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The Recolonization of Rock Surfaces and the Problem of Succession

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with 6 plates and 2 text figures

Summary

The colonization of new rock surfaces was observed experimentally as well as the recolonization of artificially denuded rock surfaces. Although in both cases the initial settlement of the larvae was successful there was a heavy mortality soon afterwards with a consequently slow rate of recolonization. This was attributed to environmental factors. It is seen that recolonization of rocks after natural denudation is very much more rapid. Seasonal number growths of *Porphyra, Scytosiphon* and *Ulva* are recorded.

Introduction

Small scale experiments were carried out in an attempt to ascertain the sequence of colonization of bare rocky surfaces on the shore in the region of Pinnacle Point at the south end of Blackman's Bay. Blackman's Bay was chosen as the area in which to conduct the experiments because it could be visited at frequent intervals, is easy of access and its fauna is reasonably well known.

In order to throw some light on the poverty of the fauna of the Midlittoral zone the original experiments were carried out in the lower part of the barnacle and the upper part of the *Galeolaria* belts. Later experiments were commenced in the *Mytilus* belt. Due to circumstances beyond my control, both series of experiments were inconclusive but certain interesting results were found.

Literature

Work has been carried out in various parts of the world on the problems of intertidal colonization. In some cases the workers have been concerned with the colonization of new rock surfaces and in others the emphasis has been placed on the recolonization of denuded rock surfaces. In Britain, Kitching (1937) and Pyefinch (1943) have been concerned with the latter aspect. In France, Fischer-Piette (1929 and 1932B), Hatton and Fischer-Piette (1932) and Hatton (1932) have studied the general aspects of the problem. Much work has been done in America on the season of attachment of sedentary marine organisms and their rates of growth. Among the American authors whose work bears on the recolonization problem are Visscher (1928), Visscher and Luce (1928), Pierron and Huang (1926), Coe (1932), Graham and Gay (1945) and Wilson (1925).

The colonization of new surfaces has been studied by several European workers. In many instances advantage has been taken of public works to supply the new surfaces. Brandt (1897) studied the colonization of the Kiel Canal, Herpin (1935A and 1935B) observed the colonization of beaches and wrecked ships and Rees (1940) noted the succession of a new sewage outfall. Moore (1939) and Moore and Sproston (1940) described the sequence of colonization of a new sea-wall at Plymouth.

There has been very little work done in Australia on this aspect of intertidal ecology. Some experiments on fouling have been described by Wood (1950) and have some bearing on the intertidal problem.

(a) Colonization of bare rock surfaces

METHOD

Two rocks were chosen for the experiment. One was of dolerite and the other of mudstone. Both had to be of sufficient weight to remain stationary under conditions of the most intense wave action experienced in the site chosen. The rocks were cubes with sides approximately one foot long.

The rocks were examined ten times over a nine-month period. Each face of the rock was examined in detail and the results of these examinations were plotted on full size, or half size, reproductions of the faces of the rock. This simplified identification of previously recognized individuals.

In order to avoid crushing any forms dwelling on the bottom surface of the rocks a smaller rock was utilised for bottom surface examinations. This smaller rock was placed beside the larger rocks and only the fauna on the under side of it was examined. The rock was placed in such a position that the under surface of it was free from the substratum.

The experiment would have been continued for a longer period than nine months, if it had not been for the fact that the rocks were thrown into deep water by some unknown persons. I do not consider that wave action was responsible for the loss as during the period the rocks disappeared there were no gales of greater severity than had already been experienced.

The site selected was in a channel on the north side of the platform at Pinnacle Point at the south end of Blackman's Bay. The channel is completely uncovered at " low low " tide and has a varied and numerous population. Wave action is not strong, the maximum being a (1-7) 1, b2. Under certain conditions of bad weather heavy surf crashing across the platform pours into the channel but the force is mostly spent by the time it reaches the channel and the rock is only subjected to a cataract of water.

The channel was inhabited by *Hymeniacidon perlevis* (Montagu), *Actinia tenebrosa* (Farq.), *Elminius modestus* Darwin, *Chthamalus antennatus* Darwin, *Ibla quadrivalvis* (Cuvier), *Corallina* sps., *Hormosira banksii* (Lam.), Decaisne, *Amaurochiton glaucus* (Gray), *Patelloida conoidea* (Reeve), and *Galeolaria caespitosa* (Lam.).

Description of the Rocks Selected

It was originally intended to use rocks of dolerite and mudstone in different parts of the shore but pressure of other work restricted the experiment to the one site with two rock types. The rocks were put in position simultaneously, but the mudstone rock only remained in position for three weeks and then vanished. The rock was not replaced as strictly comparable results could not be obtained with a rock placed in position at a later date. The value of the experiment is not very great but it is included here as several points of interest are raised by the colonization processes.

The dolerite rock was selected from a pile of this rock lying above high water mark on the beach at Sandy Bay. The rock was removed to the laboratory and thoroughly scrubbed with hot water. Chemicals were avoided in this process to avoid reactions with the minerals of the rock. The rock was left to weather for a few weeks after which it was put in position. The smaller rock for the bottom surface experiments was similarly treated. The larger rock was known as Winter Rock A and the smaller as Winter Rock B.

The nature of the rock faces and their orientation can be best expressed in Table 1.

TABLE 1

Nature, orientation and area of the faces of Winter Rocks A and B.

Smooth, sea-sheltered vertical face with vertical and inclined ridges	Landward, 419 sq. cms.
Smooth, sea-exposed vertical face with exposed vertical and inclined ridges	Seaward, 494 sq. cms.
Semi-exposed vertical face with inclined and vertical ridges	Left hand, 637 sq. cms. Right hand, 708 sq. cms.
Sea and air-sheltered horizontal face with lateral ridges	Bottom, 271 sq. cms.
Sea and air-exposed horizontal face with lateral ridges	Top, 432 sq. cms.

