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The Effects of Grazing by Gastropods and Physical Factors on the Upper Limits of Distribution of Intertidal Macroalgae

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Summary. The cover of foliose algae is sparse to non-existent above a low-level algal zone on many shores in N.S.W., except in rock-pools. Above this algal zone, encrusting algae, mostly *Hildenbrandia prototypus*, occupy most of the primary substratum on sheltered shores. Experimental manipulations at midtidal levels were used to test hypotheses about the effects of grazing by molluscs and of physical factors during low tide on this pattern of algal community structure.

Fences and cages were used to exclude grazers: molluscs grazed under roofs and in open areas. Cages and roofs provided shade, and decreased the harshness of the environment during low tide: fences and open areas had the normal environmental regime.

In the absence of grazers, rapid colonization of *Ulva* and slower colonization by other foliose algae occurred in all experimental areas. The rate of colonization by *Ulva* sporelings was initially retarded on existing encrusting algae, but after a few months, cover of *Ulva* equalled that on cleared rock.

Most species of algae only grew to maturity inside cages, and remained as a turf of sporelings inside fences. No foliose algae grew to a visible size in open, grazed areas. Grazing thus prevents the establishment of foliose algae above their normal upper limit on the shore, but the effects of physical factors during low tide prevent the growth of algae which become established when grazers are removed. Physical factors thus limit the abundance of foliose algae at mid-tidal levels.

The recolonization of cleared areas by *Hildenbrandia* was not affected by the presence of a turf of sporelings, nor by the shade cast by roofs, but was retarded in cages where mature algae formed a canopy. Even under such a canopy, *Hildenbrandia* eventually covered as much primary substratum as in open, grazed areas. This encrusting alga is able to escape from the effects of grazing by having a tough thallus, and by its vegetative growth which allows individual plants to cover a lot of substratum, and by the tendency for new individuals to start growing from small cracks and pits in the rock, which are apparently inaccessible to the grazers.

Mature foliose algae are removed from the substratum by waves, and many individual plants died during periods of hot weather. Sporelings in a turf were eliminated, after experimental fences were removed, by the combined effects of macroalgal grazers, which invaded the areas, and microalgal grazers which ate the turf from the edges inwards.

The results obtained here are discussed with respect to other studies on limits to distribution of intertidal macroalgae, and the role of grazing in the diversity and structure of intertidal algal communities. Some problems of these experimental treatments are also discussed.

Introduction

On rock-platforms in New South Wales, there are abundant foliose macroalgae dominating, and often occupying all substratum, at low levels (Underwood 1980). Mid-shore areas are dominated by sessile animals, encrusting algae (notably *Hildenbrandia prototypus* Nardo) and/or grazing molluscs (Underwood 1975, 1980). At mid- to high-shore levels on dry rock, there are some seasonally common plants (e.g., *Ilea fascia* (Muell.) Fries., *Porphyra umbilicalis* Lucas), and a number of species are common in and at the edges of pools (notably *Hormosira banksii* (Turn.) Decne and *Corallina officinalis* (L.) or amongst abundant cover of barnacles (e.g., *Caloglossa adnata* Zan.).

Two major hypotheses can be proposed to account for the abrupt discontinuity in distribution of most low-shore algae. First, the physical environment whilst emersed during low-tide may be too harsh for the survival of algae above a certain level. Second, the grazing animals (mostly gastropods and chitons) may eliminate algae above a certain level on the shore.

The effects of physical harshness during low tide (i.e., desiccation, high temperature and light intensity) have been demonstrated as important factors in the distribution of a number of intertidal algae (e.g., Castenholz 1961; Frank 1965; Moore 1939; review by Connell 1972), particularly fucoids in northern temperate waters (e.g., Baker 1909; Schonbeck and Norton 1978), and discussed by many other authors (e.g., Doty 1946; Lewis 1964; Raffaelli 1979). Several species of algae can only survive intertidally in the moist shaded conditions underneath a canopy of other species (Dayton 1975).

Investigations of grazing have demonstrated some limits to distribution of algae. For example, Castenholz (1961) observed that littorine snails could prevent the establishment of diatom slicks at high levels on the shore during summer, but physical factors could also have been involved, as the diatoms grew at high levels during winter. The establishment of opportunistic species of algae, and an increase in abundance of fucoids have been found when limpets were removed from areas of the shore (Jones 1948; Burrows and Lodge 1950; Lodge 1948; Southward 1964; Dayton 1971). These studies, however, gave little indication that grazing controlled the upper limit of distribution of the algae, even though it had a major effect on abundance, and apparently influenced the lower limits of *Fucus spiralis* (Burrows and Lodge 1950). Littorine snails were found to remove opportunistic algae from rocks and in pools, making space available for the perennial alga *Chondrus crispus* (Lubchenco and Menge 1978; Lubchenco 1978) but again this did not apparently alter the vertical distribution of any of the algae.

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May et al. (1970) examined the effect of removal of grazers from a shore in New South Wales, and observed increased abundance of a number of algae, but no apparent effects on the patterns of distribution. In their study, however, the lack of progressive succession after initial colonization of opportunistic algae was attributed to the invasion of snails into the experimental area, which occurred very rapidly.

In the present study, the effects of grazers on the upper limits of distribution of low-shore algae were examined by experimentally excluding molluscs from mid-shore areas above the natural upper limits of the low-shore algal zone. Cages and fences were used to exclude grazers. Cages and roofs were also used to cast shade and thereby reduce the harshness of the physical environment by decreasing light intensity and temperature during low tide. Experimental manipulations were done so that the effects of grazing and of reductions in physical stress could be separated. Thus, the relative importance of these different factors in determining patterns of algal distribution and abundance could be assessed.

Because grazing may affect interactions between the algae (e.g., Lubchenco 1978), different algal assemblages were examined. These were areas dominated by the perennial encrusting alga *Hildenbrandia prototypus*, and areas where foliose macroalgae had been established by previous experimental manipulation. Finally, the effects of grazing and physical factors on the recolonization of artificially cleared areas were assessed.

Materials and Methods

The study site chosen at the Cape Banks Scientific Marine Reserve was the sandstone platform most sheltered from wave action. This was selected because the effects of harsh physical factors, such as high air-temperature and desiccation, during low tide would be greatest. This area also supported very great densities of grazing gastropods (*Nerita atramentosa* Reeve, *Bembicium nanum* (Lam.), *Austrocochlea constricta* (Lam.) and the patellid limpet *Cellana tramoserica* (Sowerby)). The densities and distribution of these molluscs were very similar to those described for a nearby area in Underwood (1975). Except during severe southerly gales, no splash or spray from waves affects this platform during low tide.

Experiments were done at about mid-tidal level, some 0.6 m above the upper limit of a dense zone of foliose macroalgae which comprised mostly *Corallina officinalis* (L.), *Colpomenia sinuosa* and *Ulva lactuca* L. at the start of these experiments. This algal zone extended up to about 0.5 m, and the tidal range on the shore was about 2 m. The only algae in the experimental area were some *Corallina officinalis* and *Hormosira banksii* in pools. The general rock-surface (the 'emergent substrata' of Menge, 1976) was covered by abundant growth (80–90%) of the encrusting alga *H. prototypus*, which had been misidentified as *Peyssonelia gunniana* in some previous publications (e.g., Underwood 1975).

Three experimental (Fenced, Roofed, Caged) and one control treatment (called Open) were used. Cages and fences were used to exclude grazers which could move, at will, into Roofed or Open areas. Cages and Roofs, however, were constructed so that they cast shade and reduced the temperature of covered areas. In contrast, Fenced and Open areas were exposed to normal sunlight and temperature during low tide. This orthogonal design of experimental manipulations in theory allowed independent comparisons of the effects of grazing and reduction of environmental harshness, each in the presence or absence of the other. This proved impossible (see Results), but the experimental Roofs were planned as a separate treatment, not as a control for the effects of caging (as in e.g., Dayton 1971; Menge 1976).

