Reprinted from ECOLOGY, Vol. IX, No. 2, April, 1928

LITTORAL VEGETATION ON A HEADLAND OF MT. DESERT ISLAND, MAINE. I. SUBMERSIBLE OR STRICTLY LITTORAL VEGETATION[1]

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Purpose

In the present investigation we have undertaken to determine the precise limits of distribution, vertically and horizontally, of each littoral plant and plant association found on a high, rocky point of Mt. Desert Island, Maine, known as Otter Cliffs. Our object was the discovery of the external conditions limiting this distribution.

Most of the observations to be recorded were made during July, August and early September of the years 1923 to 1925. In March 1927 the junior author spent three days studying the late winter flora of our area, and the senior author followed the seasonal development of the vegetation from June to September of the exceptionally cool and backward summer of 1927.

Area and Methods

Otter Cliffs are on the south side of the island, close by the Ogden Station of the Mt. Desert Island Biological Laboratory, and are completely exposed to the heavy surf of the open Atlantic. They lie near 44° 19′ N. latitude and 68° 11′ W. longitude. Our work was carried on from the Weir Mitchell Station of this laboratory as a base. The area most carefully studied extends 150 feet north and south, and 300 feet east and west, and includes elevations from — 8 to + 50 feet (Chart I). It was selected because of the widely varied habitats provided by the rock surfaces of many different slopes and exposures, and by tide-pools of very different sizes at many different levels. It embraces some bottom at 4 to 8 feet below mean low water, of rocky or gravelly character, and a bit of coarse shingle and boulders between 7 and 13 feet above low water, while the rest of the littoral zone is of granite or schist cliffs and ledges, with some trap dikes. Not until the 20-foot level, 10 feet above mean high tide, is reached do we find even minute pockets of soil in

[1] Botanical Contribution No. 87 from the Johns Hopkins University. The authors gratefully acknowledge here the courtesy of the Trustees and of Director Ulric Dahlgren of the Mt. Desert Island Biological Laboratory in affording them the facilities of the Laboratory for carrying on this work. They also here express their thanks to Superintendent George B. Dorr of Lafayette National Park, for help in fastening our tide-stake to the ledges, and for transportation to the area in March 1927. They are indebted also to Doctor A. S. Hitchcock for naming the grasses and to Doctors M. A. Howe, Albert Mann, and W. R. Taylor and J. E. Tilden for identifying various algae collected in the area studied.

crevices of these ledges, where rooting plants can take hold, and only at the 30-foot level does a soil become continuous over considerable areas. There are thus, in the lower parts of our area, no pockets with mud bottoms that might bear *Zostera* (eel grass), a plant which actually withstands a very

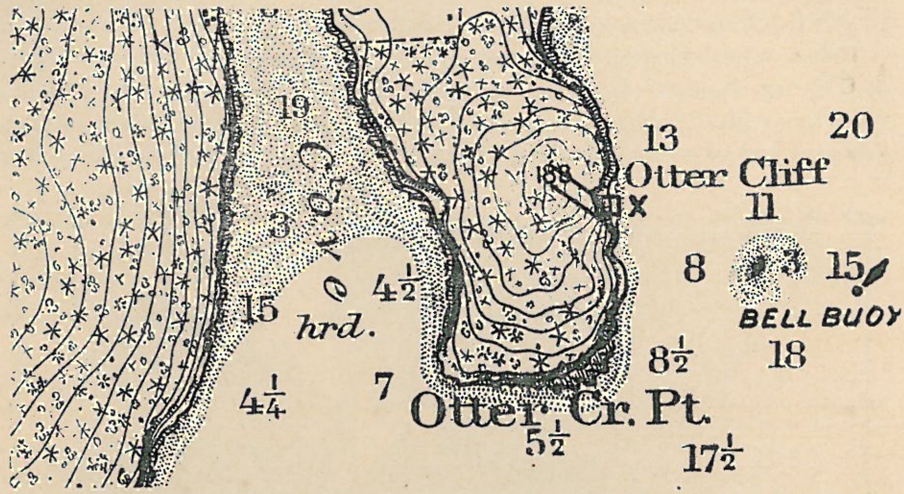

CHART 1. The Otter Cliffs portion of the U. S. Coast and Geodetic Survey Chart No. 306, showing, at X, the location of the area studied. Otter Cove is at the left and the small, offshore reef at the right. Scale 1 : 36,000.

heavy surf on adjoining shores which are muddy. Our shore is occupied by a series of varied plant associations, ranging from tangles of large kelps or crusts of corallines near low water mark to a dense spruce-balsam forest on the top of the cliffs. Each of the numerous tide-pools is occupied by a series of algae whose kinds and vegetative characters depend on its elevation, exposure and illumination.

The mean range of tide at Otter Cliffs is 10.4 feet, this being the mean derived from the ranges given for the two nearest datum points, by the Tide Tables (1924) of the United States Department of Commerce. Bar Harbor, 5 miles north of Otter Cliffs, has a mean range of 10.5 feet, and Southwest Harbor, 7 miles to the south, has one of 10.3 feet. Our zero datum level, as in the Tide Tables, is mean low water. The accurate determination of the mean low water level at Otter Cliff was finally accomplished after overcoming rather serious difficulties in anchoring our tide-staff to the smooth ledges. We finally secured the staff to timbers wedged in crevices in the ledges and braced it from 1-inch steel dowels cemented in the rock (see Pl. VIII, Fig. 1). After recording the water level at turn-of-tide (usually at low water) on a number of days with all ranges of tide, we compared these figures with the expected readings, obtained by multiplying the predicted level, at turn-of-tide at Eastport by the fixed ratio given by the Tide Tables for Mt. Desert points in relation to this, the nearest, "reference port." Our zero, so determined, brings the actual and the expected values into close agreement.

The duration of submergence and exposure at any particular level can be read from carefully recorded tide-curves, covering a twenty-five hour period, after the method employed by Johnson and York ('15, pp. 12–14, 131–136), to which reference should be made for fuller details.

Next, we established a base-mark on the highest point of the outer ledge, at 18.8 feet above M. L. W. (Pls. VIII, XII, Figs. 1, 2, 16). By levelling from this with the aid of a spirit level and a long staff, the elevation of each tide-pool and of each important topographic point up to the 50-foot level was

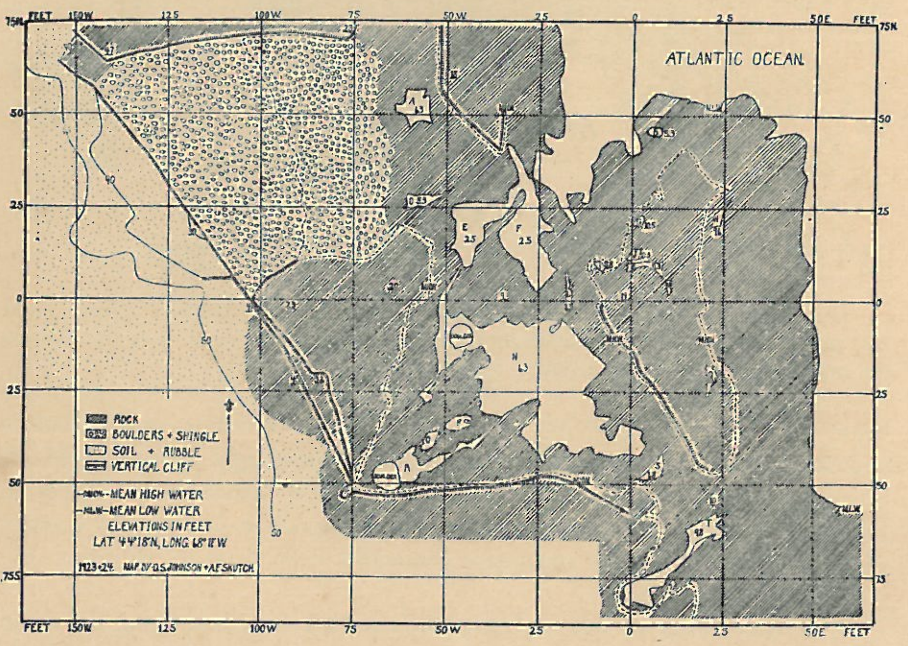

CHART II. Map of the area studied intensively, from mean low water to the 50-foot level. It shows the ledges, boulders, shingle beach and tide pools (levels indicated in feet) as they show at low tide. It also shows the mean high water line and the vertical cliff forming most of the inshore border of the littoral portion of our area. Compare with Figs. 1 and 2, Plate VIII.