The experiment was commenced on 18th April, 1948, and observations were made on 1st May, 12th May, 19th May, 29th May, 20th June, 26th June, 3rd July, 8th July, 15th July, 21st July, 14th August, 29th August, 21st September, 19th October, 3rd December, 10th January, 15th February. On the latter date only, the bottom face of Winter Rock B was examined. Winter Rock B is still in position at the time of writing (October, 1953) and it has been examined frequently since 15th February, 1949.

The first sessile organism to appear on the rocks was a small *Corallina* sp. on the landward face in May. Previous to this several errant species were seen on the faces of the rock, notably *Amaurochiton glaucus*, *Patiriella exigua* (Lam.), *Cominella lineolata* (Lam.) while below the rocks crabs (*? Petrolisthes* sp.) were sheltering. Amphipods were found in cracks on the rock. The first occasion on which large numbers of colonizing animals were noted was in June when 113 individuals appeared on the rocks. There were only nine deaths noted during this period.

Of these new individuals over 72 per cent were *Galeolaria*. These tubes were not confined to the lower part of the rock. About 25 per cent of them were found on the top surface. Barnacles appeared at the same time as the worms but in fewer numbers. A colonial diatom association, mainly of *Euschizonema* and *Melosira* sps. appeared at this time. These colonies were of a very short lived nature only, two extending from one week to the next. These diatoms are discussed below.

There were no macroscopic forms other than barnacles, *Galeolaria* and *Corallina* to successfully colonize the rock. *Actinia tenebrosa, Patelloida conoidea* and two errant annelids appeared but soon wandered away again. There was a constantly changing number of *Amaurochiton glaucus* on the rock. Several of these were marked and one was noted as returning to the rock at 2, 5 and 3 week intervals.

Table 2 shows the number of new individuals settling each month and the number of deaths per month on each of the faces of the rocks. Although during certain months the rock was visited more frequently than others, thus giving a greater number of new settlements, there is no doubt that some faces of the rock were more densely populated during some months than others. The figures, although they show an overall increase of deaths and settlements during the more frequently visited months, reflect the true picture of the trends by the ratio of these numbers.

TABLE 2

The new settlings per month on each face of Winter Rocks A and B.

	MAY		JUNE		JULY		AUGUST	
	Settlings	Deaths	Settlings	Deaths	Settlings	Deaths	Settlings	Deaths
Top	1	....	23	....	38	33	2	26
Seaward face	....	....	7	....	14	12	2	5
Landward face	1	....	1	2	26	10	4	18
Right-hand face	....	....	9	....	52	14	14	39
Left-hand face	....	....	31	....	11	37	2	6
Bottom	....	....	42	7	51	29	7	37

	SEPTEMBER		OCTOBER		NOVEMBER		DECEMBER	
	Settlings	Deaths	Settlings	Deaths	Settlings	Deaths	Settlings	Deaths
Top	5	1	4	4	?	?	....	4
Seaward face	3	....	4	5	?	?	19	6
Landward face	2	....	5	1	?	?	2	6
Right-hand face	19	6	15	15	?	?	11	19
Left-hand face	2	0	3	3	?	?	1	2
Bottom	7	6	33	6	?	?	8	36

	JANUARY		FEBRUARY	
	Settlings	Deaths	Settlings	Deaths
Bottom	5	13	8	6

Table 3 and Fig. 1 show the total number of individuals inhabiting the faces each month, while Table 4 and Fig. 2 show the new settlings and deaths of the various species per month.

From these tables and graphs it can be seen that there is a very great decrease in the total number of organisms on all faces between July 21st and August 14th and also between October and December. If the trends shown by the bottom face of Winter Rock B are true, there is also a sharp diminution of numbers in December and January.

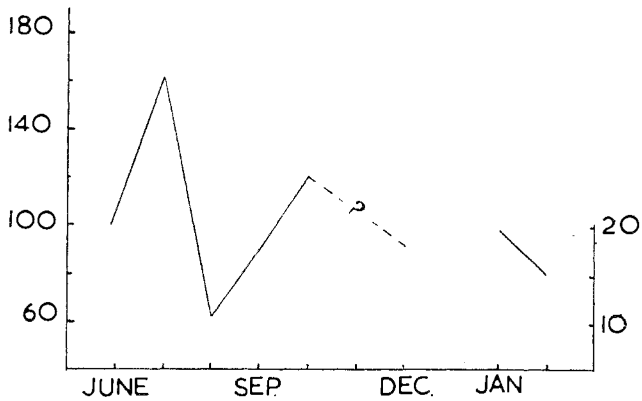

FIG. 1.—The total number of individuals inhabiting all faces of Winter Rocks A and B from June, 1948, to February, 1949.

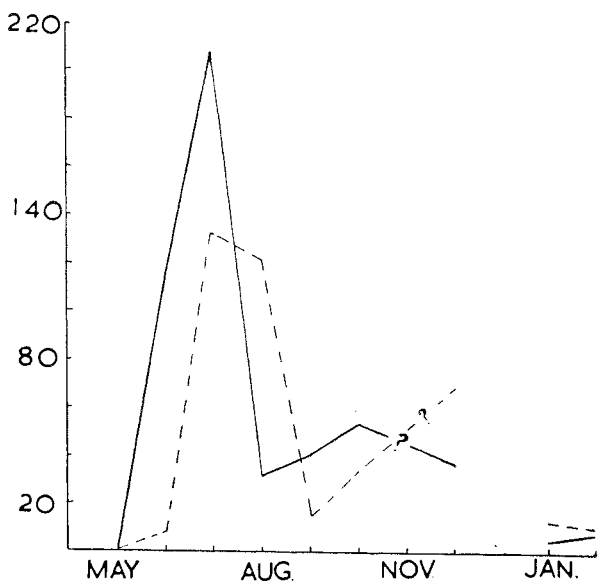

FIG. 2.—The number of settlements and of deaths (broken line) per month on all faces of Winter Rocks A and B.

TABLE 3

The total number of individuals of all species inhabiting the various faces of Winter Rocks A and B each month for the period June, 1948, to December, 1948.