Cages (28 × 28 cm × 4 cm high) were of stainless-steel mesh as described in Underwood (1978) and reduced the light intensity of enclosed areas by one-third on sunny or overcast days. Air-temperature under cages during low tide was 2–3° C (5–10%) less than open areas on sunny days and 0.5–2° C (1–5%) less on overcast days. Roofs were inverted cages raised on perspex legs 3 cm above the rock, which allowed access all round to any grazers on the shore, and to other animals such as the anemone *Actinia tenebrosa*.

Open areas were marked with screws in each corner, but not otherwise affected. Fences could not be made from stainless-steel mesh, because of lack of funds, and so were of galvanized iron 28 × 28 cm side, 4 cm high, with an out-turned lip 1 cm wide around the top and an out-turned base about 3 cm wide around the base, through which stainless-steel or monel metal screws were inserted into rawl-plugs in the rock. These fences could have influenced the microclimate of the enclosed area, because of their solid walls. In fact, this did not occur, as the fences drained during falling tides as fast as surrounding areas, and other experiments using fences of different area and different types of wire and mesh (to be described elsewhere) produced very similar results.

These treatments were done on three different types of area, cleared, normal and macroalgae. Areas were cleared by scraping with a metal scraper, followed by scrubbing with a wire brush. In early trials, *Hildenbrandia* was not completely removed, so these methods were followed by application of a few mls of concentrated acid. Trials were done using different acids and no different results were obtained with phosphoric, sulphuric or nitric acids, but hydrochloric acid caused obvious chemical discolouration of the rock. Phosphoric acid was generally used. This treatment did not cause enhanced colonization by algae compared with other acids (despite the possible enrichment by phosphates). All cleared areas were thoroughly washed with seawater immediately after treatment (and the diluted phosphoric acid caused less obvious agitation of surrounding gastropods than did some other acids). This clearing treatment removed all organisms from treated plots.

Normal algal treatments were untouched except for the removal of all grazing molluscs at the start of the experiment. Macroalgal treatments consisted of areas caged, as already described, for 18 months to 2 years before the start of the experiment. In these cages a dense cover of foliose algae developed, mostly consisting of *Ulva lactuca* but other species were common (see Results). At the start of the experiment, these areas were recaged, fenced, had a roof put over or were left open. The three different types of area allowed investigation of colonization of algae on newly-cleared substrata, the fate of experimentally established midshore stands of algae, and the influence of normal encrusting algal growth on colonization by algae under the different experimental treatments.

Four replicate sets of the 12 experimental areas (i.e., Fenced, Caged, Roofed and Open of each of cleared, normal and macroalgal areas) were used. In each set, the twelve areas were arranged haphazardly in a horizontal band on the shore, at the same height. The twelve plots (each 28 × 28 cm) were separated from each other by distances of 30–50 cm to ensure independence of the treatments. The four sets were separated by about 2 m horizontally along the shore.

Data were collected by counting all animals and measuring the percentage cover of all visible algae either directly, or, more usually, from colour photographs of the experimental areas. Percentage cover of algae was estimated from a grid of 100 regularlyspaced points placed over the area (or the photo when projected at real size), excluding a border 2 cm wide around the edges. The grid was placed in a different position on each occasion to reduce temporal dependence of the data (see e.g., Connell 1970).

Results

Algal cover at the start of the experiment

On 27th September 1976 when the experiment began, the mean percentage cover of *Hildenbrandia* in cleared, normal and macroalgal areas was 0%, 84% and 62%, respectively. Approximately 85% mean cover of *Hildenbrandia* had been removed from the cleared areas. The reduced cover in macroalgal areas must be attributed to the effects of caging and consequent growth of other algae over the encrusting forms, during the previous eighteen months but this is discussed in detail below. In addition, most areas had a cover of 1–7% of *Lithophyllum* sp., and traces of other encrusting coralline algae.

The only other algae present were in macroalgal treatments (i.e., those previously caged) which had a mean cover of 10% of *Ulva* turf, i.e., *Ulva* sporelings grown to a maximum height of 2 mm, and a further mean cover of 53% of mature *Ulva*, i.e., plants with thalli standing up to 3 cm above the substratum (see data for various treatments in September 1976 in Figs. 1 and 2). There were some other foliose algae present (e.g., *Corallina officinalis, Ilea fascia*) in small quantities, and these are discussed below.

Colonization by Ulva lactuca in Fenced areas

Immediate and dramatic colonization by *Ulva lactuca* followed the start of some experimental treatments (Fig. 1). A turf of *Ulva* sporelings began to grow in all Fenced areas within a few days of the start of the experiment, and by 23rd October, 1976, one month after the experiment began, occupied virtually 100% of the substratum in cleared Fenced areas. Cover of *Ulva* turf reached about 60% in normal Fenced areas at this time, and it is clear from Fig. 1 that *Ulva* did not colonize normal areas (which had approximately 85% cover of *Hildenbrandia*) as quickly, nor as extensively as areas from which the encrusting algae had been removed. The colonization of *Ulva* in macroalgal Fenced areas (i.e., those previously caged) was also reduced compared with cleared areas (Fig. 1).

In complete contrast, no traces of *Ulva* appeared in any of the Open or Roofed treatments at any stage in the experiment. This result can be attributed to the effects of grazing gastropods which moved into and grazed over all Open and Roofed areas from the start of the experiment.

The cover of *Ulva* turf within normal and macroalgal Fences eventually rose to the same level as in cleared Fences by February 1977 (Fig. 1). From then, until the experiment was ended in May 1978, no further change took place to *Ulva* inside these fences, except for three incursions by grazers (see below). It was obvious, however, that individual plants died and were replaced throughout the experiment. No *Ulva* grew to maturity in Fenced areas, and the turf remained at a uniform thickness of a few millimetres throughout.

Grazers appeared in the Fenced areas in April and August 1977, when newly-settled *Siphonaria denticulata* were found in some replicates. These must have settled during the previous month or so, but were not seen during March and July, nor any effects of them noticed, No newly-settled *Siphonaria* were found in any Caged, Roofed or Open areas, although many were present from April to September amongst algae at lower levels on the shore. These limpets ate patches of the *Ulva* turf in various fences, removing the sporelings down to a thin green film. The reduction in cover of turf in April and August 1977 (Fig. 1) was due entirely to the limpets, as those replicate fences with no limpets showed no decline in cover of *Ulva* (Table 1). During each of these two months, the *Siphonaria* were removed from all fenced areas.

During October 1977 adult *Bembicium nanum* (Littorinidae) invaded the Fenced areas, during a period of rough weather, and presumably by climbing over the edges of the fences. This did not occur again, except for an occasional individual during later months, and no explanation is offered for the sudden appearance of these animals. They did, however, eat the turf of *Ulva,* mainly from the edges of enclosures, thus reducing the mean cover to about 71% for all fences (see treatments in Fig. 1). Unlike *Siphonaria,* these gastropods removed all traces of *Ulva* from the grazed patches, leaving bare rock, or *Hildenbrandia* with no green film on it. The snails were removed as soon as they were found. As with *Siphonaria,* the reduction in cover of *Ulva* during August was due solely to the effects of grazing by *Bembicium,* and there was an obvious correlation between the number of *Bembicium* in any fence, and the reduction of algal cover in that fence (Table 1).

These unplanned incursions of grazers were fortuitous in that they provide support for continuous recruitment and some turnover of *Ulva,* at least during the months April to October. After grazers were removed, all affected replicates immediately returned to over 90% cover of *Ulva,* indicating that recruitment of the alga could occur very quickly throughout the autumn, winter and spring. It is reasonable to assume that individual sporelings dying for any other reason during the experiment were also replaced, and the great cover of *Ulva* turf in Fenced, ungrazed areas was thus maintained throughout the year.