determined, and marked by paint on the rocks. Through this base-mark as a center we laid out two axes at right angles, and then series of other lines parallel to each of these axes at intervals of 25 feet. The extremities and some intermediate points on these lines were marked on the rocks. By aid of these, a map was made of the area studied, showing the chief contour lines as well as the tide-pools and the few large detached boulders (Chart II). These same lines on the rock enabled us to determine the vertical and horizontal distribution, over the ledges and through the tide-pools, of the plants on this shore.

We shall find as we proceed that, while each littoral plant is confined to definite, usually narrow, vertical limits, yet the zones or belts of vegetation are less evident to the eye than they are on the gravel, sand or mud bottoms of quieter shores. One reason for this indefiniteness is that each small drainage furrow, transverse to the general shore line, has secondary vegetational belts of its own running transversely to the shore line. The algae of mid-channel in each rill are those characteristic of lower levels (where exposed), while those at each margin of the rill are algae that can withstand more desiccation. Each tide-pool also interrupts the horizontal belt in which it occurs, with its series of different algae which can thrive under constant submergence.

A striking feature of the littoral vegetation belt here, as compared with that on quieter shores, is its elevation to 2 feet or more above the actual average level of the intertidal zone. This elevation is evidently due to wave action. The precise amount of elevation at any point is determined by the effects which exposure and the conformation of the rocks produce on the height of the wave splash.

The two primary habitat zones distinguished on this shore are the true littoral, or submersible zone, extending from 6 feet below to 14 feet above mean low water, and the adlittoral, or terrestrial zone proper, from 14 to 193 feet. The lower edge of the adlittoral zone (14 to 35 ft.) is rarely wetted by wave splash (in the growing season at least), but is commonly wet solely by wind-blown spray. The whole upper portion (35 to 193 ft.) forms a non-halophytic or inland zone which is wetted only by the fine spray that may be carried far by occasional high winds. The littoral zone is occupied by three distinct belts of vegetation, and the adlittoral zone by four distinguishable belts.

The Vegetational Belts of the Submersible Zone are: 1. The Sublittoral Belt, the lowest of the series, which extends from 6 feet below low water to 2 feet above this level. It is characterized by associations of *Alaria*,[2] *Halosaccion* and *Melobesia*. 2. The Lower Littoral Belt embraces levels from 2 to 7 feet, and is characterized by associations of *Porphyra*, of *Fucus furcatus*, of *Spongomorpha arcta* and *S. spinescens*, of *Ascophyllum* and of *Rhodymenia*. 3. The Upper Littoral Belt extends from 7 to 14 feet, and is characterized throughout the year by associations of *Fucus vesiculosus*, of *Ascophyllum* and *Polysiphonia*, of *Calothrix* and of *Verrucaria*. In summer large patches of *Codiolum* appear on exposed ledges, while in winter and spring *Bangia*, *Ulothrix flacca*, *Enteromorpha minima* and *Hormiscia penicilliformis* largely replace the *Codiolum*. It may be remarked here that the

[2] In case only one species of a genus is mentioned in this work, the generic name alone is usually given. The specific name with the authority will be listed in a subsequent paper (Ecology, Vol. IX, No. 3).

floras of the tide-pools, a discussion of which will be published in a later paper, are necessarily left out of consideration in the delimitation and the discussion of the three submersible belts, and the character plants referred to here are thus those of the exposed rocks and of the shallow trickles.

It will be evident from this outline of the belts of vegetation thus characterized that the splash and spray zones do not here reach nearly so far above high tide mark as do those of the Faeroe Islands, described by Børgesen ('08, p. 708), though in a storm of August 1927 waves, at one point, splashed up beyond 40 feet.

The foregoing remarks, many of which are in the nature of conclusions and might have been reserved for a later section of this paper, are briefly presented this early in order to reveal some of the considerations on which the vertical limits of the belts of vegetation were fixed, as indicated in the succeeding paragraphs, and to suggest some of the facts it was in many cases necessary to learn before we could recognize clear zonal limits, or even to recognize any definite zonation at all.

Sublittoral or Alaria-Halosaccion-Melobesia Belt

(From — 6 to + 2 feet)

The lower limit of this belt is difficult to determine because of the constant agitation of the water. That given above is the limit of the bottom on which we could see, and feel with a long handled hook, that *Alaria* and sometimes *Saccorhiza* were attached. The upper half of this belt was studied with care during low water of spring tides, when, with the receding of the waves to 3 or 4 feet below M. L. W. (mean low water) it was possible to distinguish all larger plants growing down to these levels. The three dominant plants mentioned seem all to be perennial. At least all are common in both March and midsummer.

Alaria esculenta is the dominant plant in this belt and grows abundantly throughout both its horizontal and its vertical extent. (Pls. IX–XI, Figs. 7, 8, 12.) On one rock surface of 1 square foot, situated just above the M. L. W. level, 88 individuals, all over 10 cm. long, were attached. On another square foot nearby 74 plants of this alga were growing, all over 10 cm. long, 37 of them between 1 and 2 meters in length, and two over 2 m. long. *Alaria* may here grow to 2 or even 3.5 m. in length, and have a maximum width of 15 to 18 cm. The lower plants of *Alaria* are in general larger, while those near and above M. L. W. are decidedly smaller in size, many, at its upper limit, having a blade but 3 or 4 cm. in width and 6 or 8 cm. long.

The larger, older *Alaria* plants, pounded by the waves, become much frayed at the tip (Pl. XI, Fig. 12). The thin margins of the blade split transversely—recalling the well-known behavior of the mature leaf of the banana when frayed by the wind—while the tip of the rib is worn off to a pointed or wedge-shaped end. It seems clear that it is this fraying of the blade that often enables this alga to withstand the impact and pull of the tons of water that are constantly tumbling on it and tugging at its holdfasts. One has but to watch the surge of the waves dashing on it at low water, and see the blades writhe as they are thus lashed about, to realize how tremendous is the mechanical strain to which these large plants are subjected almost unceasingly throughout life. Tests were made to determine the actual strain necessary to break the stipes of the three kelps found in our area. The results of these tests are given in Table I. They show that the stipe of *Alaria* will support a pull of over 45 kilograms per square centimeter of cross section. This is remarkable when the large moisture content of the stipe is considered. They shrink in drying to a small fraction of the thickness they have while living.

TABLE I. *Breaking Strain of the Fresh Stipes of Kelps*

Plant	Weight causing rupture	Cross-sectional area at point of rupture	Weight per square cm.	Mean
Alaria esculenta	9730 g.	0.258 cm.^{2}	37,700 g.	45,600 g.
	8375	0.197	42,300	
	8045	0.141	56,900	
Saccorhiza dermatodea	8785	0.353	24,900	28,500
	3800	0.152	25,000	
	3725	0.132	28,200	
	3090	0.086	35,800	
Laminaria digitata	10,905	0.306	35,600	45,900
	15,770	0.335	47,100	
	13,790	0.251	55,000	

Such observations on the habit of these kelps also make it clear that it is the intercalary growing zone and the basal location of the small, fertile pinnae characteristic of this genus (Pl. XI, Fig. 12 Al), that enable it to thrive where other large Laminariaceae, with reproductive organs located on the more vulnerable, terminal blade, rarely endure long enough to accomplish reproduction.