	June	July	August	September	October	November	December	Totals
Top	23	27	3	7	7	?	3	70
Seaward face	....	9	6	9	8	?	21	53
Landward face	1	16	2	4	8	?	4	35
Right-hand face ..	9	47	22	35	37	?	27	177
Left-hand face ..	31	5	1	3	3	?	4	47
Bottom	35	57	27	28	55	?	27	229
Grand Totals	99	161	61	86	118	?	86	611

The bottom face only during January and February had 19 and 16 inhabitants respectively giving an absolute total of 646 organisms noted. These latter figures are not included in the table as they are only indications and may not be true records of actual population changes.

TABLE 4

Total number of specific settlements and deaths per month.

Settlements	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Barnacles	....	18	57	16	24	33	? .	24	2	3	177
Serpulids	....	81	130	12	11	14	?	1	3	3	255
Anemones	....	1	....	1	....	....	?	2	....	....	4
Diatoms	....	10	17	2	....	....	?	....	....	....	29
P. alticostata	....	....	....	....	1	3	?	....	....	....	4
P. conoidea	....	....	....	....	....	1	?	3	....	....	4
Patella ustulata ..	....	....	....	....	....	....	?	1	....	....	1
Corallina	1	2	....	....	....	....	?	6	....	....	9
Nereids	....	1	2	....	....	....	?	....	....	....	3
Red algae	....	....	1	....	....	....	?	....	....	....	1
Chiton eggs	....	....	....	....	3	....	?	....	....	....	3
Totals	1	113	207	31	39	52	?	36	5	6	490

Deaths	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Barnacles	....	3	13	26	1	10	?	45	13	7	118
Serpulids	....	3	94	90	13	19	?	18	....	1	238
Anemones	....	1	....	....	1	....	?	....	....	....	2
Diatoms	....	1	23	5	....	....	?	....	....	....	29
P. alticostata	....	....	....	....	....	....	?	3	....	....	3
P. conoidea	....	....	....	....	....	...	?	1	....	....	1
Patella ustulata ..	....	....	....	....	....	....	?	1	....	....	1
Corallina	....	1	....	....	....	....	?	....	....	....	1
Nereids	....	....	2	....	....	....	?	....	....	....	2
Red algae	....	...	1	....	....	....	?	....	....	....	1
Chiton eggs	....	....	...	....	....	3	?	....	....	....	3
Totals	....	9	133	121	15	32	?	68	13	8	399

The number of forms successfully settling also shows a sharp diminution in August and January. The number of deaths in July and August is very high. The large number of settlings in July possibly came from a late autumn spawning.

The seaward and landward faces of the rock never had as dense a population as the other faces.

The total population of the bottom face of Winter Rock B is still low (October, 1953), consisting of 18 occupied *Galeolaria* tubes, 22 *Chthamalus antennatus* and 12 *Chamaesipho columna* as well as a patch, 5 cms. by 3 cms. of *Hymeniacidon perlevis*. Numerous errant types dwell on the surface. Plate I shows the rock after 3½ years.

Discussion

From the above observations it can be seen that the rate of successful colonizing is very slow compared with the rate in other parts of the world where there is a much greater density of population per unit of time. It is proposed to examine some of the factors which may influence the settling of larvae on the experimental rocks.

There is a close correlation between the critical months for intertidal organisms as deduced from physical data in an earlier paper (Guiler, 1950) and the observed rates of settling and deaths on the experimental rocks. December, January and July are considered to be critical months for intertidal organisms due to the combination of adverse tidal and meteorological factors. April and October are regarded as months of slightly less strain due to the equinoctial change of tidal behaviour. From Tables 2, 3 and 4 it can be seen that there are times of high casualties and low spatfall between late July and early August and in October and December. It is further indicated by Winter Rock B (Tables 2 to 4) that January is also a month of stress, though this is not conclusive. March and April unfortunately are not included in the experiment for the reasons given above.

The black colour of the rock would certainly assist barnacle settling. The larvae being negatively phototropic (Visscher, 1928) would choose a dark surface in preference to the surrounding lighter coloured mudstone. The relative absence of surf would tend to reduce the number of successful barnacle settlings though it has been shown by Coe (1932) that test blocks exposed to heavy surf were cleared of barnacles measuring up to several millimeters in diameter. In the channel in which the experimental rocks were situated there was not nearly as great a barnacle population as there was on the exposed edge of the rocky platform. On the other hand, the seaward face of Winter Rock A which would experience whatever wave action there might be, had very few barnacles on it, having very much smaller number than either of the lateral faces. In general, it might be concluded that the channel was not very highly suited to barnacle life, though barnacles were living there.

The poverty of barnacles on the seaward face of Winter Rock A is possibly explained by the fact that the face was towards the North, i.e., it was exposed to the sun. This would drive cyprid larvae round to the sides of the rock where they would find more congenial conditions. Any larvae which had settled on the seaward face would probably be killed by the sun before the metamorphosis was complete. The right hand face, because it is sheltered from all but the early morning sun, has a comparatively rich fauna.

It has been shown by Hopkins (1935) that oysters tend to form their densest colonies on the under surface of objects. The reason for this lies in the larval method of swimming with the velum upwards. There is little evidence of this behaviour being shown by any of the larval forms encountered during the experiment.

It has been noted by Coe (1932) that the degrees of roughness of surfaces influences the population inhabiting them. In this case the faces of the rock were all of equal smoothness and the factor is not applicable to the fauna of different rock faces.

The absence of any algal grazers permanently dwelling on the rocks points to the fact that an algal film was not formed on the rock. This may have been influenced by bacteriological factors (Zobell and Allen, 1935). Wood (1950) found that bacteria do not play the role of forming the primary film but are replaced by algal spores.

The failure of organisms to colonize the rocks is due to the integration of a number of factors. The orientation and sitting of the rock and the relation of the faces to sun and wave exposure play some part. The lack of full wave action would reduce the number of barnacle settlements but ought to increase the number of *Galeolaria* settlements. The number of settlings by the worms was large but the death rate was also high. The high death rate was caused by the larvae settling in June or July and being unable to become established before the critical month of July.