When grazers were excluded large numbers of sporelings of *Ulva* were able to grow, and in all Fenced treatments, to occupy all the substratum, although the initial rate of coverage was reduced in areas where *Hildenbrandia* was present.

The corollary of this is that where grazers were present in Open areas, even though they were not in particularly great density (range from 1–14 for all Open areas throughout the study; see Table 2) their activities were sufficient to completely prevent any sporelings of *Ulva* from growing. The majority of grazers in these areas (about 80–90% of the total) were adult limpets *Cellana tramoserica*. Other grazers were the gastropods *Bembicium nanum, Austrocochlea constricta,* a few *Nerita atramentosa,* the chiton *Chiton septentriones* and the small herbivorous starfish *Patiriella exigua.*

Colonization and Growth of Ulva lactuca in Caged Areas

Inside normal and cleared Cages, a turf of *Ulva* developed within the first week or two from the start of the experiment, as described for Fenced areas. Again, the rate of colonization was slower where *Hildenbrandia* covered much of the area at the start of the experiment. From the second month of the experiment onwards, however, the growth of *Ulva* in Caged areas greatly exceeded that in Fenced areas. The sporelings forming the turf grew to mature

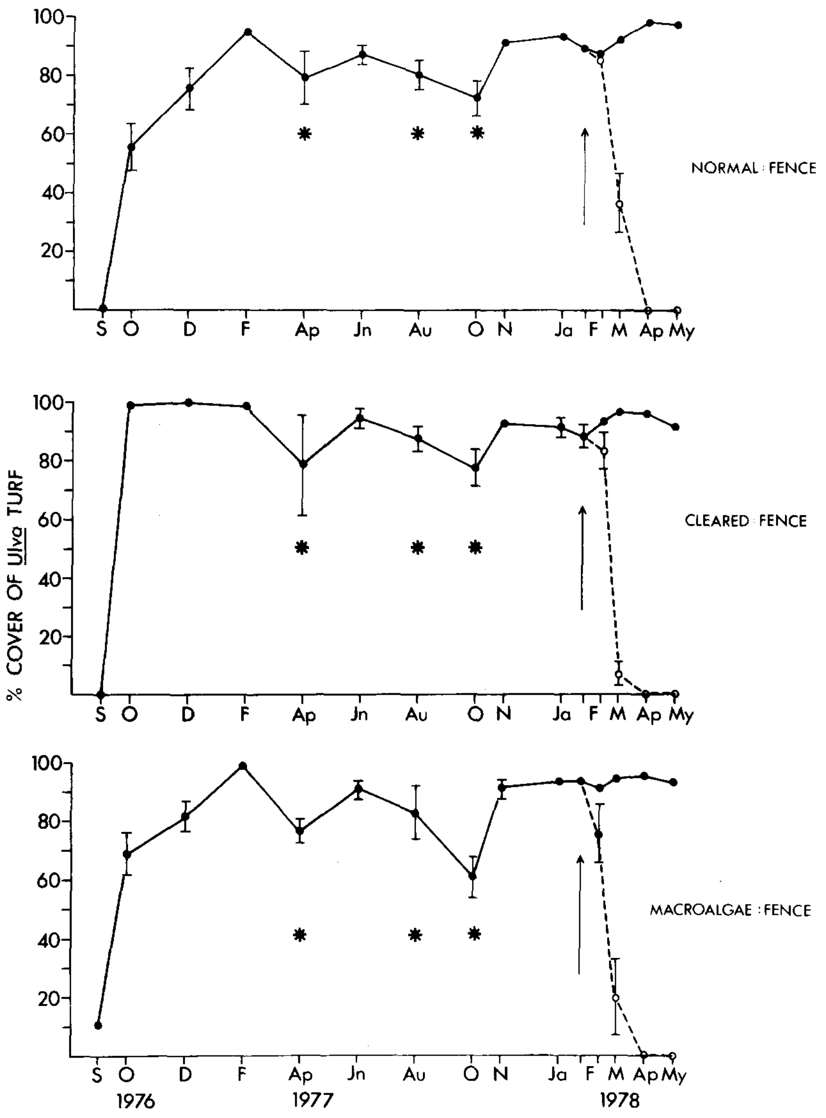

Fig. 1. Mean (±S.E., except where <2%) cover of turf of *Ulva lactuca* in experimental fences. Asterisks indicate dates of invasions by grazers (see text for further details). *Arrow* indicates removal of fences from two replicate plots after data recorded on 7th February 1978. Open circles: fences removed; Solid circles: fences intact

Table 1. Grazers invading experimentally Fenced areas

Treatment	Normal fences				Cleared fences				Macroalgal fences			
Replicate	1	2	3	4	1	2	3	4	1	2	3	4
April 1977												
No. *Siphonaria*	0	0	0	11	0	0	0	27	18	11	12	10
% *Ulva* turf	94	89	83	54	100	97	92	27	63	78	76	81
August 1977												
No. *Siphonaria*	0	12	9	4	0	4	0	15	27	0	11	0
% *Ulva* turf	91	67	78	75	98	86	90	79	62	98	74	99
October 1977												
No. *Bembicium*	14	11	14	21	2	4	9	11	21	28	19	34
% *Ulva* turf	91	72	66	62	89	84	74	60	64	60	76	42

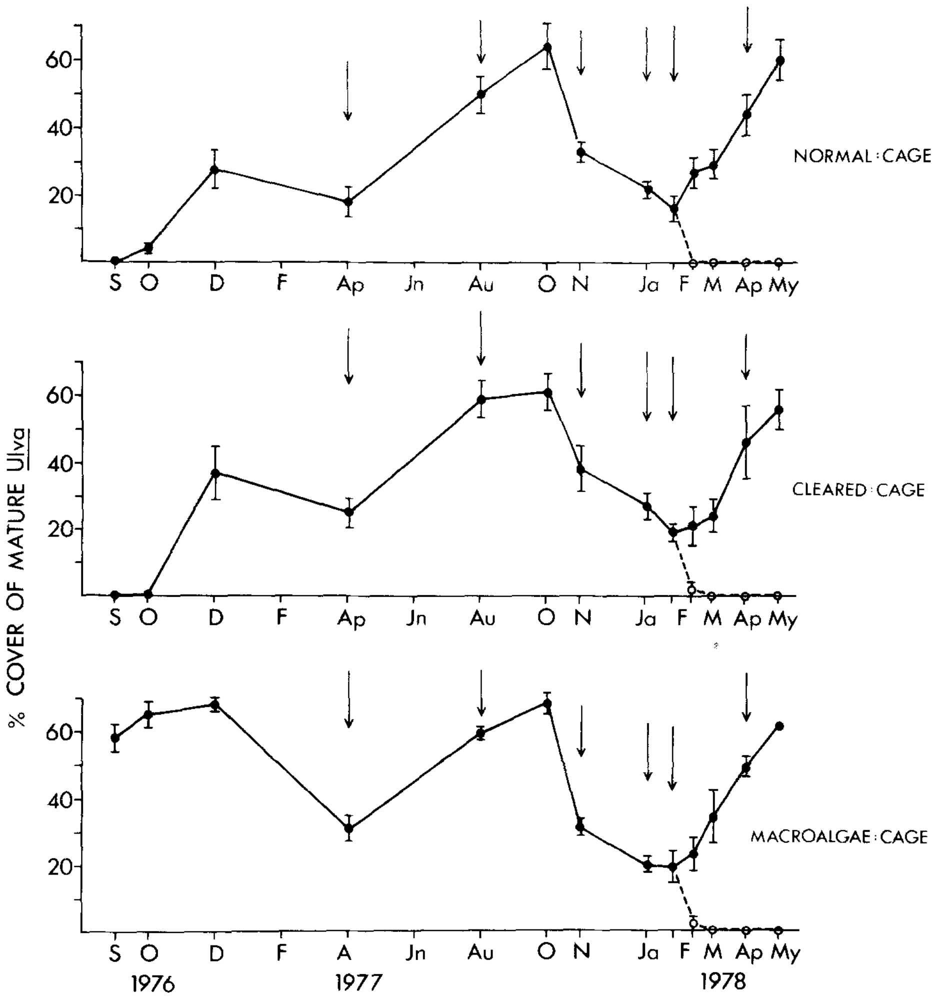

Fig. 2. Mean (±S.E., except where <2%) cover of mature *Ulva lactuca* in experimental cages. *Arrows* indicate times when cages cleaned or replaced (see text for details). Cages were removed from two replicates on 7th February 1978. *Open circles:* cages removed; *Solid circles:* cages intact

