of these factors is subject to modification primarily by wave action and the configuration of the rock.

It must be emphasized here that the results of tidal analyses and observations on the levels of intertidal organisms are approximate only, since, as Colman (1933) states, the ecological tide level is not that shown on the recorder, but that reached by the surf. Also a large amount of personal judgment enters into the determination of the upper and lower limits, as these are affected to varying extents by wave action, rock configuration and aspect. However, if a sufficient number of observations are carried out a reasonable estimate of the limits as they would be in the absence of these modifying factors, can be made.

The vertical range of the tide has little effect on the basic zonation, which is just as marked in Tasmania where the mean tidal range is only 1 foot 10 inches, as it is at Taylor's Mistake, where it is 7 feet, or on shores where it may be 30 or 40 feet. Intertidal organisms are still subjected to the same conditions of exposure and submergence no matter what the range of the tide may be, although conditions will differ according to the nature of the tides—e.g., in the region studied by Doty (1946) there occurs mixed semi-diurnal tides of such a nature that successive high and low tides are often of appreciably different heights.

The principal factors determining the upper and lower limits of plants and animals on the shore are:

(1) Submergence and exposure.
(2) Wave action.
(3) Tidal flow and ebb.
(4) Type of substrate.
(5) Topography, including aspect and angle of slope.
(6) Proximity of sand.
(7) Climatic factors such as temperature, amount of sunshine, rainfall and wind.
(8) Competition.

The above factors interact in varying combinations and proportions for different localities and for different species in the same locality. Different factors may also operate in determining the upper and lower limits—e.g., the upper limit of the barnacles *C. columna* and *E. plicatus* is determined largely by the amount of exposure and the degree of wave action while the lower limit is, in many localities, determined by competition with algae.

Rigg and Miller (1950) regard zonation as the resultant of two primary factors:

(1) " Organisms in the upper littoral have an optimum vertical range that is determined by a variety of conditions, among which are food supply and illumination; degree of resistance to desiccation when exposed to air and sunshine, and to endosmosis when exposed to rain; and adaptability to survival under the pounding of heavy surf.

(2) " Organisms characteristic of a given vertical range often survive in limited number above or below the level regarded as optimum. Their apparent restriction to a narrow vertical range is due primarily to competition from other organisms better adapted to the vertical range immediately adjacent."

The conditions which Rigg and Miller list as vertical range limiting factors are secondary factors due to combinations of the principal factors listed above. A secondary factor limiting the upper levels reached by plankton feeders, such as *C. columna, E. plicatus* and *Modiolus* is food supply. The level reached depends on the minimum coverage by water that is necessary for the animals to obtain an adequate food supply, which in turn depends on the amount of submergence and exposure and the degree of wave action. Desiccation is also an important secondary limiting factor due to a combination of several of the principal factors, including submergence and exposure, wave action, aspect, angle of slope, temperature, sunshine and wind. The influence of sand in elevating the upper limits of the species studied at Taylor's Mistake has been noted above. Notable examples are the Littorinid snails *M. oliveri* and *M. cincta,* and the algae *Bostrychia arbuscula, Ralfsia verrucosa* and *Codium adhaerens.*

Chapman (1943) has proposed a division of the ecological factors affecting the vertical zonation of intertidal organisms into three groups:

(1) Causal factors—i.e., factors which determine the upper and lower limits of a given species.
(2) Presence or absence factors—i.e., factors which determine whether a species shall be present or absent in a given locality.
(3) Modifying factors—i.e., factors responsible for modifying the vertical range or position occupied by any species.

Any of the primary factors mentioned above may, according to the species and the combination of other factors involved, be classified in one, two, or all three of the above categories. Wave action may act as a presence or absence factor, determining the presence of a species not adapted to withstand strong wave action—e.g., *Bostrychia,* or as a modifying factor, increasing the breadth of the zone occupied by many species, especially barnacles. Competition acts as a presence or absence factor where the dense *Pomatoceros* encrustations prevent the development of *Codium, Colpomenia, Scytothamnus* and *Ralfsia,* and as a modifying factor where the same encrustations considerably shorten the vertical heights of the *Modiolus* and *Chamaesipho* zones by restricting the lower level of these species to M.H.W.N.