Barnacle larvae settled throughout the year, though the critical months also caused a high death rate in these species. This is in contrast to the situation described by Moore (1939). In no sense was a pioneer community established as described by Rees (1940). The nearest parallel to colonization in South Tasmania is that described by Pyefinch (1943) who found that no inter-specific competition existed.

It can be concluded that the rate of settlement was very slow, Rock B being relatively unpopulated after 5½ years.

(b) The recolonization of depopulated rock in the *Mytilus* belt

The object of the experiment was to determine the sequence of recolonization of depopulated mussel beds. Six areas of rock, each area being one foot square, were scraped clean. The areas were in the mussel beds at Blackman's Bay on the platform at the Pinnacle. The areas are as shown in Table 5 and their distribution on the platform was selected so as to include different amounts of wave action.

TABLE 5

The experimental areas at Blackman's Bay.

Area 1.	In the *Mytilus* beds on the surface of à shelf at the seaward end of the platform.
Area 2.	In the mussel beds at a slightly higher level and further inshore than Area 1.
Area 3.	On the vertical face of a cleft which is occupied by *Mytilus* and is exposed to wave action.

Area 4. On the surface of the platform to the south of Area 3.
Area 5. In the mussel beds on a low level shelf at the southern end of the platform.
Area 6. On the under-surface of a cleft near the southern end of the platform. The mussels in this instance are *Brachyodontes rostratus.*

The areas chosen are on both wave exposed and wave sheltered parts of the same restricted area of coast.

METHOD

The areas were cleared on the 16th October, 1950. The mussels and other loosely attached organisms were pulled off the rocks, barnacles, *Galeolaria* and other firmly attached animals were removed by scraping with a chisel, without damaging the surface of the rock. Each area formed a square of sides one foot in length. It was not found necessary to wash the rock as waves were continually sweeping over the platform. Visits were made to the areas at intervals and the forms inhabiting the areas were noted. The individual animal or plant found on the rock was not removed, but identification was carried out in the field, or by the collection of an identical specimen from near-by. This was done to avoid de-populating the experimental areas.

It was not always possible to make a detailed survey of the areas. High tides during the winter and the prevalent southerly swell prevented an examination of the areas on several visits. On other occasions only a partial examination was possible. Successful or partially successful examinations were carried out on 8th November, 1950, 20th November, 1950, 27th November, 1950, 8th January, 1951, 31st January, 1951, 8th March, 1951, 29th March, 1951, 10th April, 1951, 12th May, 1951, 23rd June, 1951, 15th August, 1951, 17th September, 1951, 23rd October, 1951, 30th October, 1951, and the 7th November, 1951. During the latter part of October a very strong gale caused heavy damage on the western shores of the estuary. This gale completely denuded the rocks of all attached animals and most of the plants.

16*th October,* 1950

The areas were cleared on this date and the fauna of the mussel beds was examined and found to be the same as that noted in Guiler (1950). The mussels were covered by a fairly thick growth of *Ulva lactuca.* On Area 6 there was no *Ulva* and the fauna was different from that in the other mussel beds. As noted in Table 5 the mussels inhabiting this cleft are *Brachyodontes rostratus* (Dunker). This bed of this species does not support a large cryptofauna as do the *Mytilus* beds. The only other species found on the *Brachyodontes* beds were *Elminius modestus, Chthamalus antennatus, Chamaesipho columna* and *Actinia tenebrosa.* These species were all utilising the mussels as a substratum and were found in a similar habitat on all the other areas.

8th November, 1950

There were no attached organisms to be found in the areas. Some small *Ulva* plants occurred on Areas 1, 2 and 5. Several roving species were found on Areas 1 and 5. These were *Sypharochiton pellis-serpentis* (Quoy & Gaim.), *Patelloida conoidea* and *Fossarina petterdi* Crosse.

16*th November,* 1951

Roving species were found on all of the areas, except No. 6. A few sedentary or attached species were present. One small *Ulva* plant occurred in Area 2. Area 5 was nearly permanently waterlogged due partly to the conformation of the rock and also to the very thick growth of *Ulva* and mussels on the shelf.

There was no evidence of any settlement on Area 6.

20*th November,* 1950

The early stages of the colonization were marked by the spreading of *Ulva* from the mussels on to the areas and also by the invasions of roving species. All areas, except No. 6, showed more or less growth of *Ulva.* Area 5 was densely covered by a *Polysiphonia* sp. This weed was only common in places where the mussels had been scraped off the rocks. Area 4 was partially colonized by the same seaweed.

The roving species encountered were *Cominella lineolata, Sypharochiton pellis-serpentis, Patelloida conoidea, Cellana variegata* and *Fossarina petterdi.* The latter species was very numerous on Area 2 where 10 individuals were counted. *Cominella lineolata* was rare, only one individual being noted. Area 3 was largely populated by limpets, while Area 3 was occupied by only one chiton.

The sessile forms which appeared were in the minority and were confined to Areas 2, 4 and 5. All these areas carried a few small mussels of about half an inch in length, though on Area 5 the mussels were nearly one inch in length. *Chthamalus antennatus* was found on Areas 2 and 4. There were a large number of *Galeolaria* tubes on Area 5.

27*th November,* 1950

It was not possible to examine Areas 1 and 5 due to a ground swell which was breaking on the platforms. During the week since the last examination there had been a small barnacle spatfall. Barnacles, *Elminius modestus,* were found on Areas 2 and 4. Also on Area 4 were several small *Chthamalus antennatus.* All these barnacles had disappeared by the next examination of the areas.

It was very noticeable that the roving species were not as numerous on this date as on the previous visits. One specimen of *Patelloida conoidea* was found on Area 4 and two individuals of the same species were found on Area 3. There were no other roving species found on any of the areas.

One small mussel, *Mytilus planulatus,* was recorded on Area 4 with several *Ulva* plants. The only other sessile forms found on any other area, with the exception of the barnacles mentioned above were some *Lithothamnion* on Area 3. The growth of this alga commenced very slowly but after a few weeks the species spread quite rapidly.

