THE ECOLOGY OF THE SUBLITTORAL BOULDER BEACHES AT LITTLE BARRIER ISLAND

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ABSTRACT

The sublittoral ecology at three localities on Little Barrier Island is described. A comparison of consolidated shore and boulder beach algal floras suggests that substratum movement is an important and unique factor of the boulder beach habitat. A sequence of boulder recolonisation is tentatively outlined together with a short account of the sublittoral faunas at two of the localities.

INTRODUCTION

Only a few sublittoral ecological studies have been made in New Zealand and these have been mainly concerned with consolidated rocky shores. Boulder beaches offer a particularly interesting environment for ecological studies. Whereas the intertidal region of these beaches has been studied fairly intensively the sublittoral zone has received very little attention

Brief notes on sublittoral boulder ecology at Little Barrier have been made by Trevarthen (1954), Dellow (1955) and Bergquist (1960). The work presented here is the result of a detailed survey made in August 1963.

METHODS

Free diving together with some use of the aqualung permitted extensive observations of the sublittoral. Randon 25 cm^2 quadrats, line transects and belt transects (0 5 m wide) were used to determine the composition of the flora and variations in species distribution. Recordings were made with Chinagraph pencil on perspex or plastic sheets (the pencil marks are readily erased with 95% ethanol). Some underwater photographs were taken but unfortunately are not suitable for reproduction although they have been useful in the elucidation of results. Turf algae were removed from large boulders by scraping them directly into a plastic bag; smaller boulders were removed to the surface for more detailed examination.

TERMINOLOGY

The nomenclature used follows that of the Stephensons' (1949), except for the substitution of the prefix sub- for infra- in the case of the infralittoral and infra-littoral fringe. In their scheme the Stephensons did not further subdivide the sublittoral. A tentative scheme of subdivision for moderately exposed New Zealand stones is suggested, as follows:

(a) The Upper Sublittoral

This zone occurs immediately below the sublittoral fringe. The upper limit is determined by the upper limit of the large brown algae (typically Carpophyllum spp. or Ecklonia radiata). The lower limit is determined by the lower limit of a specific indicator plant. This is Carpophyllum maschalocarpum for northern New Zealand.

(b) The Lower Sublittoral

This begins immediately below the Upper sublittoral and in the North Island of New Zealand extends as a uniform zone to considerable depths (120' or more - Bergquist 1957). The characteristic species is Ecklonia radiata.

Abbreviations for tidal levels follow the standard procedure. The following abbreviations are used to classify species frequency -

(d) = dominant
(a) = abundant
(c) = common
(o) = occasional
(r) = rare.

THE BOULDER BEACH HABITAT

The majority of the coastline of Little Barrier Island consists of boulder beaches. These extend into the sub-littoral for considerable depths in several places on the north and east coasts. Elsewhere the sea bed occasionally becomes sandy at relatively shallow depths. Most boulders are locally derived and hence their size ranges from a few inches to several feet in diameter. They are deposited on the shore at a gradient of 10° - 20°, the gentler slopes being generally formed by the larger boulders. Individual boulders are generally well rounded and show the typical flattened elliptical shape of beach boulders. This prevents close packing, and movement is therefore quite common in both littoral and upper sublittoral zones. It is to be expected then that such an unstable substratum will support an algal association distinct from that of consolidated shores. Also, since movement is to a large extent dependent on the size of individual boulders, it may be expected that the flora will vary according to the average boulder size.

THE COMPARATIVE SUBLITTORAL ECOLOGY OF BOULDER BEACH AND CONSOLIDATED ROCK LOCALITIES

1. TE TITOKI POINT

A typical boulder beach in which the boulders are approximately 12" in diameter (although wide variations do occur) and are relatively loosely packed. Exposed to moderate south-westerly storms.