Even the mechanical features mentioned above do not prevent the *Alaria* from being sometimes torn loose by the relatively moderate summer storms. One even then sees scores of blades broken loose from the stipe, and every now and then a tangle of several blades that seem to have been torn free by the successive rupture of all of the holdfasts or stipes, as the waves threw the strain of the whole tangle of blades now on one stipe and then on another. It is evident that the more delicate, frayed blades of the *Alaria* can become tangled far more readily than the blades of the firm *Saccorhiza* do; and in this respect at least the former are at a slight disadvantage. In March and even in June, 1927, as nearly as could be determined in the tumultous surf then prevailing, few large, intact plants of *Alaria* were attached above the level of mean low water. Extending a foot or two vertically above this level was a zone of rock, which could be followed all along the shore, over which were attached numerous "defoliated" holdfasts each supporting at most a short length of stipe, from which the blade had been broken or torn away by the violence of the winter storms. These dismantled holdfasts were, of course, the remains of the uppermost plants observed during the preceding summer.

Saccorhiza dermatodea is the only other large alga that has ever been at all frequent in the sublittoral belt. This species grows to two meters in length and attains a width of ten centimeters. On the rocks directly exposed to the waves this alga in 1923 was outnumbered by *Alaria*, often 100 to 1.

In spots more protected from waves and sun, as in the little notch behind the projecting barrier of rock around 30 N. × 15 E., *Saccorhiza* may in some years be considerably more abundant and also more luxuriant. The vertical range of *Saccorhiza* is evidently decidedly less than that of *Alaria*, usually extending from — 1 foot to + 1 foot. In rather more protected tide-pools, where the alga is more abundant, small plants of it may sometimes be found even as high as 9 or 10 feet. In September 1926 and June 1927 *Saccorhiza* was not seen either in the sublittoral belt or in the tide-pools.

Laminaria digitata is infrequent on the exposed ledges, but occurs sporadically on the protected, shoreward side and is most frequent of all (in dozens or scores) in the lower tide-pools. In fact, one seldom sees elsewhere two individuals that are near enough together to touch each other. On the shoreward side of the rocks we find in some seasons 4 or 5 plants for each 10 meters of shore-line. The greatest size attained in protected areas by *L. digitata*, as far as observed in 1923, is 1.5 m. in total length and 0.5 m. in width of blade. The plants of the wave zone on the exposed side of the rocks are hardly half this size.

Halosaccion ramentaceum: This coarse, filamentous red alga is by far the most abundant plant at the upper margin of the sublittoral belt. In fact, on sloping rocks, as contrasted with vertical ones, *Halosaccion* is so abundant on the seaward side between — .5 feet and + 1.5 or even 2 feet as often to dominate these levels and form a distinct association by itself (Pls. X, XI, Figs. 8, 9, 12). The branched, often rather bushy plants of *Halosaccion* reach a length of about 10 to 15 cm. in early summer, and form dense, close-set stands. It is interesting to find this alga occupying practically the same narrow tidal zone, just above M. L. W., which was dominated by *Chondrus crispus* on the somewhat quieter shores at South Harpswell, in Casco Bay, as was observed by the senior author in 1912–1918. *Halosaccion* persists throughout the year, and plants 12 and 15 cm. long were abundant at Otter Cliffs in March and June, 1927.

Chondrus crispus: Here at Otter Cliffs Chondrus has been almost absent from the open, seaward side of the rocks near low water mark, though it does occur somewhat frequently in tide-pools and on more protected rocks at higher levels. In June 1927, though it was practically absent from our area, *Chondrus* covered many yards of adjoining ledges for a foot above M. L. W. It is hoped that further study of this and neighboring areas may suggest an explanation of the absence of *Chondrus* from the zone which it constantly occupies on the rocky shores of Long Island and of Casco Bay and on certain shores near Otter Cliffs. It at first seemed possible that the absence of *Chondrus* at Otter Cliffs in July and August of 1923 was a chance seasonal vagary and that another summer might see *Halosaccion* replaced by *Chondrus.* But a study of the distribution of these two algae in four later summers showed that Chondrus was always relatively sparse, though in September 1926, it was perhaps as abundant as *Halosaccion.* At this season, however, the latter alga was very sparse and short as compared with all previous summers.

Melobesia Lenormandi: This is, after the kelps, perhaps the most characteristic plant in the midlevels of the sublittoral zone. It is a beautiful, pink, encrusting form, found in large patches on the exposed rocks from M. L. W. downward to at least 5 feet below. It is seen also in drainage sluices from the lower tide-pools, as well as in the tide-pools themselves. In all locations where it was found, *Melobesia* is almost or quite constantly covered by water. It seems intolerant of the loss of any of the water contained in its tissues. This coralline is perennial in habit, being quite as abundant in March 1927 as in midsummer.

Ulva lactuca: This is the only green alga that seems really characteristic of the sublittoral belt on the seaward side. It occurs sparingly from M. L. W. up to 2 or 3 feet. It is found sparingly also, in both spring and summer, in sluices from tide-pools, and often abundantly, as will be noted later, in the tide-pools themselves. It is not present where it could be uncovered for many minutes together. The sheets seen are all comparatively small, the larger only a decimeter or so across. There are thus no sheets that can be compared in size with those 10 meters broad that were found on the mud-bottomed, sewage-tainted inner harbor at Cold Spring Harbor.

Petalonia fascia is an unbranched, narrow, ribbon-like, slightly ruffled, perennial brown alga which occurs rather generally along the upper margin of the sublittoral belt, especially in wetter or more shaded places. The plants reach a width of 10–13 mm. and may grow to a decimeter in length. They often form a dense colony of dozens of plants which may cover a square decimeter or more as *e.g.* in the rill shown in figure 7, plate II. It is especially abundant in spring and early summer. The lowest plants of this alga are found at or below M. L. W. but it reaches to the upper edge of this belt and, along the rills, well up into the lower littoral.

Callithamnion floccosum, bearing tetraspores, was found in March 1927 in a small pool near the upper margin of this zone. It has not been recorded during the summer.

Three other macroscopic algæ scattered in this sublittoral belt are forms which are more characteristic of the lower littoral belt, smaller or larger numbers of which wander down into the upper part of this sublittoral region. *Rhodymenia palmata* is the largest and most striking of these inwanderers from the next higher zone which push down toward, or even to, the M. L. W. level. It grows not merely on the rocks, but occurs also as an epiphyte on the stipes of *Alaria*. *Spongomorpha spinescens* is a green alga from the next zone above (Pl. X, Fig. 10) which sometimes settles, sparingly, on the rocks between the bases of the kelps of this sublittoral belt. *Chordaria flagelliformis* occurs, though rarely, associated with tufts of *Halosaccion* near the upper margin of this belt.

These three algæ, once they have found standing ground, seem to grow as luxuriantly here as they do anywhere. It seems clear that they are really kept from becoming more abundant at these levels merely because the kelps and *Halosaccion* have preempted most of the available attaching surface in the upper portion of the sublittoral zone, which is perhaps the only portion of it that affords these small algæ adequate light. Many plants of these algæ that do start on a bit of bare rock here are soon torn off by the tangles of kelps beside them.