8th January, 1951

The effect of the hot summer weather was becoming noticeable in the very sharp diminution in the number of algae found on the areas situated on the higher parts of the shore. Area 2 had only one *Ulva* plant growing on it, though this plant was still healthy. The areas at lower tidal levels were still dominated by algae. Areas 1 and 4 both had considerable growths of *Ulva* and *Polysiphonia*, though some of the *Ulva* was in poor condition. *Polysiphonia* was dominant on Area 5 which was also richly covered with *Ulva*. On Area 1 the *Ulva* plants were very much dried and tended to tear away when they were gently lifted.

Animal colonization was becoming more rapid. It was not possible to make a detailed survey of Area 1 because of a dangerous ground swell, but Area 2 had 17 small *Mytilus planulatus*, each greater than a quarter inch but less than half an inch in length. Also living on Area 2 were 25 small *Elminius modestus* and two tiny *Corallina* plants. Area 3 was not a densely colonized area, being occupied by two small *Chthamalus*. Three *Mytilus planulatus* were living on Area 5. The largest of these was about one and a quarter inches in length. Area 6 was colonized by two small *Mytilus planulatus*.

The most interesting feature was noted on Area 4 where the large mussels forming the surrounding beds were beginning to encroach on the cleared patch. The encroachment was beginning from the southern edge of the area. The importance of this encroachment was seen in subsequent examinations. The removal of mussels to form a cleared area had an interesting effect on the mussel beds surrounding Area 3, where the sea had exploited the weakening of the mussel bed. This weakening led to the denudation of a small area of rock around the experimental area.

The number of roving species found on the areas had also increased considerably. *Sypharochiton pellis-serpentis* was found on all areas except No. 6, *Fossarina petterdi* was found on Areas 2, 3 and 4, *Siphonaria zonata* on Areas 3 and 4 and *Cominella lineolata* on Area 4. *Cominella* was locally very plentiful in the cleft in which Area 4 was situated.

31st January, 1951

Most of the *Ulva* which covered the mussel beds in early January had died since the last visit, but, surprisingly, there was a number of these plants growing on and around Areas 2 and 5.

The small *Mytilus* found previously had nearly all died, only one specimen being found (Area 2) but a number of *Galeolaria* tubes appeared on this area. The roving species were still numerous. *Patelloida marmorata* was noted for the first time, appearing in Area 2. The only area which showed any increase in animal population was No. 6 where 12 small *Mytilus planulatus* were noted. The mussels surrounding this area were all *Brachyodontes rostratus*.

The encroachment on to the experimental areas by the mussels was slowly proceeding.

In general, there was a very sharp reduction in the number of plants and animals colonizing the areas, but the encroachment on to the areas by the mussel beds was slowly proceeding.

8th March, 1951

Ulva had spread across the mussel beds and covered all the areas except No. 6. There had been a very large barnacle spatfall on Areas 1 and 5. There was little change in the mussel population on any of the areas. One large *Actinia tenebrosa* was found on Area 6. The specimen was too large to have settled as a juvenile and must have migrated on to the area.

The barnacles were all *Chthamalus antennatus* and were found packed together in small clusters on Areas 1 and 5. The barnacles numbered over two hundred on each area. It was not possible to undertake a detailed count because of the water washing over the areas.

Area 4 had been colonized by a large *Galeolaria* spatfall. The worm tubes were not as gregarious in their distribution as the barnacles and were distributed more evenly over the area.

28th March, 1951

Algae were dominant on all areas except No. 6. There were only two species of seaweed, namely *Ulva lactuca* and a *Polysiphonia* sp. *Ulva* was the more common of these species and it was dominant on all of the colonized areas except No. 1.

The large barnacle spatfall which was noted in February and early March had ceased and most of the young barnacles had died. On Area 4 only one small *Elminius modestus* was noted, though there were 12 mussels on the area. The *Galeolaria* tubes were still very numerous on this area.

Roving organisms were becoming more abundant. *Cellana limbata, Siphonaria zonata, S. diemenensis* (dominant animal on Area 2), *Amaurochiton glaucus, Patelloida alticostata* and *Fossarina petterdi* were found on the areas. Area 6 was dominated by *Mytilus planulatus* although this species was not numerous.

10th *April,* 1951

On this date it was not found possible to examine Areas 1, 3, 5 and 6 due to the high tides. The very high level of the tides during most of the winter frequently prevented examination of the lower and/or more exposed areas.

The encroachment of the mussels on the areas was still progressing, e.g., Area 2 (Plate 2). The fauna and flora inhabiting Area 2 was almost the same both in numbers and species as that noted on 28th March.

Area 4 was dominated by *Galeolaria* as the *Ulva* and surrounding mussels had been removed from the rock by some unknown agencies. There were also 19 *Mytilus planulatus* and a few *Chthamalus antennatus* on this area.

Patelloida marmorata, P. diemenensis, Fossarina petterdi, Siphonaria zonata, S. diemenensis and *Cominella lineolata* were all found roving on Areas 2 and 4.

12th May, 1951

A south-westerly swell made it impossible to examine Areas 1, 3 and 5.

In spite of bad weather the mussel beds were still intact and continuing to encroach on to the cleared areas. All of the young barnacles on Area 4 had died. These animals were noted as settling in February. The roving species were not common as they had probably retired to less exposed places to avoid the storm. *Sypharochiton pellis-serpentis, Patelloida alticostata, Siphonaria diemensis* and one *Cellana limbata* were recorded.

Area 6 was unchanged with *Mytilus planulatus* still the dominant organism.

23rd June, 1951

There had been little change in the population of any of the areas with the exception of Area 5 where a *Polysiphonia* sp. had become very plentiful. This area was surrounded by mussels covered by *Ulva* but the green weed was not growing on the bare rock.

Eight barnacles were found on Area 1. Six of the barnacles were large and must have settled since the area was last examined in March. The other two were small and represented a recent spatfall. In spite of a large and successful spatfall the barnacles failed to colonize the available space.