(a) Sublittoral Fringe range: MLWM - ELWS

Species

1. Xiphophora chondrophylla var. minus (d)
2. Cystophora torulosa (d)
3. Glossophora kunthii (o)
4. Spatoglossum chapmanii (c)
5. Champia novae-zealandiae (c)

6. Corallina officinalis (c)
7. Cheilosporum elegans (o)
8. Jania micrarthrodira (o)

The two dominant algae form a more or less distinct fringe above the true sub-littoral zones.

(b) Upper Sublittoral range : ELWS - 10' below ELWS

1. Carpophyllum plumosum (d)
2 Cystophora retroflexa (d)
3. Laurencia distichophylla (a) also ep.* on 1, 2, 6, 7, 8, 17, 26, 49
4 Spatoglossum chapmanii (a)
5. Glossophora kunthii (a)
6. Zonaria angustata (a)
7. Pterocladia lucida (a)
8. Halopteris spicigera (a)
9. Corallina officinalis (a)
10. Enteromorpha nana (c) also ep. on 1
11. E. procera var. minuta (c)
12. Ulva lactuca (c) also ep. on 1, 8
13. Cladophoropsis herpestica (c)
14. Cladophora sp. (o)
15. Microdictyon mutabile (c)
16. Bryopsis plumosa (o)
17. Derbesia novae-zealandiae (c) ep. on 6, 8
18. Halicystis sp. (r)
19. Caulerpa sedoides (o)
20. Ectocarpus spp. (o)
21. Colpomenia sinuosa (c) also ep. on 1
22. Ecklonia radiata (o)
23. Xiphophophora chondrophylla var. minus (r)
24. Sargassum sinclarii (c)
25. Carpophyllum maschalocarpum (o)
26. Cystophora torulosa (o)
27. Erythrotrichia hunterae (o)
28. Bangia fusco-purpurea (o)
29. Asparagopsis armata (c)
30. Lithothamnion spp. (c)) rock-encrusting algae
31. Lithophyllum spp. (c))
32. Melobesia sp (c)
33. Cheilosporum elegans (o)
34. Cheilosporum corymbosa (o)
35. Jania micrarthrodira (c)
36. Lomentaria umbellata (c) ep. on 1
37. Champia novae-zealandiae (o)

* ep = epiphytic.

38.	C. laingii		(c)
39.	Antithamnion adnatum		(c) ep. on 2
40.	Ceramium	(o) ep. on 1,49	
41.	Myriogramme denticulata		(o) ep. on 7
42.	Abroteia suborbicularis	(o) ep. on 1,24	
43.	Nitophyllum decumbens	(o) ep. on 1,24	
44.	Lenormandia coronata		(c)
45.	Polysiphonia sp.		ep. on 6
46.	Laurencia virgata		(o)
47.	Symphocladia heteroclada		(o)
48.	Dipterosiphonia heteroclada	(c) ep. on 1,37	
49.	Euzoniella incisa	(c) ep. on 6,7,8,49	
50.	Pterocladia capillacea		(o)

The algae of the upper sublittoral exhibit a mosaic pattern of distribution which is largely related to the size of the boulders composing the substratum. The large brown algae Carpothyllum maschalocarpum and Ecklonia radiata occur only on the larger, more stable boulders. Elsewhere Carpophyllum plumosum, Cystophora retroflexa and Glossophora kunthii dominate as a thick canopy with an undercover of smaller reds (Pterocladia spp, Champia, Laurencia), browns (Halopteris, Zonaria, Spatoglossum) and greens (Cladophoropsis, Microdictyon, Ulva etc.)

The ability of these plants to tolerate substrate movement is due probably to the operation of one or more of the following factors :-

(1) rapid growth
(2) extensive reproductive season with germination taking place all year round.
(3) vegetative spread by proliferation (e.g. Carpophyllum plumosum)
(4) plant form

(e.g. Ecklonia stipes are broken very easily, while the slender flexible stipes of Cystophora retroflexa can tolerate abrasion and/or burial by the boulders).

(c) Lower Sublittoral range: from 10-20' below ELWS to an undetermined depth.