Table 2. Densities of grazers in experimental areas at various times. Mean no. (and S.E.) of all grazers per plot (784 cm^2), pooled from Cleared, Normal and Macroalgal treatments; $n=12$ except where stated

Treatment	Open	Roof	Cage
Oct 1976	6.2 (0.8)	26.3 (2.7)	1.0 (0.1)
Dec	5.9 (0.6)	25.7 (11.6)	0.5 (0.5)
Feb 1977	3.6 (1.3)	15.5 (3.2)	0 (0)
Apr	4.9 (0.8)	(No data)	0 (0)
Jun	5.5 (0.8)	23.7 (4.6) ($n=6$)[a]	0.3 (0.05)
Aug	7.2 (1.5)	26.5 (8.3) ($n=6$)[a]	0.5 (0.05)
Oct	4.8 (0.7)	32.7 (8.6) ($n=4$)[a]	0.2 (0.05)
Jan 1978	6.5 (0.8)	34 (9.1) ($n=4$)[a]	0 (0)
Apr	5.7 (0.8)	31.7 (2.0) ($n=4$)[a]	0 (0) ($n=6$)[b]
May	4.2 (0.8)	28.7 (1.3) ($n=4$)[a]	0 (0) ($n=6$)[b]

[a] Some rooves were lost and not replaced

[b] Cages were removed from two replicates in each treatment in February 1978 (see text)

thalli of *Ulva,* which grew as high as the tops of the cages (3 cm). An artefact of the experiment then appeared, as *Ulva* and some *Enteromorpha intestinalis* and *Porphyra umbilicalis* began to grow over the top of the cages and formed a turf (as described in experimental fences) covering much of the mesh of the cage. This caused a major decline in the cover of algae inside Caged areas, and the cages were cleaned, or replaced. This had to be done at intervals throughout the experiment (see Fig. 2). Except for the summer of 1978 (November to February, see Fig. 2), the removal of algae from the tops of cages was followed by regrowth of an *Ulva* turf and an increase in the cover of mature *Ulva.* At some times during the experiment, the algal growth on the tops of cages was not complete, but confined to central regions, and at no stage was there any growth on the sloping sides of the cages. Observations during high tide indicated that limpets, *Cellana,* and snails, *Bembicium nanum,* were active around the cages and climbed from the surrounding rock and grazed over the outsides of the cages. Animals were never observed on the tops of cages, nor on experimental roofs (see below).

By grazing over the outer edges of the tops of cages, animals prevented a complete growth of algae over the cages. It was thus possible to examine the effects on algae inside the cages of the increased shading caused by algae on the cages.

Photographs of the tops of the cages and the substratum under the cages were compared. A grid of 100 points was placed on the photograph of the top of a particular cage, and the presence or absence of algal turf noted for each point. The corresponding picture of the substratum in the same cage was then examined, keeping the grid of points in exactly the same place. For all replicates of Caged treatments in April and November 1977 and January and April 1978 (dates when cages were replaced or cleaned, see Fig. 2), there was complete correspondence between the presence

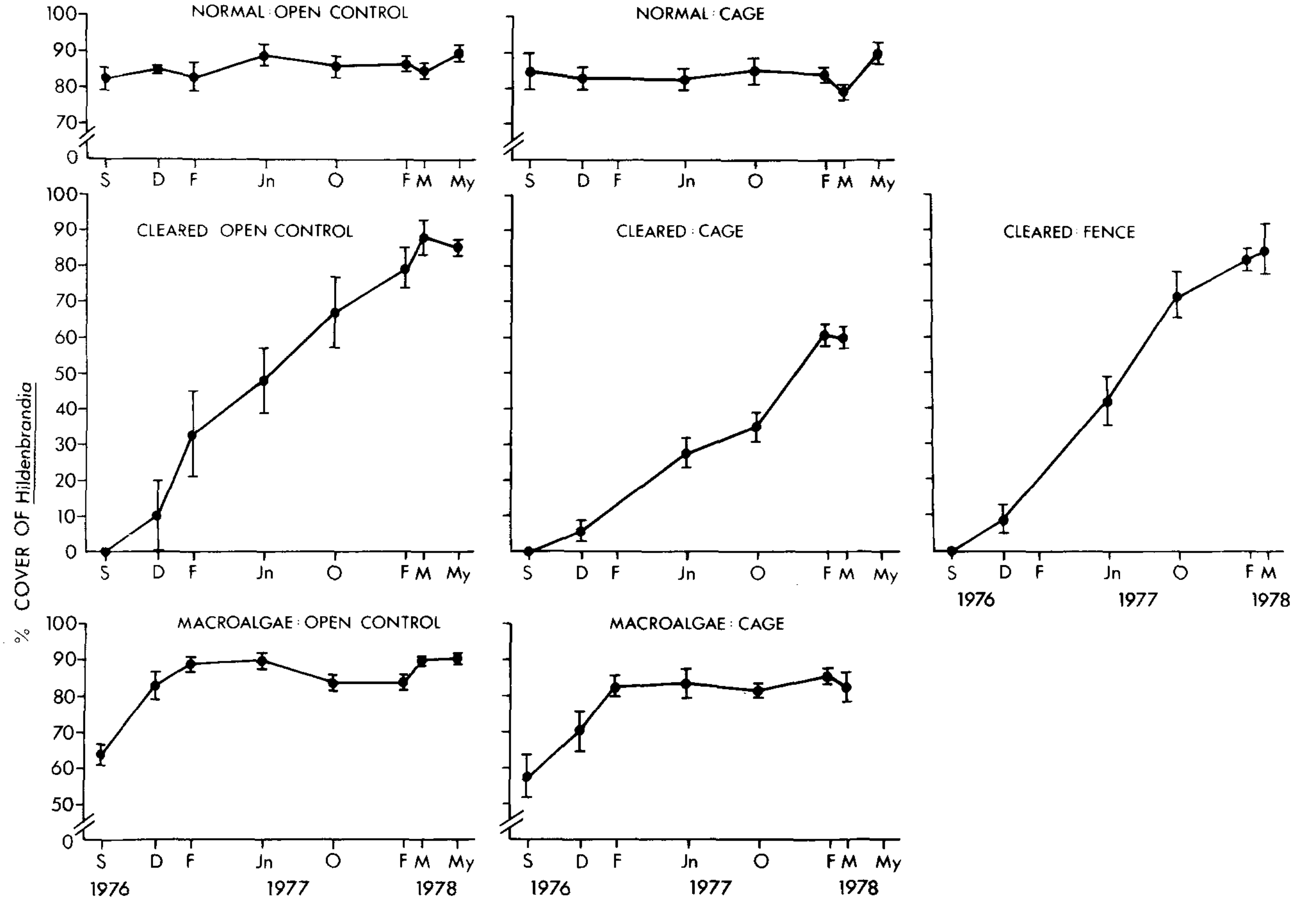

Fig. 3. Mean (±S.E.) cover of encrusting *Hildenbrandia prototypus* in various experimental treatments

of an algal turf at any point on the top of a cage, and the lack of *Ulva* below it. Similarly, whenever there was no algal growth on the top of the cage, mature *Ulva* were found on the substratum. From this it can be concluded that complete shading, caused by growth of an algal turf over the tops of cages, prevented the growth of *Ulva* underneath the cages. This artefact of the experiment explains the reductions of percentage cover of mature *Ulva* indicated in April and November, 1977 in Fig. 2. It does not completely explain the lack of recovery of *Ulva* after cages were replaced during November 1977, and January and February 1978, which implies some additional seasonality in the growth of mature *Ulva*, which is apparently slow during such summer periods.