Lower Littoral or Porphyra-Fucus Furcatus-Spongomorpha Belt

(From 2 to 7 feet)

The belt so limited is dominated by a distinct set of plants which are found here only (at least in any abundance), though there are also plants of several other species that wander up from below or spread downward from the next belt above. The characteristic plants which distinguish this belt are, in the order of their prominence: *Porphyra umbilicalis, Fucus furcatus, Spongomorpha spinescens, S. hystrix, S. arcta, Rhodymenia palmata, Ascophyllum nodosum, Rhizoclonium tortuosum, Ralfsia verrucosa, Chordaria flagelliformis, Elachistea fucicola, Ectocarpus littoralis, Enteromorpha compressa,* and *Hormiscia Wormskjoldii.* Certain of these algæ may be found as far as a foot or more below this belt, and in particularly wet or shady places some of them may occur a foot, or two, above it. The zone of their general, and really abundant occurrence, however, has the width above indicated.

Of other forms living in this belt, most are species that occur more abundantly just above or just below it. Such algæ are *Chondrus crispus, Petalonia fascia* and *Halosaccion ramentaceum,* which creep up from below, and *Fucus vesiculosus, Codiolum longipes,* and *Polysiphonia fastigiata,* which push downward from the zone above.

Porphyra umbilicalis is, on the whole, the most widespread alga of the lower littoral belt. It grows especially abundantly on sharply sloping rocks, often on those thickly covered with barnacles (Pls. X, XII, Figs. 9, 10, 17). Most commonly it is attached to the rock itself, but occasionally to barnacles, and it may also, though rarely, grow as an epiphyte, *e.g.*, on *Polysiphonia fastigiata*, which is itself an epiphyte on *Ascophyllum*. The exposed plants of *Porphyra* may here attain 10 or 15 cm. in length, barely half the size it may reach in more protected areas nearby, *e.g.* at Northeast Branch on Mt. Desert Island and at Sullivan's Falls just across Frenchman's Bay. The constantly submerged plants of the lower tide-pools of our area are decidedly larger than those of the exposed ledges. In some places, between the two-foot and the six-foot levels, there may, in midsummer, be as many as five or even ten plants of *Porphyra* to the square decimeter of rock, and the fronds may completely cover the surface for many square decimeters with several layers of their iridescent sheets. Throughout much of the horizontal extent of this zone, however, *Porphyra* is often far less abundant, with only half a dozen or perhaps a dozen plants to the square meter. During low tide on a bright day, these sheets of *Porphyra* dry down to form quite tough, papery layers, much like thin sheets of dried gelatin, which stick closely to the barnacles or to the surface of the bare rock (Pl. X, Fig. 10). With the first few waves of the returning tide the *Porphyra* again becomes flexible, and the individual sheets are soon freed from each other as they are lashed back and forth by the surf. In March 1927, *Porphyra* was fairly common. In June of 1927, it was extremely abundant, often covering 90 per cent of areas 2 or 3 meters square with plants up to 5 centimeters broad (Pl. XII, Fig. 17). It may be pretty completely ground off the exposed rocks by the floating ice during the winter (See Davis '13), though Kjellman ('78, p. 11) found it abundant in Sweden in winter. The plants shown in figure 17 were almost completely washed off by a summer storm two months later.

Fucus furcatus: This wrack forms the next most important element in the vegetation of the lower littoral belt, and occurs on the wetter, or more shaded areas throughout its whole vertical extent. It is much more abundant, however, in the lower half of the belt, where it may grow in the sun; but it flourishes best on the shaded, inshore side of the outer ledges and beside the narrow channels or furrows through the ledges, which, by confining the waves and causing them to splash higher, subject it to more frequent wetting. In some of these localities *e.g.*, on the ledges just east of our tide-stake, also near 100 S., the long, dichotomous, flat and pointed branches of this *Fucus* cover small patches of the ledge, 30 to 40 decimeters across, as completely as *Porphyra* does elsewhere (Pl. X, Fig. 9). Over most of the belt, however, this *Fucus* is scattered rather sparsely, and wherever the midday sun reaches it for more than an hour during low tide, it shows the dwarfing effect of exposure (*i.e.*, desiccation). Near its upper which it occurs higher up, as we shall see. In March and June 1927, the *Ascophyllum* bore scores of ripe fertile clubs on a single plant (Pl. XII. Fig. 15). In midsummer very few of these are seen, and in August, 1927, all mature clubs had dropped off.

Rhizoclonium tortuosum: Though this striking green alga is absent from the exposed, well-drained rocks throughout this belt, its felted tangles do occur, somewhat above, as well as below the water surface of pools and rills (Pl. XIV, Fig. 24). It is therefore merely mentioned here, but will be described more fully in a later paper dealing with the tide-pools.

Ralfsia verrucosa: This encrusting brown alga, although not conspicuous, is very frequent in the lower littoral belt, where it may grow on well-drained rocks, and has a wide vertical distribution, being found in pools even above mean high water level (March 1927). It is restricted to shallow water at the edges of tide-pools, and to trickles over the rocks. In such places it forms velvety, sometimes warty, brown, irregular patches on smooth rock surfaces, sometimes several centimeters across.

Chordaria flagelliformis: This coarsely filamentous brown alga is found in the lower littoral belt more abundantly than anywhere else, though it may, on the exposed seaward side of a ledge, go down into the upper portion of the sublittoral belt, where it is, as noted above, frequent among the tufts of *Halosaccion*. In the lower littoral belt it is found almost exclusively either in or close beside tide-pools, or in little gullies, chiefly in the lower half of the belt. Most frequently the much-branched individuals of *Chordaria*, 2–3 dm. long, occur singly, and these are always attached directly to the rock. This is apparently also a summer species with us, and a careful search in March, 1927, failed to reveal its presence. Young plants, 6 or 8 centimeters high, were common by June 15, 1927. Plants up to 5 centimeters were growing on boulders that had been *sterile* when placed in Pool N on March 30 preceding.

Elachistea fucicola: The distribution of this small, epiphytic brown alga in our area follows closely that of its host, *Fucus furcatus,* which the *Elachistea* infests quite generally throughout its range. It was not found on *F. vesiculosus*. In general, *Elachistea* is most abundant near the upper margin of the range of its host. Copious tufts of it were present in June, 1927. The extreme range noted for *Elachistea* is from the 4-foot level (at 10 N. by 40 E., and 40 N. by 20 W.) up to 7.5 feet (at 40 N. by 30 E.).

Ectocarpus littoralis: This small, delicate brown alga occurs sparsely on the flatter and wetter ledges from mean low water up to 4 or 5 feet. On the whole it is rather more frequent in this belt than in the sublittoral belt, though never conspicuous in either.

Ectocarpus sp. an epiphyte on *Fucus vesiculosus* near Pool A, was found fruiting in March 1927. It may be found elsewhere in winter.

Enteromorpha compressa: This green alga occurs most abundantly, in summer at least, in the upper half of the lower littoral belt, though it is also found in the lower half of the upper littoral. The lowest plants seen were at about the 3-foot level, the highest at 10 feet. It is more abundant on the shoreward side of the ledges, where it is usually restricted to well lighted, but not too well drained, areas. This is a moderately coarse *Enteromorpha* which grows in dense tufts, often of dozens of plants per square decimeter. The individual filaments often reach a length of a decimeter and have a diameter ranging from 2 to 4 mm.

Hormiscia Wormskjoldii: This is another green alga, which though not found at all in summer, did dominate over a restricted area near the 3-foot level, near 25 N. × 15 W. in March, 1927.

Turning now to the half dozen algæ which though more abundant in either the sublittoral belt or the upper littoral, may nevertheless occur more or less frequently in the lower littoral, we will consider first the invaders from below.