This zone was only briefly investigated to a depth of 40'. Below this level it appears to remain uniform for some distance and therefore the lower limit has not been defined.

Species

1.	Carpophyllum flexuosum		(d)
2.	Ecklonia radiata		(d)
3.	Sargassum sinclarii		(a)
4.	Sphacelaria pulvinata	(o) ep. on 1	
5.	Zonaria subarticulata		(o)
6.	Laurencia distichophylla		(o)
7.	Halicystis sp		(r)
8.	Microdictyon mutabile		(o)
9.	Enteromorpha nana		(o)

10.	Cystophora retroflexa	(a)
11.	Spatoglassum chapmanii	(r)

In this zone movement of boulders is probably considerably less than in the upper sublittoral because of the reduction in turbulence caused by wave motion. Possibly a more important factor than boulder movement in determining species distribution is the occasional burial of smaller algae by sand.

2. POHUTUKAWA FLAT

The rock fall at Pohutukawa Flat consists of large angular debris together with smaller rocks. The coast here is considerably more exposed than at Te Titoki Point, and this has contributed to a firm packing of the substratum in the sublittoral.

The sublittoral fringe dominated physiognomically by Xiphophora chondrophylla and Cystophora torulosa has the composition characteristic for all moderately exposed shores in northern New Zealand.

The composition of the upper sublittoral is little different from that of consolidated shores Carpophyllum maschalocarpum is abundant on the larger debris together with frequent Melanthalia abscissa, Vidalia colensoi, Pterocladia lucida, Halopteris spicigera and occasional Carpophyllum plumosum. On the smaller debris Cystophora retroflexa and Carpophyllum plumosum dominate together with the smaller turf algae such as Laurencia, Pterocladia, Enteromorpha and Ulva.

In the lower sublittoral Ecklonia radiata is the sole dominant, forming a conspicuous canopy with an undergrowth of Zonaria angustata and Plocamium costatum.

3. NGATAMAHINE POINT

A consolidate rocky shore with the same slope and aspect as Te Titoki Point. Wave exposure at these two localities is thought to be approximately the same

(a) Sublittoral Fringe range : MLWM - ELWS

Composition of the fringe is the same as that for the boulder shore at Te Titoki Point except for the notable absence of Spatoglossum chapmanii.

(b) Upper Sublittoral range : ELWS - 10' below ELWS

	Species	
1.	Carpophyllum maschalocarpum	(d)
2.	Ecklonia radiata	(a)
3.	Carpophyllum plumosum	(c)
4.	Zonaria angustata	(c)
5.	Sargassum sinclarii	(c)
6.	Vidalia colensoi	(c)
7.	Abroteia suborbicularis (c) ep. on 1	
8.	Halopteris spicigera	(c)
9.	Glossophora kunthii	(c)
10.	Laurencia distichophylla (c) ep. on 3, 4, 8, 14	

11.	Corallina officinalis		(a)
12.	Pterocladia lucida		(c)
13.	Derbesia novae-zealandiae	(o) ep. on. 4, 8	
14.	Colpomenia sinuosa		(o)
15.	Asparogopsis armata	(o) ep. on. 4, 12	
16.	Lithothamnion spp.	(c))	
17.	Lithophyllum spp.	(c)) rock-encrusting algae	
18.	Melobesia sp.	(o))	
19.	Cheilosporum elegans		(o)
20.	Cheilosporum corymbosa		(o)
21.	Champia laingii	(o) also ep. on 1	
22.	Dipterosiphonia sp.	(o) ep on 3, 10, 12	
23.	Euzoniella incisa	(o) ep on 4, 8. 12	

In addition all other species listed for Te Titoki Point occur here infrequently except for Lenormandia coronata, Microdictyon mutabile and Symphocladia sp.

