ZONATION OF SUBLITTORAL ROCKY BOTTOM MARINE LIFE AND ITS CHANGES FROM THE OUTER TO THE INNER HAURAKI GULF, NORTH-EASTERN NEW ZEALAND

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SUMMARY

Rocky bottom marine habitats and their associated biota fall into a sequence of zones, in much the same way as zones are apparent on the rocky shore. Underwater, the zones are dependent mainly on light intensity (related to depth and water clarity), and degree of water movement. In north-eastern New Zealand, on a steeply shelving rocky bottom in moderate wave exposure, the following sequence of zones usually occurs with increasing depth: (1) shallow mixed weed zone, with species of *Carpophyllum* dominant; (2) rock flats zone, large algae rare or absent, but abundant kina or sea-eggs (*Evechinus chloroticus*); (3) kelp forest, with abundant *Ecklonia radiata*; (4) deep zone, with sponges and sparse *Ecklonia*; (5) very deep zone, with abundant sponges and other suspension feeders, and no large algae. The sequence is often truncated by a change to a sediment substrate, and irregular topography of the rocky seabed often makes the sequence difficult to observe. In very sheltered water, such as the inner Hauraki Gulf, the *Ecklonia* of the kelp forest is usually replaced by, or mixed with, a forest of tangled bladder wrack (*Carpophyllum flexuosum*), and the rock flats zone is absent. On entering the Gulf from the outer islands, the depth of the boundaries between the zones becomes progressively shallower with decrease in water clarity and wave-induced water movement.

INTRODUCTION

Zonation of rocky shore organisms of north-eastern New Zealand has been extensively documented in a number of works, beginning with early studies at the Poor Knights Islands by Cranwell and Moore (1938). Since then, the most accessible detailed accounts have appeared in various books, for example Morton and Miller (1968), Miller and Batt (1973), and Westerskov and Probert (1981). A further account is included in this volume (Morton and Walsby 1983).

Studies of zonation of rocky bottom marine life below the tidal zone were hampered by difficulty of access, until the advent and subsequent popularisation of SCUBA-diving techniques in the early 1960s. It is fitting that some of the earliest work on zonation of underwater life was
carried out at the Poor Knights Islands, where the major early work on
intertidal zonation was also undertaken. Wade Doak’s pioneering book
on underwater life, “Beneath New Zealand Seas” (Doak 1971), first
described and illustrated the changes from low tide to maximum
SCUBA depths some 60 m below the surface. The second edition of
Morton and Miller’s “The New Zealand Sea Shore”, which appeared in
1973, contained an additional chapter exclusively devoted to patterns of
marine life beyond the shore. Other books which discuss rocky bottom
marine life are those by Doak (1979) and Westerskov and Probert
on the Hauraki Gulf Maritime Park, discusses and illustrates rocky
bottom zonation in the Hauraki Gulf.

A series of pamphlets on the marine reserve at Leigh is being
produced, some of which discuss underwater zonation and details of
marine habitats, e.g. Walsby (1982). Some specific habitats were
discussed by Ayling in the New Zealand Nature Heritage series, e.g.
kelp forests (Ayling 1974a, 1974b). From the early 1970s, a series of
papers in Tane outlined rocky bottom zonation at a number of offshore
island localities: Red Mercury Island (Grace 1972), White Island (Grace
1975), Moturoa Islands (Grace and Puch 1977) and Mokohinou Islands
(Riddell 1980).

Classification and mapping of rocky bottom zones and habitats was
pioneered by Ballantine, Grace and Doak (1973) at Mimiwhangata.
Since that time ideas on the classification and naming of marine rocky
bottom habitats has evolved, and is continuing to evolve. Between 1975
and 1979, detailed mapping of marine habitats in the marine reserve at
Goat Island, Leigh, was carried out. The habitats were outlined by
Gordon and Ballantine (1976) and described by Ayling (1978), and
published in detailed coloured map form through the Department of
Lands and Survey (Ayling, Cumming and Ballantine 1981). An area at
Paparahi, near Mimiwhangata, was mapped in 1981 (Grace 1981),
extending the area mapped at Mimiwhangata in 1973. A direct
comparison of the habitats defined and mapped at Paparahi (Grace
1981), Mimiwhangata (Ballantine, Grace and Doak 1973), and Goat
Island, Leigh (Ayling, Cumming and Ballantine 1981), is given by Dart,
Drey and Grace (1982), so that the slightly different classifications and
names given in each of those works can be related to each other.