Because there were periods of complete shading caused by algal growth over the cages, detailed interpretations of changes in cover of *Ulva* turf and mature *Ulva* thalli are impossible, and the data on *Ulva* turf are not described here. *Ulva* only grew to maturity in cages, and never grew beyond a short turf in experimental fences. The maximum cover of mature *Ulva* in Caged areas fluctuated around 60%, which was very similar to that in macroalgal plots at the start of the experiment (Fig. 2).

Cages were not completely effective in excluding grazers, because tiny gastropods could enter through the mesh. Small *Austrocochlea constricta* were fairly common (a mean density of about 5 per cage in all treatments) throughout the year. These were never larger than 4–5 mm diameter and were removed from cages at roughly monthly intervals throughout the experiment, so that their effective density would be somewhat less at any given time. Although no data can be presented, it is unlikely that these had any effect on the colonization of algae in the cages. In other, unpublished, experiments, densities of 30–40 juvenile *Austrocochlea* have been maintained in identical cages at similar levels on the shore, and no differences in algal growth observed from those described here.

In addition to these animals, some juvenile *Cellana* and tiny grazing starfish (*Patiriella exigua*) were found inside cages. They were rare, usually 0–1 per cage (see Table 2) and were removed whenever found. Effects of these animals were assumed negligible and were not estimated. In contrast to the Fenced areas (see above) there were no *Siphonaria* inside cages.

Colonization and growth of Hildenbrandia prototypus.

The cover of the major encrusting alga *Hildenbrandia prototypus* was not sampled as often as *Ulva*, because in many treatments other algae grew over it. Some sampling was done directly in the field. Only in very clear photographs was it possible to distinguish, reliably, the primary cover of *Hildenbrandia* from bare sandstone, under the secondary cover of other algae.

In Open and Roofed areas, where no algae grew over *Hildenbrandia*, its cover was easily sampled at all times. There was no change in cover in normal Open and Roofed areas throughout the period of observation (Open areas in Fig. 3). In cleared Open and Roofed areas, *Hildenbrandia* gradually grew in from the undisturbed growths on the edges of the plots, and spread from areas of newly-established thallus within the plots (Fig. 4). There was slow, continuous vegetative growth at all times of the year from both sources, until the original cover was re-established near the end of the experiment (Fig. 3). Careful examination of the photo-

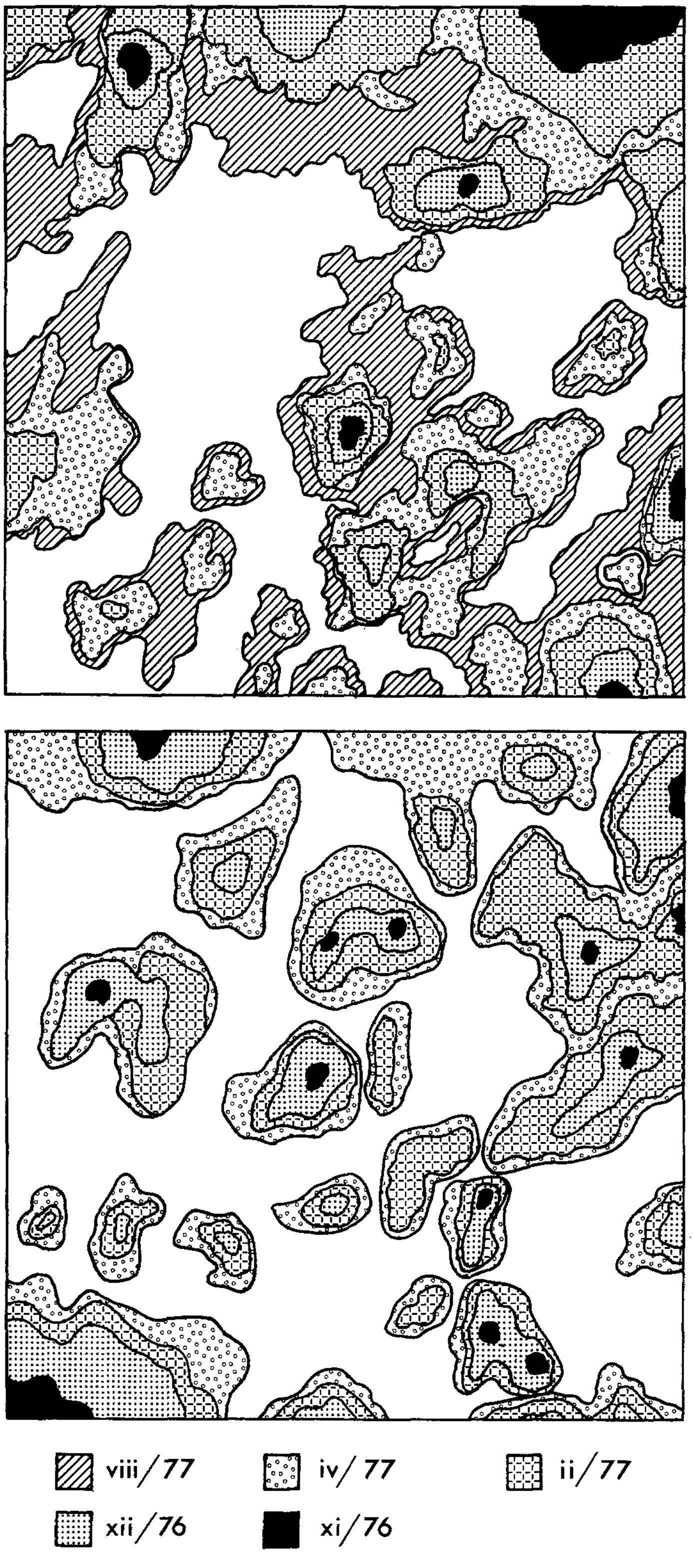

Fig. 4. Growth of *Hildenbrandia prototypus* from tracings of photographs of two cleared *Open plots*. Different types of shading indicate the cover of *H. prototypus* on the given dates

graphs revealed that all centres of newly-established *Hildenbrandia* in Open, grazed treatments were in tiny cracks running through the sandstone substratum. Not all such cracks in experimental plots formed sites for colonization of *Hildenbrandia*. The contribution to recolonization of cleared areas by growth from established cover at the edges of plots and from new individuals within plots was approximately equal.

Recolonization in cleared, Fenced areas was virtually identical to that in cleared, Open areas (Fig. 3) despite the nearly complete overgrowth of *Ulva* turf which covered the rock before the slower-growing *Hildenbrandia* became established.

The recolonization of *Hildenbrandia* in cleared Caged areas was at a much reduced rate compared with that in other experimental treatments. After 20 months, the mean cover of *Hildenbrandia* was only 60% in cleared Cages, compared with approximately 85% in Open and Fenced areas, and in normal Open areas. This reduction in growth of *Hildenbrandia* must be the result of the combination of mature *Ulva* growing in the cages, and of the shaded conditions inside the cages. There was no effect of cages on established *Hildenbrandia,* as the cover of this alga in normal Caged areas did not differ from that in normal Open areas during the experiment (see Fig. 3).