Carpophyllum maschalocarpum is the principal physiognomic dominant forming a thick canopy just below MLWS. This canopy gradually thins out at greater depths, and is replaced in the lower sublittoral by Ecklonia radiata. Ecklonia also occurs in the upper sublittoral in shaded couloirs and on vertical faces. Common sub-canopy species in this zone are Pterocladia, Halopteris, Zonaria and Glossophora.

(c) Lower Sublittoral, range : ELWS to an undetermined depth.

Species

1.	Ecklonia radiata	(d)
2.	Carpophyllum flexuosum	(c)
3.	Zonaria angustata	(o)
4.	Vidalia colensoi	(o)
5.	Plocamium costatum	(o)

The full range of this zone was not fully investigated but the upper part shows definit similarities in species abundance and composition to the lower sublittoral elsewhere in the Hauraki Gulf (Bergquist 1957, Dromgoole 1964).

SUMMARY AND CONCLUSIONS

(a) In striking contrast to the intertidal region of boulder beaches the sublittoral zone supports an exceedingly rich algal flora. This is probably due to the fact that desiccat ion in the intertidal region of such shores is extreme (boulder packing does not allow any retention of water as the tide recedes) and operates as a pressure or absence factor (Chapman 1962) for all algal species Near the level of low tides, however, desiccation is not so severe and a number of algae manage to survive.

(b) A sublittoral fringe is present on both consolidated and boulder shores, althou in the latter it is less distinct from the sublittoral. Its composition is similar at all localit studied

(c) On consolidated rock the upper sublittoral is dominated by Carpophyllum maschalocarpum and Ecklonia radiata. However on boulder beaches these species are largely replaced by Carpophyllum plumosum and Cystophora retroflexa. It should be noted that C. maschalocarpum and Ecklonia radiata do not disappear altogether on boulder shores but occur occasionally on the larger stable boulders.

(d) The distribution of species on consolidated shores can be easily referred to a zonation sequence of successive belts each dominated by one or two algae. For example, the zonation at Ngatamahine Point can be represented by the following diagram :-

Xiphophora chondrophylla Cystophora torulosa	SUBLITTORAL FRINGE
Carpophyllum maschalocarpum Ecklonia radiata	UPPER SUBLITTORAL
Ecklonia radiata	LOWER SUBLITTORAL

There is no succession in time and succession in space is essentially static.

The distribution of species on boulders beaches however is not easily referred to a zonation sequence (although this has been attempted in the brief descriptions presented above), and is best described as a mosaic. Successions in time and space are dynamic (see section on boulder recolonization).

(e) Subsidiary species of the upper sublittoral such as Halopteris spicigera, Laurencia distichophylla, Colpomenia sinuosa, Glossophora kunthii and Pterocladia dapillacea occur in greater abundance on the boulder shores (cf. species lists for Te Titoki and Ngatamahine Points).

(f) The differences between the two types of communities which have been summarised in (c), (d) and (e) above are considered to be due primarily to a difference in the nature of the substratum. Movement of the substratum at Te Titoki Point prevents the establishment of slow-growing species such as Carpophyllum maschalocarpum (Dromgoole 1964) or those which cannot tolerate burial or abrasion e. g. Ecklonia radiata. These species can, however, dominate on the consolidated rocky shores where there is no substratum movement.

(g) In the lower sublittoral the 3 localities examined show few differences. This is to be expected since movement of the boulders in this zone is infrequent, owing to decreased turbulence.

BOULDER RECOLONIZATION

Because boulder movement is common in the upper sublittoral and the sublittoral fringe it is likely that bare rock surfaces (i. e. previously uncolonized by algae) may occasionally be uncovered. The new rock surfaces are soon colonized by a number of algal species. Provided that the boulders remain stable for long enough, plants with large thalli such as C. maschalocarpum and Ecklonia radiata will become established. However, stability is dependent to a large extent on boulder size, and therefore, in the sublittoral, a number of stages of recolonization can be seen on the various boulders. This results in a mosaic pattern of small boulders with young plants and larger, more stable boulders with the older, and generally larger, plants. Even on the same boulder a number of stages of recolonization can exist together, since different parts of the boulder may be exposed or buried at various times.