So far little attempt has been made to generalise about changes in the
zonation in relation to physical changes in the environment as we
proceed from the “oceanic” conditions of the outer Hauraki Gulf, to the
“harbour” conditions of the inner Gulf and Waitemata Harbour. There
is, however, a considerable wealth of information on the effects of light
and water movement on rocky bottom marine life of the marine reserve

This paper summarises the characteristics of each of the underwater
rocky bottom zones and habitats, and makes a preliminary attempt to outline changes from the outer to the inner Gulf. These changes are somewhat analogous to those illustrated by the classical exposure/shelter diagrams of rocky shore zonation (e.g. Morton and Miller 1968, fig. 93, p. 268), but some of the major factors controlling the changes are different underwater from those on the shore.

UNDERWATER ZONATION

Because of the light-absorbing properties of seawater and the planktonic and detrital material suspended in it, the quantity of light reaching the seabed decreases with increasing depth. As depth increases, the quality of light also changes, with light at the red end of the spectrum being absorbed first. Since plants require light in order to carry out their vital process of photosynthesis, there comes a depth at which there is no longer sufficient light to support seaweeds. Different kinds of seaweeds need different amounts and quality of light. They are also able to tolerate different degrees of water movement. As a result, a zonation pattern has developed on the rocky seabed in much the same way as zones are apparent on the rocky shore. Underwater, the major factors influencing the zonation are light and water movement, both of which are generally related to depth.

In the outer Hauraki Gulf, the greater vertical extent of the subtidal zones, combined with the irregular topography of the seabed, often makes the zonation sequence underwater more difficult to observe than intertidal zonation. In addition, the zonation is often disrupted where changes in substrate (e.g. rock to sand) prevent a continuous sequence from shallow to deep water. Where a steeply shelving, continuous rocky bottom occurs, however, a clear zonation pattern is evident.

In north-eastern New Zealand, on a steeply shelving rocky bottom in moderate wave exposure, the following sequence of zones usually occurs, in order of increasing depth:

1. Shallow mixed weed zone.
2. Rock flats zone.
3. Kelp forest.
4. Deep zone.
5. Very deep zone.

OUTLINE DESCRIPTION OF ZONES

1. Shallow mixed weed zone (Fig. 1 & 2)

   This zone occurs in shallow water from low tide to about 6 m, but is often restricted to the shallower part of this range. It fringes most of the rocky shores and reefs. The substrate in this area is often, but not always, very broken and dissected, with tumbled boulders, ridges and
crevices: clearly related to the alternative name of "shallow broken rock" for this zone (Ayling 1978).

Several species of large brown algae are the dominant life forms. The most abundant is usually the bladder wrack (*Carpophyllum maschalocarpum*), often with small plants of the common kelp (*Ecklonia radiata*) in the deeper areas or more sheltered parts of the zone. Where wave action is moderate or heavy, the upper part of the zone is characterised by a fringe of the wave-exposure-tolerant surf wrack (*Carpophyllum angustifolium*), which forms a dense swirling carpet, the vertical extent of which is determined largely by the degree of wave turbulence. Usually *C. maschalocarpum* appears immediately below *C. angustifolium*, but in the most wave-exposed areas it may be replaced or accompanied by either or both of the red seaweeds *Pterocladia lucida* and *Vidalia colensoi*. In maximum wave-exposure, another surge-loving weed occurs in the deeper parts of this zone. This is *Lessonia variegata*, which appears superficially similar to *Ecklonia radiata* but differs in having a divaricating stipe or stalk. Also in heavy wave-exposure, the oak-leaved kelp *Landsburgia quercifolia* frequently occurs as scattered plants amongst the other seaweeds. Tolerant of a wide range of wave exposure, and occasionally forming monotypic stands, is the smaller finely-branched *Carpophyllum plumosum*.