The encroachment of the mussels on to the areas was slowly continuing. One large adult mussel was found near the centre of Area 1. The mussel measured 2½ inches in length and was too large to have grown from a larva. Area 5 was difficult to examine in detail due to a more or less permanent flow of water over the shelf on which the area was situated. It was possible to determine that a *Polysiphonia* sp. was the dominant form on the area, but the surrounding mussel beds were covered with *Ulva*. Area 6 showed no change.

Area 3 was slowly becoming colonized by a purple-pink coloured *Lithothamnion* sp. This alga was spreading from the top of the area down towards the bottom. One specimen of *Balanus trigonus* had settled in the bottom seaward corner of the area. A few small patches of the black lichen, *Verrucaria* were also noted as well as two small *Catophragmus polymerus.*

15th August, 1951

It was not possible to examine Areas 1, 3, 4 and 5 due to the state of the weather. Area 6 was unchanged from the June visit. Area 2 was covered by *Ulva* and it could be seen that Areas 1 and 5 were similarly populated.

23rd October, 1951

No large spatfalls had occurred on any of the areas since August.

The original foot square cleared to form Area 1 was greatly reduced by the encroachment of the mussels from the surrounding beds. Four large mussels had also moved into the centre of the area (Plate 3). Only five barnacles were found, four of these being *Elminius modestus* and the other one was a *Chthamalus antennatus*. Some *Ulva* plants were living on the seaward corner of the area.

Area 2 was also being slowly covered by the mussels. Some roving species (*Patelloida alticostata, P. pauperata* and *Siphonaria diemenensis*) were found as well as six *Elminius modestus*. A few *Ulva* plants were also growing on the area (Plate 4).

Area 3 was dominated by *Verrucaria*. The neighbouring mussels did not invade this area. One large *Catophragmus polymerus* was found on the area as were also *Siphonaria zonata, S. diemenensis* and *Patelloida alticostata*. The *Corallina* plants noted earlier had vanished from the area and the *Lithothamnion* invasion was proceeding slowly.

Area 4 was being populated by *Galeolaria*. A few *Patelloida alticostata, Siphonaria diemenensis* and *Mytilus planulatus* were also on the area.

The mussels surrounding Area 5 were encroaching on the cleared patch, which was completely covered by *Ulva*. Six *Elminius modestus* and several *Patelloida alticostata* and *Siphonaria diemenensis* were also living on Area 5.

Area 6 showed no change.

30th October, 1951

During the latter days of this month a very heavy southerly gale blew into the estuary of the River Derwent. A visit was made on this date to ascertain the damage inflicted by the storm on the mussel beds. A heavy swell was still running and it was not possible to get within 100 feet of the mussel beds.

7th November, 1951

As a result of the storm noted above the mussel beds and cleared areas ceased to exist (Plate 4). The regeneration of the mussel beds will take several years and must take place from a residual stock which survived in sheltered situations on the platform as shown in Plate 5.

Discussion

The experiment, although incomplete at the time of the storm had progressed sufficiently far to enable certain conclusions to be drawn. In the case of Areas 1, 2 and 5 there was considerable encroachment by the surrounding mussels on to the cleared areas. If permitted to continue this encroachment would have been complete and recolonization of the rock would have been achieved in a comparatively short time (two or three years).

Area 3, which was situated in a vertical cleft, was not being recolonized by mussels although there were thick beds beside the area. On these vertical beds there must be little or no force pushing mussels outwards into the cleared area. The encroachment by the mussel beds on the areas noted above was caused by such a force acting parallel to the rock surface. This force is probably gravitational, resulting from the very dense mussel population on the beds. On the vertical face this force would be downwards in direction and would tend to promote a mechanical instability in the mussel beds.

The mussels surrounding Area 4 were denuded early in the experiment. *Galeolaria* became the dominant organism. The recolonization by the serpulid was rapid but incomplete. It is probable that in time the mussels will re-occupy the area temporarily taken over by the serpulids, though the recent gale will greatly extend the time required for this process.

Area 6 showed very little sign of recolonization. The area is higher on the shore than the other places and this probably affected the rate of settlement of larvae as well as diminishing their chances of survival after settlement. The mussels surrounding the area were not as closely packed as at other areas and were also of a different species, namely, *Brachyodontes rostratus.*

Both experiments show that there is a very slow rate of colonization of rock surfaces. Winter Rock B, after 5½ years in the sea was only partly colonized. Similarly those cleared areas where there was no pressure from surrounding mussel beds showed very little recolonization. From both experiments it seems as if barnacle spatfalls take place throughout the year. In the colonization experiment a large spatfall took place in July, while in the recolonization experiment, a heavy spatfall occurred in March. Dakin and Colefax (1940) found barnacle larvae at all times of the year off the New South Wales coast. In both experiments the initial settlement seemed to be quite successful but soon afterwards some factor or factors caused very severe casualties to, if not total annihilation of, the young barnacles. This high death rate was probably due to a combination of tidal and climatic factors as noted in Guiler (1950).

The presence of many grazing forms, e.g., the chitons and patelloids, points to the presence of a good supply of minute algae. Wood (1950) notes that a bacterial film does not form on submerged test plates but he notes that the small algae are plentiful on the same type of substratum.

The growth rates of the mussel, *Mytilus planulatus,* appears to be very rapid in the early stages. The mussels on Area 1 grew to a length of 2½ inches in a period of about nine months and certainly they were above the minimum size for reproduction. It seems probable that the barnacles also grow to a reproductive size in one season.

The main conclusions to be drawn from the above experiments are that colonization or recolonization is very slow. In the mussel beds, recolonization is achieved by encroachment of the mussels except on vertical faces where a slower settlement process operates. The encroachment is by population pressure round the edges of the square as well as by a few large mussels wandering across the cleared area (Plate 4). There was very little successful mussel settlement.

The mussel beds are subject to catastrophic changes which greatly affect, if not stop, all recolonization by encroachment. Almost two years after the gale which denuded the rocks there is an almost continuous bed of mussels over nearly all the area previously colonized. However, the mussels are all small in size. This rapid recolonization could not have been achieved by encroachment and must have come about by successful larval settlement. From the size of the mussels it would appear that two periods of successful settlement took place. Thus the recolonization after a natural denudation is more rapid than that taking place after artificial clearing of a surface.