Chondrus crispus is, as we have seen, relatively sparse in the sublittoral belt. A few patches of it, however, do get above the lower edge of the lower littoral, outside the tide-pools, in which it is generally present. For example, in a shaded crevice at 40 N. × 20 W. *Chondrus* grew at the 7.5-foot level. At 30 S. × 8 W., where protected by mats of *Fucus* and *Ascophyllum,* diminutive plants of *Chondrus* reach the 9-foot level. In exposed situations, however, it rarely gets more than 3 or 4 feet above M. L. W.

Petalonia fascia: The narrow, ribbon-like fronds of this brown alga are more characteristic of the upper 2 or 2.5 feet of the sublittoral belt, but are still common in the lower part of the lower littoral. Here, however, it is practically confined to the rills that drain the tide-pools, or to those on the seaward side of the ledges where the water concentrates as the splash from each wave runs downward from the rocks above. In these rivulets the plants may, as in 1923, occur in dozens or scores in a meter's length of the narrow rill (Pl. IX, Fig. 7), *i.e.,* as thickly as they do in the sublittoral belt The highest plants of *Petalonia* seen were those in Pool T at 10 feet and Pool G at 10.5 feet. In early September 1926, no *Petalonia* could be seen either in the lower littoral or at the edges of tide-pools, where it had been abundant in midsummer in previous years. In June, 1927, ribbons of this alga, 8 to 12 cm. long, were found in tufts of a dozen or more plants attached to *Mytilus* and *Balanus* as well as to the rock, along the rill from Pool T.

Halosaccion ramentaceum: This is another of the Florideæ from the sublittoral belt that creeps up about a foot into this lower littoral. Like the *Petalonia* found in this belt, it is confined to wetter places, *i.e.,* to the little drainage gullies and to the edges of tide-pools.

Four algæ characteristic of the upper littoral belt often overlap into the lower littoral.

of the belt, while the third alga, *Calothrix scopulorum,* and the lichen, *Verrucaria striatula,* are confined to the upper two-thirds of it.

Near the lower edge of this belt the perennial epiphytic *Polysiphonia fastigiata* is found accompanying its host *Ascophyllum,* while *Porphyra umbilicalis* is represented here by a sparse scattering of invaders from the lower littoral.

Toward the upper edge of this belt there are blackish green patches of *Calothrix,* some of which are nearly pure, while others show, at the proper season for each, more or less of an admixture of *Bangia, Ulothrix* or *Hormiscia. Enteromorpha minima* is most frequent in early spring; but may also persist on wetter ledges till midsummer or later. In fresh water trickles near this upper edge of the belt and somewhat above it, *Enteromorpha micrococca* forms curly tangles (apparently perennial) on shaded vertical cliffs.

In summer another set of algæ are found in patches variously interspersed with the perennial species mentioned above. Velvety felts of *Codiolum longipes* and less frequent coatings of *Enteromorpha compressa* may then form almost pure stands over square meters of the rounded bosses of the ledges and boulders which have not already been occupied by the perennial species or by barnacles.

In winter and spring still another set of algæ, all three of which are absent, or inconspicuous in summer, appear in pure or mixed stands on the same bosses which in summer bear *Codiolum* or *Enteromorpha.* These three algæ are: *Bangia fuscopupurea, Ulothrix flacca* and *Hormiscia penicilliformis.* A fourth species: *Monostroma grevillei* is found scattered sparsely over these levels in spring and early summer.

In addition to these perennial and transient species of algæ that grow exposed on the ledges here, half a dozen other (perennial?) algæ of this belt are confined to the bottoms or edges of the tide-pools or of the rills that drain them. The chief of these are: *Ralfsia verrucosa, Gigartina mammillosa, Spongomorpha spinescens, Rhizoclonium tortuosum* and *Fucus filiformis.* The distribution of these algæ will be discussed in a general description of the denizens of the tide-pools that is to be published later.

The precise distribution of each of the characteristic algæ of this upper littoral belt, outside the tide-pools, is given in the following paragraphs.

Fucus vesiculosus usually dominates on steep, moist or shaded ledges of the upper littoral belt, just as (in summer) *Codiolum* dominates on exposed ones. Its chief competitor in such areas in the lower half of this belt is *Ascophyllum,* of which we shall speak in detail later on. The *Fucus,* like *Codiolum,* is found at all levels across the whole of this belt. It is most abundant and most luxuriant between the 8-foot and the 12-foot levels, where it often dominates considerable stretches of the shore. This species of *Fucus* flourishes about Tide-Pool N where it finds the shaded rocks and large boulders that suit it best. (Pl. XII, Fig. 16). Between 8 and 10 feet above M. L. W. this Fucus grows in dense stands of plants that may, in summer, often reach 2 dm. in length and bear numerous fertile receptacles. Above the 10-foot level, the plants, except in wetter crannies, gradually become smaller, more scattered and nearly or completely sterile.

This *Fucus* bears few epiphytes as compared with the *F. furcatus* which grows lower down. It seems clear that the more rigorous conditions, especially the desiccating power of the air, which restricts the size and the upward spread of the *Fucus* itself, are still more quickly effective on the epiphytic *Elachistea,* and thus prevent it from growing at levels as high as those which its host can endure. The highest plants of this *Fucus* were found at 14 feet, in the shaded recess of the cliff at 52 S. by 75 W., where the atmosphere is kept moist by a fresh water trickle from the rocks.

Ascophyllum nodosum: We mentioned, when speaking of its occupation of the lower littoral belt, that this alga forms its densest growths, attains its greatest size and bears the densest population of epiphytic *Polysiphonia* near the lower edge of the upper littoral belt, *i.e.,* between the 6-foot and the 8.5 or 9-foot levels, as *e.g.* about Tide-Pool N, where it dominates large areas of the almost horizontal rock surface from 6.5 feet upward. At low tide, the long, monopodially branched fronds of this alga lie on the rocks, or float over the *Spongomorpha* on the bottoms of the pools (Pls. VIII, XII, Figs. 1, 16). Though the gentler slopes are usually more completely covered by *Ascophyllum,* there are also many vertical, shaded rock faces which also bear an abundance of this alga. In the tide-pools, *Ascophyllum* is often present where its fronds float at, or slightly above the surface. This alga is rarely found where it would be submerged at low tide, except in a couple of the most elevated and sunny pools, such as a portion of Pool K at 11.3 feet.

Ascophyllum ranges in size from mere stumps, with short "renewal branches," such as are found on the seaward side of the ledges at levels from 4 to 7 feet, up to abundantly branched fronds 5 or 6 dm. in length. Such large plants occur between the 6-foot and 9-foot levels on the somewhat protected areas about Tide-Pools N, E, F, etc., and on the lower rocks of the boulder beach, west of the tide-stake. It is in these more sheltered areas with gentler slopes, between the 7-foot and 8-foot levels, that the large plants of *Ascophyllum* dominate completely (in some seasons at least) over *Fucus* and *Codiolum.* The latter succeeds the *Ascophyllum* above, often occupying the upper part of the same boulder that bears *Ascophyllum* (or *F. vesiculosus*) a few inches below, as on rock 7 in figure 22, plate XIV. Though abundant each summer this alga has usually borne very few fertile clubs. In March and early June, 1927, however, the mature plants were fruiting heavily (Pl. XII, Fig. 15). By August, 1927 all mature clubs had dropped off. Large tangles of *Ascophyllum* were torn loose by the storm of August 24, 1927, but the dense mats about Tide-Pool N. still persisted.

Calothrix scopulorum is a perennial alga that forms the most abundant and most constant constituent of thin blackish green crusts, which cover many square meters of the outer ledges between the 9-foot and 12-foot levels (Pl. VIII, Fig. 4). Another frequent constituent of these crusts is a globular, apparently protococcoid alga. These crusts, which sometimes (Fig. 4) almost merge into the nearly jet black crusts of the lichen *Verrucaria,* evidently persist throughout the year, as they are as well developed in spring and early summer as in the autumn (see Kjellman, '78, p. 12).