On entering more sheltered conditions approaching the Waitemata Harbour, the character of the shallow mixed weed zone gradually changes. *C. maschalocarpum* becomes confined to a very narrow band close to low water level. *Ecklonia radiata* appears very quickly below low tide, and is often accompanied by the tangled bladder wrack (*Carpophyllum flexuosum*) and *Cystophora retroflexa*. *Sargassum sinclairii* is another brown seaweed which becomes increasingly common approaching greater shelter. In the inner harbour itself, *Carpophyllum* species tend to disappear and *Ecklonia* extends right up to low tide.

In the outer and middle Gulf, the sea-egg or kina (*Evechinus chloroticus*) is common in this habitat, usually nestled into holes, crevices and depressions, where it can gain some shelter from wave action. Here it generally feeds on drift algae torn off the rocks by waves. Kina seem to be less common in sheltered waters closer to Auckland. In the outer Gulf, and particularly around the offshore islands, the spectacular purple-spined urchin *Centrostephanus rodgersii* also occurs occasionally in this zone, usually under slight overhangs or on vertical faces. It is excluded from the inner Gulf possibly by reduced salinity, rarely occurring south of Kawau Island. An abundance of brightly coloured sponges and other filter-feeders lives in darkened crevices and under ledges.

This zone is one of the most varied and interesting, and provides some of the best areas for snorkel diving. In the middle and outer Gulf, the
greatest abundance and variety of reef fishes occurs in this habitat, particularly where reef-top gullies and canyons dissect the rocky shore around islands and reefs.

2. Rock flats zone (Fig. 3)

Below the mixed weed zone is an area characterised by a lack of large brown seaweeds, the rock surface giving the appearance of being bare and relatively barren. Although described as rock flats, since most of the areas classified as such are of fairly low relief, the topography may be much more broken and of quite high relief. This habitat may also occur on a boulder bottom.

In the outer Gulf, the rock flats zone commonly begins at a depth of about 3 to 6 m, and extends to about 8 or 10 m, although the depth of the boundaries varies within wide limits. Often the rock flats zone is absent from very sheltered water, and particularly from the inner Gulf south of about Tiritiri Island.

Although appearing barren, nearly the whole rock surface is covered with a thin film of mauve to pink encrusting coralline seaweed. The most conspicuous animal here is the kina, which is often present at a density of 5 to 10 per m², but locally may be even more abundant. It is the grazing activity of the kina which maintains the habitat in its relatively barren state, since recently settled algae and encrusting animals are removed before they have a chance to grow. The five-pointed star-shaped teeth marks of kina can sometimes be seen on the surface of the pink coralline seaweed. Kina also feed on drift weed which has been torn from the rocks by the waves, and occasionally they eat living seaweed on the edge of adjacent weed beds.

Despite its barren appearance, this zone is highly productive with a rapid turn-over of biological energy, although at any one time the standing stock is relatively low. Several species of small grazing molluscs live here, such as the stellate limpet (Cellana stellifera), and the green top shell (Trochus viridis). Larger grazing molluscs include our largest chiton (Eudoxochiton nobilis) and the Cook’s turban shell (Cookia sulcata), a rough-surfaced gastropod about 100 mm in diameter. The Cook’s turban shell is occasionally eaten by the eagleray, which crushes the shell in its powerful jaws and leaves a tell-tale pile of iridescent shell fragments.

Sometimes kina move into areas where large seaweeds are growing, and deliberately cut down seaweed plants for food, leading to an extension of the rock flats zone (up to 5 m per year - Ayling 1978) at the expense of the adjacent seaweed-dominated zones. This has happened widely in the Hauraki Gulf, Northland east coast, and Bay of Plenty in the past twenty to thirty years. Evidence from a time-series of aerial photographs is confirmed by long-term diving observations in several areas, e.g. Mimiwhangata. It has been suggested that the apparent
increase in kina leading to extension of the rock flats zone may be a
result of heavy fishing for snapper and crayfish, both important
predators of kina.