Long term changes also alter the status of mussel beds and such a change has been noted at Coles Bay where the mussels replaced *Hormosira* on the shore (Guiler, 1953).

(c) Seasonal growths

It was noted in Guiler (1950) that a diatom growth appeared on the shores in 1948, but this growth did not appear in 1949 or 1950. The winter of 1951 showed some diatom growth on the shore but the density of the colonies was not nearly as great as in 1948. The winters of 1949-51 were notable for the lack of rain and it is possible that this factor prevented the establishment of a strong diatom growth. In 1952 and 1953 the diatom growth was very marked.

(2) Algae

Apart from secondary colonization of the diatom region by several species, as noted above, there are only three algae which are found forming a seasonal growth on the shore. They are *Porphyra columbina* Mart., *Scytosiphon lomentarius* (Lyngb.) J. Ag. and *Ulva lactuca*, L. These first two species were very common on the shore in the winter of 1951, being recorded from Howrah, Kingston, Blackman's Bay, Eaglehawk Neck and Dover. The algae formed two permanent bands in the Midlittoral. *Porphyra* was found as high as the barnacles but in some places the weed was found as high on the shore as the littorinids. Below the *Porphyra* belt was the *Scytosiphon* belt. This belt extended as far down the shore as the mussel beds. These mussel beds may be covered by a dense growth of *Ulva* so that the shore in winter presents the unusual feature of an algal zonation . . *Melaraphe, Porphyra, Scytosiphon, Ulva, Cystophora.*

The algal growth usually appears in late August (Plate 6) and persists until early November. By that time, the algae were becoming very dry and only just managing to survive. The growth disappeared shortly later, when the heat of the early summer sun was experienced.

There are three varieties of *Scytosiphon*. These varieties occur at different tidal levels. The variety to be seen at the highest level on the shore is a stunted form with very poorly developed internodes. This variety, when dry, looks like withered or dead *Zostera*.

The varieties found about the level of the barnacles show development of the internodes while the variety found above the mussels has very well developed internodes and is more fleshy in appearance than either of the other two varieties.

Ulva lactuca can be found at all times of the year on the mussel beds but in the spring and early summer the species forms a complete cover for the mussels. The dense growth of *Ulva* does not survive for long into the summer, only scattered plants being found on the mussels. The ponds of the Infralittoral fringe usually have *Ulva* growing in them all summer. Womersley (1950), Dellow (1950) note the seasonal growth of *Porphyra* in South Australia and New Zealand and Newton (1931) and Chapman (1950) both note the seasonal occurrence of the genus in Europe.

Often associated with the appearance of these three algae is the upward extension of the range of certain of the roving gastropods, such as *Cominella lineolata* and *Austrocochlea obtusa.* I have not noticed any appreciable change in the distance the limpets are found above the mussels. *Gelidium* and some other red algae extend further up the shore but on the disappearance of the original algae all these species soon disappear. Young mussels, *Mytilus planulatus,* have been noted to settle very far up the shore during the period of algal growth. It is possible that the mussels found high on the shore in such places as Kettering are enabled to settle during a period of algal colonization. Bishop (1947) notes that mussels settle on a colonized surface and the presence of an algal growth on the rocks fulfils this condition.

(3) Animals

The only seasonal animal migrations are those which occur in the early or late summer or as a result of the unusual algal or diatom growths. In the early summer numerous roving forms are found in the Infralittoral fringe and the ponds of the Infralittoral fringe. There are small fish, *Scutus antipodes, Nudibranchs,* tectibranchs, the urchin *Helocidaris erithrogrammus* and a Crinoid which breeds under stones. These species all return to deeper water in the autumn.

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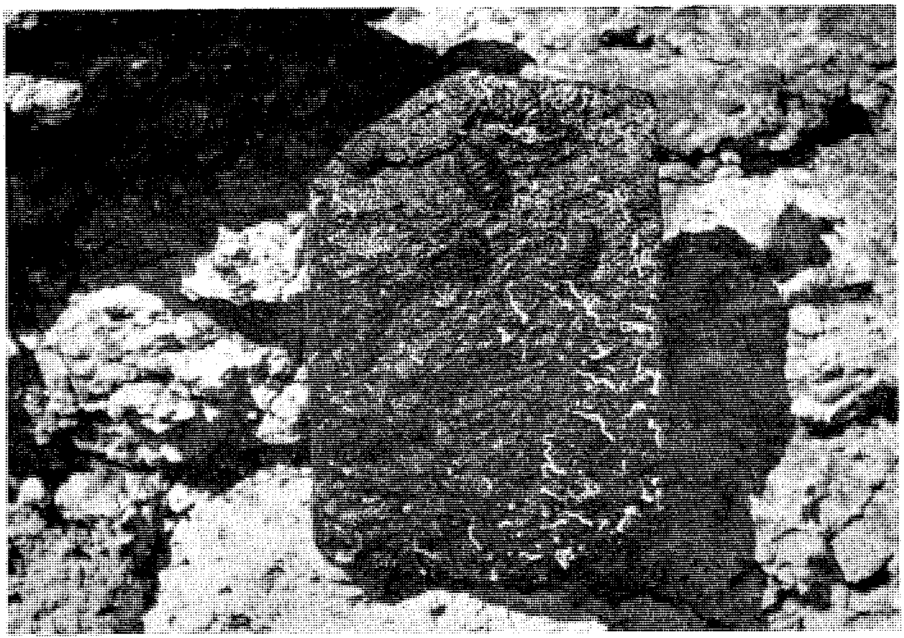

Plate 1.—Winter Rock B, November, 1951. The chitons are *Amaurochiton glaucus*, and the serpulids are *Galeolaria* with some *Serpula*. Note the almost complete absence of barnacles.