Verrucaria striatula is a lichen that is very abundant, especially on the shaded rocks of the upper half of this upper littoral belt. On the exposed, sunny sides of ledges it forms scattered dots, or splashes, in the damper pits in the surface of the rocks. On the shady side of a ledge this lichen often forms continuous black coatings over many square decimeters of rock down to, and even in among, the higher *Fucus* and *Balanus* (Pls. VIII, XII, Figs. 3, 16). On the sunny side the lowest crusts of *Verrucaria* lie close to, or mingle with, the uppermost *Codiolum* and even *Bangia.* These black patches of *Verrucaria* persist throughout the year and probably for many years in succession.

This *Verrucaria* is one of the few lichens that can withstand prolonged submergence in salt water.[3] When high tide occurs at night they must often stay *saturated* with salt water for 10 or 12 hours continuously, though actual submergence may last but 2 or 3 hours. With this capacity for withstanding salt water, it seems probable that it is the reduction of the light by overlying water at high tide that fixes the lower limit of distribution of this lichen. This explanation would be quite in accord with the findings of Plitt ('21, p. 61) who shows that lichens in general are distinctly partial to at least moderately well-lighted habitats.

Polysiphonia fastigiata: This blackish species of the Florideæ is the most conspicuous macroscopic epiphyte in the whole of our area. It is often very abundant indeed in the lower third of the littoral belt. It is always epiphytic and is practically always on *Ascophyllum* (Pl. XII, Fig. 15). In a few cases young plants of *Polysiphonia* grew on older ones. It forms dense, dark tufts attached to the main axes and older lateral branches of the *Ascophyllum,* with sometimes half a dozen tufts per running decimeter of such a branch. Each tuft of *Polysiphonia* is 4 to 6 cm. in height and consists of scores of branches in its upper part, though all of these spring from one parent basal filament. The blackish color of the epiphyte distinguishes it sharply from its lighter colored host.

Like its host, this Polysiphonia seems to be persistent throughout the year. It was abundant and mature in both March and early June, 1927.

Polysiphonia violacea: Bits of this species were identified among algæ collected at Otter Cliffs in March 1927. It has not been seen in summer.

[3] Dr. C. C. Plitt finds 5 intertidal species of *Verrucaria* on the protected, north shore of Mt. Desert Island.

Porphyra umbilicalis: This relative of *Bangia* is so capable of enduring submergence that it occurs abundantly, as we have seen, down to the lower limit of the lower littoral belt at 2 feet. But *Porphyra* is nevertheless so well able to withstand prolonged desiccation that on steeper cliffs, exposed to the full force of the waves, this alga may be found several feet above the upper edge of the lower littoral zone. In particularly favorable places well-developed plants of *Porphyra* may even be found at the 11-foot level. *Porphyra* also occurs occasionally in the tide-pools of this belt.

Enteromorpha micrococca: is a fine perennial species which forms curly tangles on steep rocks wet by dripping fresh water. These tangles occur in the lower edge of the next higher vegetational belt, but at two points in our area they follow these trickles down into this upper littoral. Figure 20, plate XIII, shows a fine tangle of this alga growing 50 yards south of our chosen area.

Codiolum longipes: While *Codiolum* may occur sparsely, as we have seen, in the upper portion of the *lower littoral,* it is in this *upper littoral* belt that it grows most abundantly, and in most summers is widely distributed across the whole belt. Here it is most luxuriant on the convex, gently sloping bosses and ledges of the seaward side, and on stable boulders of the shingle beach where fully exposed to both the sun and the waves (Pls. IX, XIV, Figs. 5, 22). In such places *Codiolum* forms, from midsummer on, dense, smoky green, lubricous turfs, which when wet make walking on these rocks extremely treacherous. *Codiolum* is distinctly a summer species. It was not to be found in March 1927, and in June of that year it formed only a very thin coating, a few decimeters square, not covering the rock surface, though quite continuous. The individual plants were 1/3 mature size. These felts may in some places and in some summers, extend pretty continuously from the 6-foot level, up to 11 feet or even higher, and may far exceed *Fucus vesiculosus* in area covered on the exposed ledges. In the summers of 1923 and 1924 *Codiolum* colonies covered many square meters on the seaward side of the outer ledge of our area (Pl. IX, Fig. 5), completely excluding all other megaphytic algæ and forming pure stands. Now and then at lower levels a sheet of *Porphyra* would be found in the midst of such a colony of *Codiolum,* attached either to the rock itself or to the shell of a barnacle. In other summers, as in 1925, 1926, and 1927, the same rock surfaces were largely occupied by barnacles (Pls. IX, XII, Figs. 6, 14) whereas in 1923 these animals had been confined, at the high levels, to the moister furrows between the convex bosses of the rock (Pl. XII, Fig. 13). In March and June of 1927 this part of the ledge was practically bare of *Codiolum.* The major part of the surface was occupied by *Balanus* while the rounded bosses were often completely covered with *Bangia* (Pls. IX, XI, Figs. 6, 11).

Toward the end of August and in early September, 1923, the epiphytic diatom *Fragilaria striatula* covered extensive areas of the *Codiolum* turfs, as well as the shells of the barnacles growing between them, with a rusty brown coating that gave the *Codiolum* the appearance of being sunburned and dying. Just what harm this smothering brown layer may inflict upon the *Codiolum* is as yet undetermined. It is of interest to note that Mt. Desert Island apparently marks the southermost point on our Atlantic Coast at which this diatom has been collected.[4]

While *Porphyra* and the diatom just mentioned may thus be very closely associated with the *Codiolum,* it is noteworthy that usually when barnacles occur near this alga, each barnacle or each group of them is separated from the *Codiolum* by a ring of bare rock about a centimeter broad (Pl. XIII, Fig. 18). No explanation of the apparent inability of the alga to occupy the rock next to a barnacle has yet been found, and it is but fair to mention that in the case of old established colonies of the crustacean, the *Codiolum* may grow almost in contact with the animal's shell. It has not, however, been found actually attached to the shell of a barnacle. On a nearby part of the shore, at Seawall, boulders were found in the upper littoral belt with the whole seaward side covered continuously with the *Codiolum,* except for several circular areas about 2 cm. in diameter in the center of each of which was a small depression about 5 mm. in diameter (Pl. XIII, Fig. 19). This depression was always found occupied by a small snail which had evidently kept the ring bare by feeding upon the *Codiolum.* The alimentary tracts of the snails from such depressions were often full of *Codiolum.*

With every low tide on a sunny day the club-shaped filaments of *Codiolum* cling together laterally in little tufts, which separate from neighboring groups to expose the colorless stipes in irregular whitish lines surrounding the areas where the dark green tips adhere. (Pl. XIII, Fig. 18). The appearance of these patches of *Codiolum,* when dried out, is a perfectly characteristic one that recalls the color contrasts or "grain" of so-called Spanish leather.