There was, however, an anomalous result in macroalgal areas. These areas had been caged for the previous twelve to eighteen months. By the time the experiment started, in September 1976, the mean cover of *Hildenbrandia* in all macroalgal areas was 62% (S.E. = 1.8%; $n = 16$ combined from all plots which subsequently were Fenced, Roofed, Caged or left Open). This indicates a highly significant reduction from the mean of 85% in surrounding areas, previously uncaged. In these macroalgal areas, *Hildenbrandia* increased its cover during the first five months of the experiment (until February 1977, see Fig. 3) until the cover no longer differed from that in uncleared Open normal areas. The fact that *Hildenbrandia* cover increased in macroalgal caged areas indicates that the reduced rate of colonization in cleared Caged plots during the experimental period would not lead to a permanently reduced cover.

There is no simple explanation for the reduction in cover of *Hildenbrandia* found in macroalgal areas which were caged during 1975. No reduction in *Hildenbrandia* was observed in normal Caged areas during the experiment.

Other Foliose Algae

At various times during the experiment, but after a minimum of six months, various other species of algae appeared in Caged areas. A few of these species also appeared in tiny amounts inside fences, and most of them were present in macroalgal areas at the start of the experiment. Most of these species occupied only 3–5% of the experimental plots, and some, such as *Sargassum* were only one or two individual thalli. Their occurrence is reported here simply as presence or absence in replicate plots of each Caged treatment (Table 3) and there was no discernible difference in the frequency of occurrence of any species from treatment to treatment. There were marked patterns of seasonality in the occurrence of some species (e.g., *Colpomenia sinuosa, Chaetomorpha* sp., *Ilea fascia*) which were present only in cooler months and absent during the summer (February data). In contrast, *Ralfsia* sp. was present only during the warmer months and may have been overgrown by other algae during autumn, although no detailed data are presented. Other species (such as *Corallina officinalis*) appeared during the first autumn after the experiment began (i.e., March to June, 1977) and persisted and grew throughout the experimental period. Yet other ephemeral species, such as *Enteromorpha* and *Porphyra,* were present at all times of the year after January 1977, but individual plants disappeared and new ones grew.

Table 3. Algae present in experimental cages

No. of replicates alga present	Normal cages		Cleared cages		Macroalgal cages	
	Oct. 1977	Feb. 1978	Oct. 1977	Feb. 1978	Oct. 1977	Feb. 1978
Chaetomorpha sp.	2	0	1	0	3	0
Cladophora sp.	2	0	1	0	2	0
Colpomenia sinuosa	3	0	2	0	2	0
Corallina officinalis	2	2	1	2	2	1
Enteromorpha intestinalis	3	4	3	2	3	4
Ilea fascia	2	0	1	0	1	0
Laurencia pinnatifida	1	0	0	0	2	0
Lyngbya sp.	0	1	0	2	0	1
Porphyra umbilicalis	3	4	4	2	3	3
Ralfsia sp.	0	1	0	1	0	2
Sargassum sp.	0	0	1	0	1	0
Unidentified red alga 1	1	1	1	1	1	2
Unidentified red alga 2	1	2	1	1	1	1
Unidentified blue-green alga	2	1	3	1	3	2

Inside fences, very few of these algae prospered, and the only species which grew beyond a short turf were the brown alga *Ilea fascia,* some individuals of which grew thalli up to 6 or 7 cm in length, and *Chaetomorpha* and *Cladophora* both of which grew as large as can usually be found in lower, algal-dominated regions on the shore, i.e., about 8–12 mm long. Perennial algae such as *Sargassum* and *Laurencia pinnatifida* were not seen in Fenced areas, but 1–3% cover of stunted plants (2–3 mm) of the ephemeral *Porphyra* could be found at all times of the year. One or two of these plants grew to maturity (3–4 cm thalli) in two or three Fenced areas during September/October 1977 but disappeared during the following summer.

Effect of Roofs

Roofed treatments were intended to allow evaluation of the effects of grazing under conditions of reduced environmental harshness. They produced, however, entirely unpredicted effects on the densities of grazers. Large numbers of gastropods, mostly adult *Austrocochlea constricta,* took up residence under the roofs during low tide, increasing the density of grazers to about 4–6 times that in open treatments (Table 2). No foliose algae grew under roofs, and the growth of encrusting algae in cleared Roofed treatments was virtually identical to that in Open and Fenced areas (as shown in Fig. 3).

As described above for cages, there was considerable growth of algal turf (mostly *Ulva lactuca,* but some *Enteromorpha intestinalis* and *Porphyra umbilicalis*). No grazers were ever observed on the roofs, and algae were removed at intervals. Growth of algae on top of the roofs cannot account for the lack of colonization of foliose algae under the roofs, because no such algae developed even when there was no growth on the top of the mesh. No further data are presented for Roofed treatments and some were destroyed (by people) during June and October 1977, and were not replaced.

Table 4. Mean no. (and S.E.) of *Actinia tenebrosa* per 784 cm^2 in various treatments ($n = 4$ except where stated)

Treatment		September 1976	December 1976	August 1977
Open:	Macroalgal	7.2 (1.0)	0 (0)	0 (0)
Fence:	Macroalgal	9.5 (1.5)	1.7 (0.2)	1.2 (0.6)
Roof:	Normal	0 (0)	0.7 (0.2)	7.0 (1.0)[a]
	Cleared	0 (0)	0.7 (0.7)	7.5 (0.5)[a]
	Macroalgal	9.7 (0.8)	7.7 (0.2)	7.5 (0.5)[a]
Cage:	Normal	0 (0)	4.2 (1.4)	9.7 (1.2)
	Cleared	0 (0)	2.0 (1.0)	5.2 (1.3)
	Macroalgal	6.0 (0.8)	7.5 (2.1)	6.2 (2.5)

[a] $n = 2$; some rooves lost and not replaced

Sea-anemones in Experimental Treatments

Adult anemones, *Actinia tenebrosa,* moved considerable distances (at least 3 m in some cases) from surrounding rock-pools and established themselves under roofs (data for some months, as examples in Table 4). No anemones ever appeared in any of the open areas, but many juveniles became established and grew to maturity inside cages. This had previously happened in the areas caged to create macroalgal treatments, so that there were some *Actinia* present in all macroalgal treatments at the start of the experiment in September 1976. These disappeared within two months from Open macroalgal areas (Table 4), and presumably moved away to pools, or perhaps to some of the Roofed areas. Many of the *Actinia* in Roofed macroalgal areas remained there throughout the experiment, as did some of the anemones in Fenced areas. There was, however, an initial decline in densities of *Actinia* in Fenced macroalgal areas during the first two months of the experiment (September to December, 1976: Table 4). Some of these animals were seen climbing over the fences, and the few which remained for the period of observation were observed to move from one corner to another of the fences as the sun moved during low tide, presumably to avoid being in direct sunlight whilst in air.

By August, 1977 (after 11 months) juvenile anemones which had appeared in Caged treatments reached adult sizes (approx. 15–25 mm diameter) and similar densities to those in macroalgal areas at the start of the experiment (Table 4). There was no difference in density of *Actinia* between Caged and Roofed treatments, for any of the three original algal conditions from August 1977 onwards (2-Factor analysis of variance of data in Table 4; experimental treatments, algal conditions and interaction all non-significant, $P > 0.05$). Clearly, the anemones were influenced by shade and reduced temperature and desiccation under roofs and in cages, but were not apparently affected by the great numbers of grazers under roofs, nor the cover of algae in the cages. *Actinia* in cages occupied a very small percentage of space ($< 3\%$) in the areas measured, and no corrections for this were made for measurements of cover of algae.