3. Kelp forest (Fig. 4 & 5)

In shallow to medium depths, the rocky bottom is often covered with
a forest of the common kelp (*Ecklonia radiata*) (Fig. 4). Most commonly,
the top of the kelp forest is bounded by the rock flats zone, but in
sheltered areas the kelp forest often occurs adjacent to the shallow
mixed weed zone, and may imperceptibly intergrade with it. In many
coastal areas the bottom of the kelp forest drops abruptly on to sand.
Kelp forest is extensive along the Northland coast and offshore islands,
the Hauraki Gulf, and Bay of Plenty.

Kina are almost entirely absent from the kelp forest, despite the
obvious abundance of food. Kina do, however, on occasions attack the
boundary of the kelp forest, and over a period of several years can
seriously reduce the area occupied by *Ecklonia*, converting it to a rock
flats habitat.

The canopy of *Ecklonia radiata* greatly reduces the light intensity on
the rock surface beneath. This creates favourable conditions for small
encrusting animals such as bryozoans, hydroids, sponges and ascidians,
which in shallow water live only under darkened ledges.

*Ecklonia* may exist as an unbroken forest on extensive low-relief rock,
but often occurs on a substrate of high relief rock. In these
circumstances *Ecklonia* grows on the well-lighted tops and ridges, with
rich encrusting life occupying the vertical and overhanging walls of
canyons. This is spectacular SCUBA-diving country, where the large-
scale scenery and wealth of encrusting life provide a good range of
subject material for the underwater photographer.

*Ecklonia radiata* is one of the few larger brown seaweeds which ranges
from the outermost islands such as the Poor Knights, to the inner
Waitemata Harbour. At the Poor Knights it still occurs as scattered
plants on the outer coast to a depth of 55 m because of the very clear
water, whereas in the turbid waters of the inner Waitemata Harbour it
is rare below 1 or 2 m.

In the most sheltered rocky bottom areas, protected from heavy wave
attack by islands and reefs, and in the sheltered waters near the mouths
of harbours, a thick, almost impenetrable kelp forest of the tangled
bladder wrack (*Carpophyllum flexuosum*) occurs (Fig. 5). It can extend
from just below low water in sheltered harbour situations, to at least 20
m in South Harbour at the Poor Knights. It often seems to replace
*Ecklonia radiata* in the more sheltered areas, although close to
Auckland *C. flexuosum* and *Ecklonia* frequently form a mixed forest.
*Ecklonia radiata* often tends to dominate on ridges, while *C. flexuosum*
is prevalent in hollows.
Fig. 1. The shallow mixed weed zone fringes most of the rocky shores and reefs. Several species of large brown algae are the dominant life forms.

Fig. 2. In maximum wave-exposure, the shallow mixed weed zone is characterised by *Carpophyllum angustifolium* and *Lessonia variegata*.

Fig. 3. The rock flats zone is devoid of large algae, because of the grazing activities of the kina *Evechinus chloroticus*, which reaches maximum densities in this zone.

Fig. 4. In shallow to medium depths, the *Ecklonia* forest, characterised by the common kelp *Ecklonia radiata*, occupies extensive areas of the rocky bottom of north-eastern New Zealand.

Fig. 5. In sheltered rocky bottom areas, a thick forest of the tangled bladder wrack, *Carpophyllum flexuosum*, often occurs, individual plants often reaching 4 or 5 m in height.

Fig. 6. In deep water, where there is insufficient light to support large seaweeds, the very deep zone is occupied by a wide range of filter-feeding animals. In the outer Hauraki Gulf, gorgonian fans and sponges are dominant.
Individual plants of *C. flexuosum* often reach 4 or 5 m tall, and diving in these areas can give a true feeling of being in a forest. The abundance of kina varies in the *C. flexuosum* beds, but it is never very common here, although individual kina may reach a very large size.