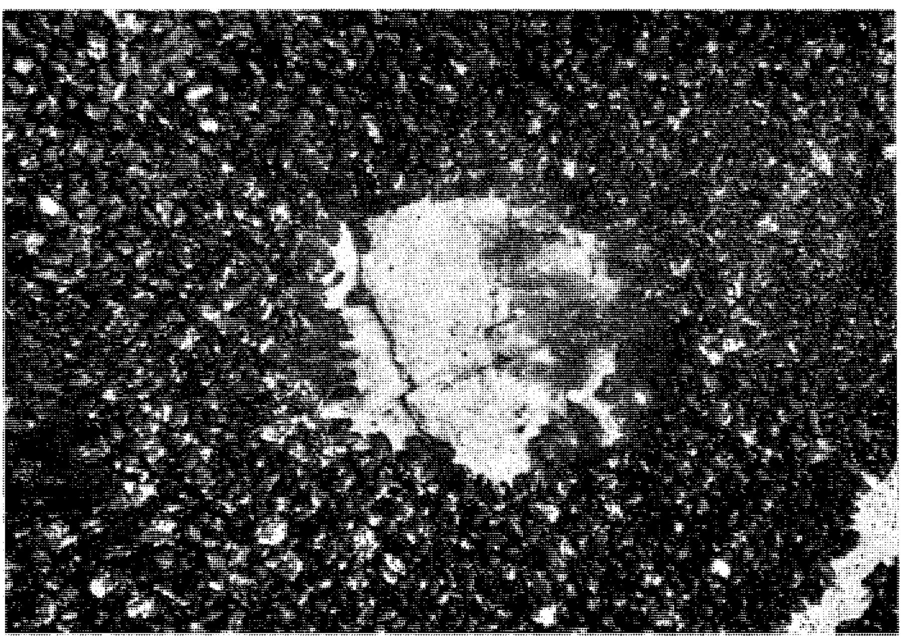

Plate 2.—Area 2, 10th April, 1951. Note the encroachment by mussels on to the cleared area. The seaweed growing on the area is *Ulva*.

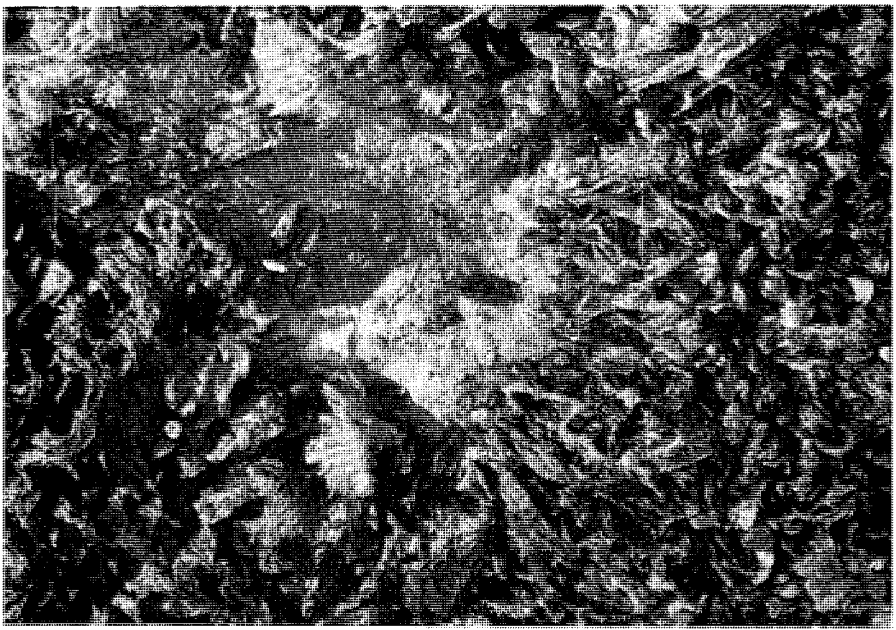

PLATE 3.—Area 1, October, 1951. The encroachment by mussels is most obvious and large mussels which have migrated into the centre of the area can be seen. The alga is *Ulva*.

PLATE 4.—Area 2, October, 1951. Note the barnacles and molluscs which have invaded the area.

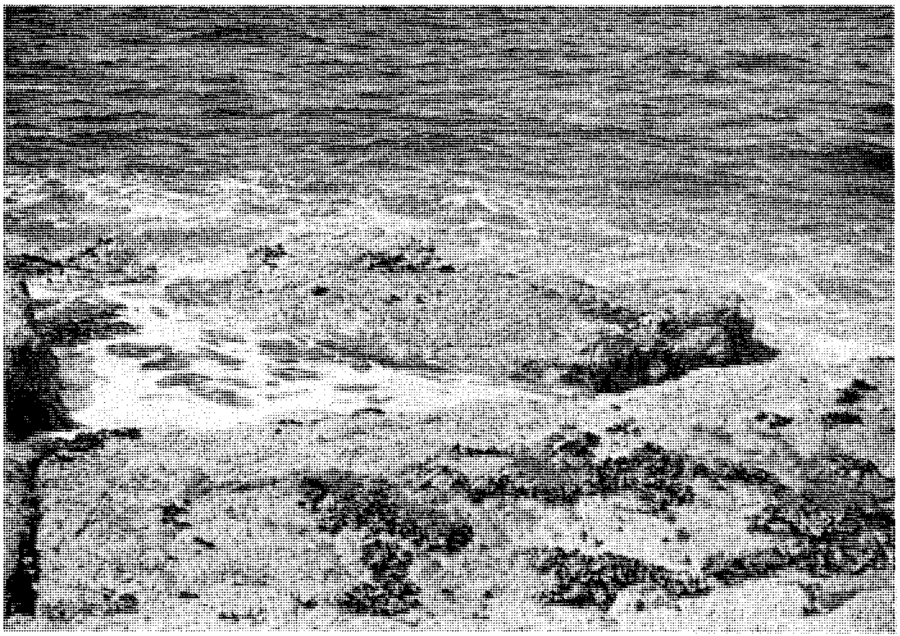

PLATE 5.—The mussel beds after the gale which destroyed most of the mussels. Area 1 was situated on the small shelf in the middle of the photograph.

PLATE 6.—A dense seasonal growth of *Scytosiphon lomentarius* at Blackman's Bay, September, 1951.