Fate of Established Algae

The fate of established macroalgae could be examined in two ways in this experiment. First, in macroalgal plots where stands of algae had grown in cages before the start of the experiment, the algae were observed after the cages were removed in September

Table 5. Mean (and S.E.) percentage cover of established mature *Ulva* in macroalgal treatments for the first few months of the experiment ($n = 4$) (Note that cover of *Ulva* turf is not included)

	Open	Roof	Fence	Cage
September 1976	57 (5.0)	58 (3.0)	54 (4.0)	58 (4.1)
October	0	2 (1.5)	16 (5.3)	65 (3.7)
November	0	0	0	63 (4.0)

1976. Some of these plots were fenced, some were caged, some had roofs placed over them and some were left open. The data for Caged macroalgal plots have already been described (see Fig. 2). Second, on 7th February 1978, the fences and cages were removed from two of the four replicate plots of each algal condition and subsequent events were compared with the two plots where the experimental treatments remained (see Figs. 2 and 3).

Removal of cages from macroalgal areas in September 1976 resulted in a rapid reduction of cover of mature *Ulva*. Some plants disappeared within a few days, and were apparently ripped off by waves. No animals were seen consuming mature plants, and those which survived the first few days lasted for a few weeks. During a period of warm calm weather in early October, however, many of them were bleached white and then disappeared. By early November (six weeks after the start of the experiment) there were no mature *Ulva* left in any of the uncaged macroalgal plots (Table 5). The more rapid decline in percentage cover of mature *Ulva* in Open and Roofed areas compared with that in Fenced plots (Table 5) is attributable to the reduced impact of wave-action inside the fences. Even though the mesh of the Roofs reduced the light intensity by approximately one third (see Methods), *Ulva* under the roofs also became bleached and died during October.

Of the other algae in macroalgal areas at the start of the experiment (as in Table 3) *Colpomenia sinuosa* were dislodged by waves. This often happens during rough weather in established algal beds at lower levels on the shore (personal observations). Most other species disappeared during October 1976. Because these species were present in such small quantities (3–5% of the substratum) no detailed account of their mortality can be attempted.

One foliose alga, the calcareous red *Corallina officinalis*, was an exception to the above account. This alga occupied a few percent of the area in several macroalgal plots at the start of the experiment and persisted as thalli 1–2 cm high until a period of very hot weather in January 1977, when all plants died and the dead calcareous skeletons washed away.

When cages and fences were removed in February, 1978, mature *Ulva* disappeared rapidly, as found in macroalgal Open areas at the start of the experiment. The reduction in cover of mature *Ulva* in these latter plots was, however, much more rapid (mostly within 2 weeks, see Fig. 2) and, during this warmer period of the year, all plants began to bleach, and many died, very quickly. There was no indication of healhy plants being washed away, nor was there any sign of grazing on these plants.

In contrast, sporelings of *Ulva* forming the turf in Fenced and Caged areas were eaten by grazers when the enclosures were removed in February 1978 (Fig. 2). A few adult *Siphonaria denticulata* were seen grazing in most plots within a few days from the removal of the fences. These were eating the *Ulva* turf. No *Siphonaria* were seen in any Open or Roofed plots during the experiment. In addition, *Cellana tramoserica* and *Bembicium nanum* moved around the edges of the turf and gradually ate the sporelings. Within a few weeks, the combined efforts of these grazers removed all turf algae, including the small percentage cover of *Porphyra, Enteromorpha* and unidentifiable juvenile red algae (see Fig. 2).

Discussion

Problems with the Experimental Manipulations

Experimental roofs in this study were considered as a separate treatment, not simply as a control for the effects of shading, etc., caused by cages. The abnormally high densities of grazers under the roofs (Table 3) make them useless as a control for other treatments. This is probably not a unique situation, although not discussed in some other studies. For example, the experimental roofs illustrated by Menge (1976; Fig. 5) show a marked increase in the density of the whelk *Thais lapillus* compared with the density in open, untouched areas (Table 2 of that paper). Such artificially great densities under roofs would presumably cause an artificially enhanced impact on surrounding populations of prey. For this reason, it is important that different experimental treatments should not be immediately adjacent to each other, otherwise adjacent open areas could not possibly serve as realistic controls for various manipulations.

Experimental cages introduce another artefact because algae grow over them. Fences served as more realistic exclosure treatments in the present study, but were somewhat less effective at excluding snails. The use of solid-walled fences is open to criticism, because they may seriously impede water-flow, cast shade around the edges and generally alter the microclimate. In the present study, it is improbable that any of the results could be attributed to such artefacts. Other experiments have been done using fences of much less substantial construction. These could not modify environmental factors to the same extent as was possible by the fences used here. Yet, other types of fences have generated similar results to those discussed here; these will be described elsewhere. To investigate the effects of grazing molluscs when even a few animals reinvade experimental areas is likely to lead to misleading or equivocal results (May et al. 1970; Raffaelli 1979; see below), and the use of fences and cages can be justified if realistic controls are designed. In other experiments (Underwood and Jernakoff, in preparation) the use of fences to enclose and exclude grazers has produced a satisfactory compromise between the necessities of manipulating grazers and the artefacts produced by the manipulations. Similar results to those in the galvanised iron fences described here were obtained.

Grazing and the Upper Limit of Distribution of Foliose Algae

The results clearly demonstrate that the exclusion of grazers from mid-shore levels led to immediate colonization by foliose algae, well above the normal upper vertical limit of their distribution on the shore. This result is in marked contrast to the results obtained by May et al. (1970) on a nearby shore, and by Raffaelli (1979) on shores in New Zealand. There are, however, important differences in the design of the experiments, which may account for the differences in the results. In both of the other studies, grazers could re-invade the cleared areas, sometimes very rapidly (May et al. 1970). Raffaelli (1979) indicated that about 5% of the original biomass of grazers could be found in experimental areas, and the present results indicate that relatively few grazers can have a profound effect on the establishment of algae. The mean density of grazers in open plots was about 5 (Table 2) throughout this study, yet these managed to keep plots clear of all sporelings of foliose algae. Whenever animals did invade exclosure treatments, they had an obvious and profound effect. The only way to be sure about the effects of grazing molluscs is to exclude all of them. The results of May et al. (1970) are confounded by the presence of 'rare' quantities of some species of foliose algae at mid-shore levels at the start of the experiment. Their experiment was done in an area characterized by numerous small pools (personal observations), in which a number of foliose algae can be found. These algae are not present on surrounding rock surfaces. Their presence in pools, which were not included in the present experiments, could mask the upward extension of some algae on non-pool surfaces when grazers were removed. An alternative possibility, that the results obtained in the present experiments are an artefact caused by changes in microclimate associated with experimental fences and cages, has been considered above.

Remarkably few studies have been published which discuss experimental analyses of the effects of intertidal grazers on the vertical distribution of intertidal algae. This is in marked contrast to the numerous studies on the role of grazing in the distribution and abundance of sub-tidal algae (e.g., Vance 1979; Paine and Vadas 1969; Vadas 1977; Kain and Jones 1966; and many others) and in the abundance of intertidal algae (e.g., Southward 1964; Pyefinch 1943; Aitken 1962; and many others). Castenholz (1961), however, demonstrated that grazing by littorine snails prevented the upward spread of a diatom mat during summer, and that the grazers were incapable of doing this during winter. In the present study, the foliose algae *Ulva lactuca, Chaetomorpha* sp., *Cladophora* sp., *Colpomenia sinuosa, Corallina officinalis, Enteromorpha intestinalis* and some unidentified red algae settled and grew in areas above their normal upper limit on dry rock when grazers were removed.