Except at the Poor Knights Islands, the seaweed, and the rock substrate of the *C. flexuosum* beds, is nearly always covered with a thin layer of fine detritus settled out from the relatively calm waters. This detritus, rich in organic matter, provides food for a range of specialised detritus and deposit feeders, such as the sea-cucumber (*Stichopus mollis*), found on the rocks and in crevices beneath the weed canopy. This large brown holothurian, about 150 mm long, licks detritus from the rock surface, and digests bacteria and other nutritive material from the deposit.

With increasing exposure to wave action, *Carpophyllum flexuosum* forest often intergrades with *Ecklonia* forest, but towards low tide usually gives way to *Carpophyllum maschalocarpum* and a narrow strip of the shallow mixed weed zone. In sheltered areas of the East Coast Bays of Auckland, a mixed forest of *Ecklonia radiata*, *Carpophyllum flexuosum*, and *Cystophora retroflexa* often occurs in shallow water, grading into pure stands of *C. flexuosum* in deeper water.

4. Deep zone

As light levels diminish in deeper water, kelp plants become more scattered, and the larger sponges start to appear. Within this zone, light levels become so low that *Ecklonia radiata* is barely able to carry out photosynthesis at a sufficient rate to replace energy lost through respiration. Large algae here are living close to their limits of tolerance, and are poorly equipped to compete with other organisms.

Freed from severe competition with the larger algae for living space, several sponges become important with increasing depth. In this zone the usual types are the massive grey *Ancorina alata*, the yellow *Cliona celata*, the yellow or orange football sponge *Polymastia granulosa* (particularly close to the rock/sand boundary), the related brown football sponge *P. fusca*, the orange branching *Raspailia* sp., the tall finger-sponge *Calyspongia ramosa*, the brownish “tennis-ball” sponge *Aaptos aaptos*, and sometimes the massive orange cup sponge *Stelleta crater* or its crimson relative *S. hauraki*.

A few of the smaller encrusting bryozoans and sponges which were found under ledges in shallower water, begin to appear on open rock surfaces in this zone.

In the sheltered, turbid waters of the inner Gulf, this zone may become vertically compressed, and often the dominant seaweed remaining would be the tangled bladder wrack *Carpophyllum flexuosum*. 
5. Very deep zone (Fig. 6)

When there is no longer enough light to support the large brown seaweeds, a very deep zone contains a rich growth of filter-feeding animals of varieties accustomed to dim light and quiet water. The general lack of violent water movement allows the development of delicate and diverse branching structures, much needed in quiet water to increase the filtering surface and food-gathering ability of the organisms. Tall, branching sponges, such as *Iophon*, *Raspailia*, *Desmacidon* and *Calyspongia* dominate the scene. In the outer Hauraki Gulf, from about the Chicken Islands northwards, the sponges are accompanied by pink gorgonian fans of a species of *Primnoides*, which in places carpets the rock surface with its delicate upright branches 100 to 300 mm tall. The fans tend to be aligned across the prevailing current to maximise the food-gathering surface for the tiny bead-like polyps occurring in rows on the branches. In maximum SCUBA depths (about 45 to 60 m), occasional ghostly-white branching “trees” of the antipatharian black coral can be found where there is a gentle current.

The rock surface between the larger branching forms of marine life is a kaleidoscope of small colourful encrusting animals, including bryozoans, simple and compound ascidians, encrusting sponges, hydroids, cup corals, and tube worms. Small red seaweeds are also found here, including encrusting types and a few delicate branching forms, being able to tolerate much dimmer light than that required by the larger brown seaweeds. In the outer Gulf, some spectacular starfish are also found in this zone, such as the multi-coloured fire-brick star *Asterodiscus truncatus* and the brilliant yellow *Knightaster bakeri*.