As previously mentioned, the sandy beach at Taylor's Mistake is subject to considerable scour, the sand level on the inshore rocks varying up to two feet in vertical height. In such localities the proximity of sand often acts as a presence or absence factor eliminating completely the infralittoral fringe with its characteristic algae. *Laurencia* is one species that can tolerate considerable coverage by sand. It also acts as a modifying factor raising the upper limit of the typical species of the midlittoral zone. The fixed animals of this zone have different ranges of tolerance towards coverage by sand, and can be arranged in the following series of increasing tolerance, *E. plicatus, C. columna, M. planulatus, E. modestus, P. coeruleus* and *M. neozelanicus*. The latter species is definitely the most tolerant and on the rocks in the centre of the beach there is often a band of *Modiolus,* up to a foot in width below the abrupt lower limit of *M. planulatus* and *C. columna.*

Wave action is one of the most important factors causing variation in the pattern of distribution of intertidal organisms, and its effect will be discussed in more detail.

At Taylor's Mistake, as in other parts of the world, there is a definite correlation between the intensity of wave action and the distribution of the algae. However, the majority of the algae are confined to the infralittoral fringe, and there does not occur an invasion of the mid-beach barnacle zone by fucoids with decreasing intensity of surf, as described by Evans (1947b) for the Plymouth region, Great Britain. There the invasion proceeds from low water and from high water towards the centre of the beach, until finally the barnacle belt is more or less obliterated. Apart from restricting the lower limit of the barnacles under certain conditions, the algae at Taylor's Mistake have little influence on their distribution.

The only species of algae that occurs in quantity in the upper littoral is *Bostrychia arbuscula.* For this species wave action acts as a presence or absence factor, the species being absent in exposed situations and the vertical height of the zone shows little variation. Wave action also acts as a presence or absence factor for the majority of the algal species of the midlittoral zone, *Scytothamnus, Colpomenia, Splachnidium* and *Codium* occurring only in semi-exposed to sheltered situations.

For the algae of the infralittoral fringe wave action acts both as a presence and absence and as a modifying factor. A gradual change in the species of algae can be seen from the outer, exposed headlands to the sheltered areas near the beach. In situations of extreme exposure the single dominant algal species is *Durvillea willana* or *Durvillea antarctica,* with an underflora consisting almost entirely of "Lithothamnion." *Corallina* may replace the Lithothamnion where the wave action is slightly less intense. With increase in shelter *Macrocystis* appears and *Durvillea* is replaced by *Carpophyllum,* with the addition of *Cystophora* with further increase in shelter.

As a modifying factor the action of surf may elevate the upper limit of the infralittoral algae several feet. On steep faces subject to considerable wave shock the upper limit is not affected, while in localities where the actual wave shock is lessened by broken outer reefs, but where there is still considerable surge, the upper limit may be considerably raised. This effect is also noted on steep faces at right angles to the wave front. Such faces, while protected from direct shock, are still subject to considerable swell.

For the animals studied at Taylor's Mistake wave action, as for the plants, acts as both a presence and absence factor, and as a modifying factor. The animals studied can be divided into two groups: one consisting of species, including *Melaraphe oliveri, Chamaesipho columna, Elminius plicatus, Cellana radians, Notoacmea parviconoidea,* and *Sypharochiton pelliserpentis,* which can withstand very exposed conditions; the other of species which are found only where there is shelter from excessive wave action, notably *Lepsiella scobina, Cellana radians, Melagraphia aethiops* and *Pomatoceros coeruleus.* Many of the species in the first group, especially *M. oliveri, C. columna* and *E. plicatus* extend to the more sheltered regions, while *Mytilus planulatus* and *Modiolus neozelanicus* occupy an intermediate position between the above two groups, extending from exposed to sheltered situations. Generally wave action, acting as a presence or absence factor, plays an important part in determining the density of the animals studied. The action of this factor is subject to considerable modification by other factors, particularly rock configuration.

As a modifying factor the effect of surf in elevating the upper limits of *Chamaesipho brunnea, C. columna, Elminius plicatus, Melaraphe oliveri, M. cincta, Cellana radians, Mytilus planulatus, Modiolus neozelanicus* and *Sypharochiton pelliserpentis* has been noted above. Exposure to surf also lowers the lower limit of *C. columna* and *E. plicatus.*

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