The lowest patches of *Codiolum* seen were at the 5.5-foot level, the highest at 14 feet. The largest patches of *Codiolum* on the convex surfaces of the seaward side of the ledges are between the 8- and 12-foot levels. It is here that the treacherous velvet carpet is most prominent as one looks over the shore as a whole. Back of the barrier ledges, where the waves break on or splash over great boulders or a gentle slope of the ledge, there may be considerable patches of *Codiolum* at still higher levels, up to 13 or even 14 feet, which resemble the turfs just mentioned but are not as extensive, as completely continuous, nor are they often as dense as those near the 10-foot level (Pl. IX, Fig. 5). The largest boulders of the shingle beach (*e.g.* near 25–50 N. × 75 W.) often bear dense felts of *Codiolum* on their

[4] Communication to the authors from Professor C. S. Boyer, who kindly determined the specimens.

exposed tops, while the smaller, mobile boulders bear no algæ at all. The storm of August 24, 1927 rolled the boulders of the shingle beach about so vigorously as to grind off much of the *Codiolum,* or left the felts of the alga on them turned directly townward and so destined to perish from lack of light. From the distribution of *Codiolum,* it is clear that this alga is one which can withstand pretty prolonged drying, though it is rarely out of reach of the waves of each high tide, or at least of their spray. It is thus practically always washed twice a day, and is of course pretty sure to keep moist during darkness, or even when shaded, by moisture attracted by the salts left in it after the sea water evaporates. The higher patches especially are subjected to prolonged wetting and leaching by fresh water, during the rains which occur while the tide is low.

Codiolum plants attached to a boulder withstood 7 days of drying on a shelf in our laboratory, and others 8 days drying on a ledge above high tide, and when later returned to the beach the plants in both cases continued to live. This experiment shows the ability of *Codiolum* to withstand more prolonged desiccation than it would normally be subjected to anywhere between the extreme tide levels at Otter Cliffs. On the other hand, while *Codiolum* can withstand prolonged drying, and also wetting by fresh water, it is evident from its distribution that it cannot endure submergence in sea water continuously, or even nearly continuously. For no patches of *Codiolum* are found nearer mean low water than 5.5 feet. None occur where submerged in tide-pools nor, as we have seen, does this alga grow in the furrows of the rock, where the water draining from tide-pools would run over it during low tide. Its inability to endure continuous submergence was also proved experimentally. Boulders covered by this alga were left submerged in Tide-Pools N and O, and were found bare of all living plants of *Codiolum* after 15 to 25 days. These relations of the plant to exposure and submergence are similar to those presented by many algæ of both the upper and lower littoral belts. Such algæ, though very different in vegetative structure from the mosses and seed plants of the seashore, evidently have something in common with them physiologically, since, like all the latter on this shore, they cannot endure continued submergence. It is, however, difficult to understand why this *Codiolum,* whose relatives succeed so well where constantly submerged, should never grow thus itself. The only suggestion offering itself is that this habit may be connected with the permeability of the cell walls. But it is hard to see how the diosmotic exchange of substances through such a gelatinous wall as that of *Codiolum* could be less satisfactory when the plant is constantly submerged than when it is alternately dried and wetted.

Enteromorpha minima: After *Codiolum,* this *Enteromorpha* is, in summer, the most characteristic green alga of this belt, outside the tide-pools. It is found (1923 to 1927) chiefly on somewhat shaded, steep faces of the cliffs, where often splashed by the waves, but out of reach of wave-flow rivulets. At higher levels, 10 feet and upward, it is oftenest found where shaded or moistened more or less by trickles of fresh water. In such places it may completely cover the rock surface for many square decimeters with a bright green turf, which when dry becomes whitish or milky green in color. During low tide of bright, windy days these plants dry out to a crisp, so that they may be rubbed to a powder between the fingers. In spring and early summer an *Enteromorpha* of apparently this same species is common on the seaward slope of the ledges, *e.g.* near the outlet of Tide-Pool T. This *E. minima* is connected by a seemingly complete series of intermediate forms with typical *E. micrococca,* the distribution of which was noted above.

Enteromorpha compressa: Though this *Enteromorpha* may, in summer, be rather frequent below the zone we are discussing, it is in spring a common constituent of this upper littoral belt. It is here restricted to wetter places at the edges of pools and of small rills, where it forms tufts of simple filaments that stream back and forth with the surging water, as in the drainage furrow shown in figure 7, plate IX. It nowhere grows densely enough to cover considerable areas, but seems rather to fill in small bits of rock surface that chance to be left bare of *Fucus* and barnacles. This alga seems limited to areas where it can never be dried out as completely as *E. minima* may often be, and where it is clear of fresh water. In such situations, it is distributed generally through the lower third of this belt. *E. compressa* is not as abundant at Otter Cliffs as *E. intestinalis* is at similar levels (but always near fresh water rivulets) at Cold Spring Harbor (see Johnson and York, '15, p. 96).

We now turn to the three algæ that are nearly, or quite, lacking from this belt in summer, but which appear, and may become rather prominent in winter and spring.

Bangia fusco-purpurea: This often diminutive red alga, like *Codiolum,* differs markedly in abundance in different summers, but whenever present, is practically confined to this upper littoral belt. It has been found as low as 4.5 feet and as high as the 13.3-foot level, but it is never abundant except between the 8-foot and 12-foot levels.

This alga occurs most abundantly on the rounded, wave-beaten bosses of the outer ledges and on the smooth tops of boulders. Here, on portions of the rock surface not occupied by *Codiolum* or barnacles, *Bangia,* in July 1923, formed very scattered, brownish tufts rarely more than a centimeter or so in height. In other summers these tufts may stand close enough together to form open patches of a decimeter in diameter. The patches have, in midsummer, never been large enough or numerous enough to form a distinct zone on any part of the shore. In more protected areas, behind the outer ledge, *Bangia* is found occasionally, usually much scattered, and here it may grow to longer filaments than where beaten severely by the waves, as it is on the ocean side of the ledge. In March 1927, continuous patches of *Bangia*, often half a square meter in area, grew on the outer faces of the ledges. These were present in June, 1927, but by July had disappeared as if by weathering off, from the middle outward. By August 15, few clumps larger than one's hand were to be seen. The patches of *Bangia* when dry had a light tan color, while when wet they became a dark chestnut brown. The length of the filaments of *Bangia* in spring was often 6 centimeters or more as compared with the 1 or 2 centimeters in the sparse tufts found in midsummer. One patch 3 or 4 decimeters in diameter persisted till September 6, 1927 (near 100 N. × 70 W.).

Ulothrix flacca was found in March, 1927 growing abundantly on the smooth seaward face of the outer ledges and on the boulders of the shingle beach, up to the 10-foot level, or even the 12-foot level. It formed, by itself, or often mixed with *Hormiscia*, a thin slimy, green coating over areas half a meter in diameter or more. A few patches of this alga were still to be seen on June 15, 1927, but all had disappeared by August 1. Further observations are needed to show whether it is a regular occupant of these ledges.

Hormiscia penicilliformis is another green alga that was first seen in March, 1927, and which also persisted till early summer. It may grow in relatively pure stands, of filaments 2 or 3 cm. long, on the ledges or boulders, or it may be mixed with *Ulothrix flacca.* Toward its upper limit *Hormiscia* often mingles with *Calothrix* in forming the blackish crusts on exposed rocks, as at the 16-foot level near our bench mark. On the outer face of the ledge *Hormiscia* is most abundant in the lower half of the upper littoral belt.

Monostroma grevillei is another Ulvaceous genus which may occasionally appear in this belt. It then usually occurs toward the lower border of the belt and on the rocks and in rills of the exposed seaward side.

The vegetation of this upper littoral belt is then, as we have now seen, more varied than that of the sublittoral one. In fact, if we include the tide-pool species of these levels, the vegetation is about as varied as that of the lower littoral belt. In midsummer, most of the plant-covered surface, outside the tide-pools, bears *Fucus vesiculosus, Ascophyllum, Codiolum,* and, near the upper margin of the belt, *Calothrix* and *Verrucaria.* In winter and spring *Bangia, Ulothrix* and *Hormiscia* occupy much the same areas that in summer are commonly covered by *Codiolum.* The algæ characteristic of this belt are in general those able to withstand a considerable amount of desiccation. There is no alga of the lower littoral belt that shows a resistance equal to that of *Codiolum,* save only *Porphyra,* which may sometimes cover square meters of rock surface in the lower half of this belt, as *Fucus* and *Codiolum* do farther up.