In many coastal areas, the very deep zone cannot develop because of the change from a rocky to a sediment substrate before a suitable depth is reached. This zone commonly occurs around the offshore islands, however, and is seen at its best at the Poor Knights Islands. Closer to Auckland, the few areas where sufficient depth is reached on a rocky bottom, show that the character of the very deep zone is rather different from that developed around the offshore islands. The much higher sediment loading in the waters of the inner Gulf is apparently responsible for the exclusion of many of the more spectacular branching forms of filter feeders, their delicate filtering devices being unable to cope with the silt load.

Most of the organisms of the very deep zone of the inner Gulf and Waitemata Harbour are capable of removing quantities of silt which steadily rains down over their surface. Sponges, such as the red encrusting *Microciona*, the orange golf-ball *Tethya aurantium*, and the brownish tennis-ball *Aaptos aaptos*, are well-adapted for life in silty harbours, where the “very deep zone” may start only a few centimetres below low tide level. Equally at home here are the bryozoans *Dakaria*
subovoidea and Bugula flabellata, the simple ascidians Microcosmus kura, the pink Corella eumyota and the purple Asterocarpa coerulea, and the little pink or purple “mushrooms” of Hypsistozaa, a compound ascidian. The few taller branching species able to tolerate the silt load of the harbour include the gymnoblastic hydroids Tubularia larynx and Pennaria australis.

In slightly less silted conditions where there are moderate currents, such as the Tiritiri Channel, spectacular brightly coloured fluorescent masses of the corallimorph jewel anemone Corynactis haddoni add welcome splashes of brilliant colour to an otherwise relatively drab very deep zone of the inner Gulf.

Other habitats
Several other rocky bottom habitats have been recognised, for example the “Sponge garden”, and “Sediment-covered rock flats” at Goat Island, Leigh (Ayling 1978). These are rather localised in occurrence, and are beyond the scope of this general treatment of sublittoral rocky bottom zones.

CHANGES ON ENTERING THE HAURAKI GULF

The succession of rocky bottom zones is affected by depth, as related to light levels and water movement on the bottom. The more turbid waters of the inner Gulf restrict light penetration to shallow depths, with the result that the larger seaweeds cut out progressively shallower on entering the Gulf. Other changes relate to increasing shelter from wave action in the inner Gulf, such as the loss of Carpophyllum angustifolium, and the more widespread appearance of C. flexuosum. Increasing sediment load in the waters on entering the Gulf undoubtedly excludes some of the more delicate filter-feeding organisms so prevalent in the very deep zone of the outer Gulf and offshore islands. Reduced salinity of the inner Gulf may be partly responsible for the disappearance of the rock flats zone dominated by kina.

Although the depth of the boundaries between the zones varies considerably, even within a relatively small geographical area, as a result of variations in wave exposure, water movement, angle of slope of the rocky bottom, aspect to sunlight, etc., there is nevertheless a trend apparent as we proceed from the outer Gulf to the inner Gulf. In general, the boundaries between the zones occur in progressively shallower water on entering the Gulf, and, as previously noted, some of the zones change character dramatically, and other zones disappear altogether. An attempt to summarise this trend is illustrated in Fig. 7, based on information from seven localities from the Poor Knights Islands to the Waitemata Harbour. Detailed localities are on the more open coasts in each area, where possible on a steeply shelving rocky bottom.Sources of
Fig. 7. Diagrammatic representation of the major changes in zonation of underwater rocky bottom marine life from the outer to the inner Hauraki Gulf (Poor Knights Islands to Waitemata Harbour).

information are as follows: Poor Knights Islands (Doak 1981, personal observation); Mimiwhangata (Dart, Drey and Grace 1982); Chickens Islands (personal observation); Goat Island (Ayling, Cumming and Ballantine 1981, Walsby 1982, Grace 1983, personal transect data); Tiritiri Channel (personal observation); Castor Bay (Grace 1980); Northcote Point (personal observation, Morton and Miller 1968). The information on which the diagram is based is fairly precise in some places but sketchy in others. It is hoped that, by making this first
attempt, others will be encouraged to improve on the information, and refine the diagram.

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