Movement of the boulders may also result in burial of boulders supporting algal growth. These buried algae soon die and decay leaving only a light covering of microfauna. Thus there is a return to the initial phase in recolonization.

By comparing the algal floras growing on boulders of the same and different sizes, it has been possible to determine a general sequence of recolonization. Stages in the sequence are outlined below :-

(1) Initially the bare rock surface, even if it has not been previously colonized will have a slimy covering of marine bacteria and other microfauna. A covering of microscopic organisms together with minute inorganic particles provides a favourable surface of recolonization (Coe and Allen 1937). Thus boulders (formerly carrying algal growths) which are buried and uncovered at a later stage will undergo a more rapid recolonization process than newly exposed surfaces.

(2) The first noticeable phase of colonization is the appearance of a smooth light brown covering of colonial diatoms. These soon become subordinate in importance, although they persist throughout the complete sequence quite often as an epiphyte on the larger algal species.

(3) The earliest macroscopic algae to appear are several species of Enteromorpha including E. nana and E. procera f. minuta. These species are however transitory and are gradually replaced by a light cover of Ulva lactuca, Bangia sp., Erythrotrichia kunterae and Bryopsis plumosa.

(4) After the Enteromorpha/Ulva phase there follows another dominated by Ectocarpus spp, Scytosiphon lomentaria and Colpomenia sinuosa. These species flourish for a time after which they disappear almost completely.

It may be that this phase is also an alternative to the Enteromorpha/Ulva phase, since the appearance of perennial algae of slow growth, which is the next major phase can occur after either of these stages.

It is interesting to note that at Cape Peninsula Enteromorpha dominates the initial phases (Bokenham 1938) whilst at La Jolla Ectocarpus occupies the early stages of the sequence of recolonization. (Wilson 1925). In New Zealand the particular phase may depend on the time of year at which recolonization takes place.

At approximately the same time as Ulva and Enteromorpha appear there is also a settling of barnacle larvae In the sublittoral this growth is not heavy and is generally subordinate to the algal phases.

An important modification of the colonization process is the impregnation of the Ulva/Enteromorpha mat by sand particles. This particular substrate favours colonization in the later phases by Carpophyllum plumosum.

(5) Following the appearance of phases dominated by species of relatively rapid growth and transient appearance there is a phase in which perennial slow-growing species of Gelidium, Chaetangium, Laurencia and Champia dominate. The encrusting Coralline species also appear at approximately the same time.

(6) Phase (5) may persist for some time or else it may pass into a phase of growth dominated by Glossophora and Spatoglossum, together with zoning plants of C. plumosum and Cystophora retroflexa. Juvenile plants of Ecklonia radiata and C. maschalocarpum

are often found at this stage but because of their intolerance to substrate movement they never mature and therefore do not dominate in the final phase.

(7) The final phase (climax) is represented by a dominance of either C. plumosum or Cystophora retroflexa, with smaller turf-forming algae such as Pterocladia lucida, Glossophora kunthii, Spatoglossum chapmanii, Laurencia spp., Zonaria angustata and Champia novae-zealandiae.

Any one phase can return to any other preceding phase (by abrasion) or to the initial phase (by burial and subsequent uncovering) but the forward sequence of phases is always maintained in the order outlined above. This sequence should, however, be regarded as tentative only. It is based on comparative observations above and as Bokenham (1938) and others have shown that recolonization depends upon :-

(i) time of denudation
(ii) population of adjacent rock (boulders)
(iii) level of the denuded patch (boulder)
(iv) degree of wave exposure.

It is realised that further work is necessary to confirm the above conclusions.

BOULDER BEACH FAUNA

The sublittoral fauna of the boulder beach is not as rich as that of the consolidated shore. Movement of the substrate at Te Titoki Point appears to be responsible for the absence of large species such as Cookia, Evechinus and Buccinullum.

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