Summary and Conclusions

1. The foregoing is part of a report of an ecological study of the vegetation of a rocky, exposed area on the ocean shore of Mt. Desert Island, Maine. It was made during the summers of 1923 to 1927, and in the last week of March 1927.

2. The area studied extends 150 feet along the shore line, while perpendicular to this it reaches from 6 feet below mean low water upward to the top of the Peak of Otter at 193 feet above mean low water. The portion of this area dealt with here, includes a series of intertidal rounded ledges and of steep cliffs, facing the open Atlantic, among which nestle numerous tide-pools of all sizes and at all levels. It includes also an intertidal strip of shingle beach strewn with rounded pebbles and boulders, from a few inches up to several feet in diameter.

3. One main aim of this study was to determine the exact vertical distribution, with reference to tide levels, of the plants found here. We attempted also to correlate the observed vertical and horizontal distribution with the character of the substratum, and with all those other environmetal factors, such as light, temperature, salinity, acidity, and evaporation, which are affected by the alternating submergence and exposure of the plants by the tides.

4. The mean range of tide on our shore is 10.4 feet. After determining the mean low water level, by aid of a tide-staff, we fixed a bench mark on the top of an outer ledge at the 18.8-foot level. The elevations of the various plants and plant habitats were determined by levelling from this bench mark. The horizontal distribution of each plant was determined by aid of a system of coordinates of which the bench mark was the center.

5. In the littoral or submersible region three zones, occupied by characteristic belts of vegetation are recognized: *a*. The sublittoral belt, extending upward to 2 feet above mean low water and characterized by the kelp *Alaria esculenta* and by the red algæ *Halosaccion ramentaceum* and *Melobesia Lenormandi*. *b*. The lower littoral belt, extending from 2 to 7 feet above mean low water and characterized by *Porphyra umbilicalis, Fucus furcatus,* and 3 species of *Spongomorpha*. *c*. The upper littoral belt covering levels from 7 to 14 feet, and characterized the year through by *Fucus vesiculosus, Ascophyllum, Calothrix* and *Verrucaria*. In summer *Codiolum* is abundant, while in winter and spring *Bangia, Ulothrix, Hormiscia* and *Enteromorpha minima* replace the *Codiolum*.

6. Because of the almost constant wave action there is an upward displacement of all of these vegetational belts to some 2 or 3 feet above the levels they would occupy on quiet shores, where the distribution of algæ matches average tide-limits, rather than average wave limits.

7. The horizontal zones of vegetation on this shore are often broken

by rills from the tide-pools, which run tranversely to the shore line, and thus allow algæ which do not tolerate desiccation to push upward to levels higher than they can attain on exposed rocks. The aspect and algal components of the plant covering of a given rock surface, especially of the upper littoral belt, may differ greatly in different years and even in different seasons of the same year.

8. It has been demonstrated experimentally that *Codiolum* cannot tolerate continuous submergence. *Ascophyllum* does not grow where continuously and completely submerged. Neither alga persists where continuously exposed. Further discussion of the relation of distribution to environment will be published in a later paper.

9. Annual variations in the makeup of the littoral vegetation of the same area have been observed. In August 1925, *e.g.*, barnacles occupied much of the rock surface which had been covered by *Codiolum* during the same month in 1923. *Chondrus* also shows marked annual fluctuations in abundance and distribution.

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DESCRIPTION OF FIGURES[1]

Plate VIII

Fig. 1. General view of the intertidal portion of the area studied, looking southeast from 50 north by 125 west; bench mark at +; tide stake at *S*; tide-pools indicated by *K, N,* and *T* are those bearing the same letters on the map, Chart II. The numbers 1 to 7 indicate the same rocks in this and in figure 2. Tide at 2 foot level. Photographed July, 1923.

Fig. 2. View of area studied, from 0 north by 100 west, looking east, at high tide; symbols and numbers indicate bench mark, pools and rocks as in figure 1. A short reef and bell buoy in background. Photographed July, 1923.

Fig. 3. Peak of ledge near 90 N. and 40 W. from 6- to 12-foot levels showing contrast in algal covering on shaded and sunlit sides of the same rock. The dark N. W. side, at left, bears a dense stand of *Fucus vesiculosus* (with rarely an *Ascophyllum*)

[1] The photographs are by D. S. Johnson, except figure 19.

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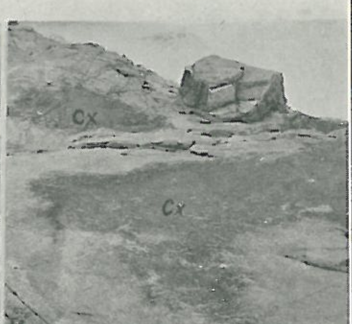

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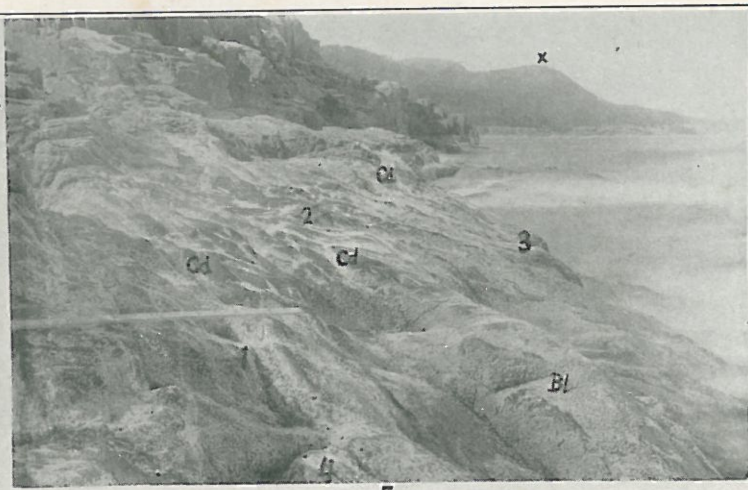

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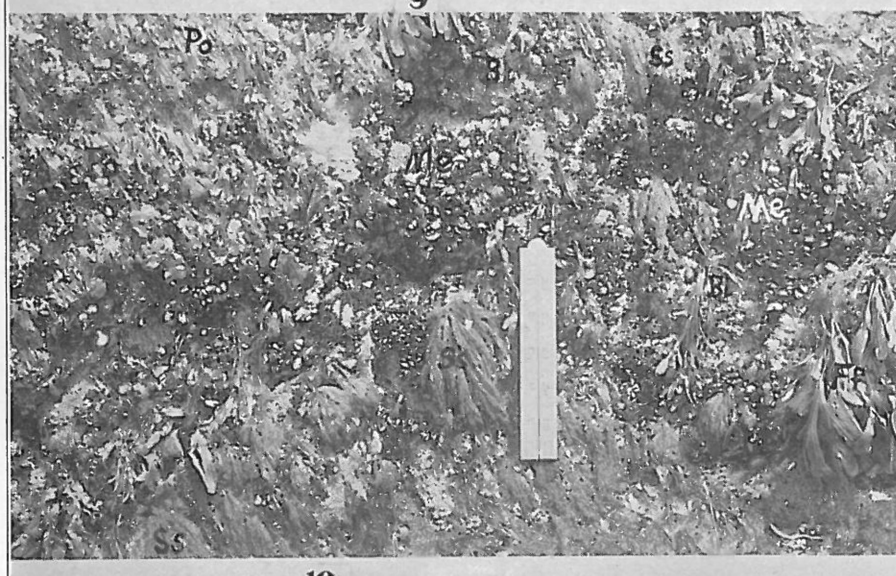

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