The abundance and diversity of algae above the upper limit of the main algal zone (see Underwood 1980) are affected by physical factors. In these experiments, none of the algae in fenced areas grew to maturity, although they did inside cages and more species appeared in cages. These results suggest that, in the absence of grazers, although sporelings of some algae can survive at higher levels than they are normally found, the physical harshness of the environment limits their growth, and presumably prevents some species from becoming established (e.g., *Laurencia* and *Sargassum* which were present in cages but not in fences). Two exceptions to this were *Porphyra umbilicalis* and *Ilea fascia* which grew to mature thalli inside fences, but not in grazed open areas, even though individuals can be found amongst grazers at mid- and high-tidal levels at some times of the year (Underwood 1980). How these algae occasionally escape from their grazers is not known.

Natural conditions providing shade and moisture at mid-tidal levels are sparse on many shores in New South Wales. There is no dominant fucoid canopy (except in some areas where *Hormosira banksii* provides this, but only in pools) which would provide shelter for understorey species (see Hatton 1938 and particularly Dayton 1975). Shaded areas, such as under ledges and in caves are either covered by the barnacle *Tetraclitella purpurascens* (Wood) (Denley and Underwood 1979) or have great densities of grazers. In the present experiments the provision of shade in plots accessible to grazers (Roofed areas) led to abnormally great densities of gastropods, which prevented the establishment of foliose algae. This does not happen in some other parts of the world where shade is provided by large algae which form a canopy (e.g., Dayton 1975). Southward (1964), however, described much greater densities of juvenile limpets under a fucoid canopy than in areas where the canopy was lacking.

Much of the greatly increased density of grazers under roofs in the present experiments was due to the immigration of *Austrocochlea constricta* which is usually very much confined to pools during low tide (Underwood 1976). This is probably a response to the effects of temperature and desiccation, although no data are available on this. The bahaviour and densities of the anemones *Actinia tenebrosa* in various experimental treatments provides support for this interpretation, as the distribution of this anemone is apparently influenced by desiccation (Ottaway 1973) as are other anemones (Dayton 1971).

In a number of studies, it has been asserted, without direct experimental evidence, that upper limits of intertidal algae are due to physical factors prevailing during low tide (see e.g., Doty 1946 and review by Lewis 1964). This view has been criticized by Chapman (1973) because the natural zonation of a number of species is not consistent with experimental evidence for intertidal and subtidal algae. There are, however, studies where the upper limits of species of algae can be demonstrated to be very strongly correlated with physical factors (e.g., Schonbeck and Norton 1978). In other studies, some support for this view is provided by the higher extension of algae where moist conditions or running water ameliorated the physical environment during low tide (e.g., Castenholz 1961; Dayton 1971; Frank 1965; Moore 1939). In none of these studies, were the effects of this treatment on any grazing animals investigated. It is possible that the moister conditions reduced the efficiency of grazers, or increased the survival and/or growth of sporelings to a point where they satiated the grazers. These effects would suggest that the actual cause of upper limits of the algae was a combination of physical stress and grazing, not just the former. Such interpretations, however, remain speculation until further experimental evidence comes to light.

Several authors have transplanted adult algae to higher levels on the shore than they are normally found (e.g., Schonbeck and Norton 1978); these plants usually die. While providing evidence that the physical environment kills these plants above their normal upper limit, such experiments do not provide evidence for the causes of their natural absence from these levels. This may still be due to physical factos, but could also be the result of a lack of settlement of spores, or removal of spores by grazers. Only where specific experiments are done which can identify and distinguish between such alternative hypotheses will the causes of limits to distribution be known.

A study similar in many respects to the present one was that on *Durvillaea antarctica* by Hay (1979). He demonstrated in one area that the upper limit of spores and sporelings of the kelp was raised to higher levels where he had experimentally removed limpets. The sporelings died during warm weather in early summer, and it is clear that the upper limits of the kelp were set by desiccation, not by grazing. Although he did not discuss the results in this context, Hay (1979) demonstrated that a number of other algae (*Porphyra columbina* and *Enteromorpha* sp.) appeared in higher areas when grazers were removed, and these apparently survived the rigours of the physical environment at levels higher than they were found before the experiments. In the present experiments, the algal turf inside fences survived the rigours of the environment, and were only eliminated when grazers invaded the fenced areas, or invaded the areas after the fences were removed.

Diversity of algae and structure of intertidal communities

A number of authors have investigated recolonization of algae on intertidal substrate after clearing, or the initial colonization of new surfaces (e.g., Hatton 1932; Pyefinch 1943; Moore 1939; Rees 1940; Dayton 1971). The general pattern of colonization seems to be diatoms, followed by opportunistic ephemeral algae such as *Ulva, Enteromorpha* and *Porphyra.* In northern temperate waters, fucoid algae appear later, and they, or other canopy species, can dominate the algal community. Controversy surrounds the interpretation of such observations as a true succession (Connell 1972; Connell and Slatyer 1977) and the development of an algal community may depend solely on rates and times of dispersal of the component species. There have been experimental demonstrations, however, that early arrivals may create favourable environmental conditions for later colonists (see Hatton 1932; Hruby and Norton 1979) indicating that succession may be occurring according to the Facilitation model of Connell and Slatyer (1977).

An analysis of succession is not the purpose of the present study. It is noticeable, nevertheless, that the sequence of algal colonization at mid-shore levels in N.S.W. was restricted for the most part to the earliest stages of that described in northern temperate waters. In the absence of grazing, even in the benign physical conditions inside cages, after three years no fucoid algae or other dominant canopy species developed (see Results: macroalgal cages which were caged for a total of three years prior to and during the experiments). May et al. (1970) suggested that rapid re-invasion of highly motile gastropods may prevent further 'colonizing succession'. This is not the case, as further changes in the algal community did not occur in the present experimental areas even though animals were kept out for 3 years. Probably, the harsh physical environment during low tide prevents the establishment of any but the hardiest species, most of which are widely-dispersing and short-lived.

Lubchenco (1978) discussed an intertidal system where ephemeral species can outcompete perennial algae in rock-pools and the successional sequence does not progress unless grazers remove the ephemeral algae. In such a system, the effect of grazers on community structure is extremely important. In the area studied in the present experiments, the opportunistic (ephemeral) algae, which are the first colonists, have no effect on the rate of recolonization by the dominant perennial encrusting alga *Hildenbrandia prototypus,* except in caged areas where there was a reduced rate of growth of *Hildenbrandia.* In fact, the converse appeared to be true in that the rate of colonization by *Ulva* sporelings was slower on *Hildenbrandia* than on cleared rock. This retardation was not long-term, and within five months of the start of the experiment, the turf of *Ulva* was equal on *Hildenbrandia* and on cleared rock. The nature of the effect of *Hildenbrandia* is unknown, but may be by production of allelopathic toxins, as have been found in a number of intertidal algae (Sieburth and Conover 1966) but not in *Hildenbrandia prototypus* (Conover and Sieburth 1966). There are, however, alternative explanations such as physical effects of the presence of *Hildenbrandia,* which might influence the retention of water, the temperature of the substratum, or rate of desiccation of sporelings. No data are available on this. The only suggestion, in the present study, that opportunists may deleteriously affect the perennial algae comes from the results of macroalgal cages, where the cover of *Hildenbrandia* was reduced at the start of the experiment. This did not happen in normal areas caged during the experiments, and the effect did not persist in macroalgal cages throughout the study. No explanation for this phenomenon can be offered, but it should be noted that details of processes in macroalgal cages were not monitored prior to the start of the experiments, and any of a number of possible factors may have been operating. During the period of close observation, no competitive superiority of ephemeral algae over *Hildenbrandia* was observed. This intertidal algal community thus has some similarities to the 'emergent substrata' discussed by Lubchenco (1978), but the successional sequence is not really affected by the herbivores in the way she discussed. In the system studied here, the presence or absence of grazers made no difference to the rate of occupation of primary substratum by the perennial *Hildenbrandia,* and no competitive interaction for primary substratum between this and other species was observed (compare data for cleared Fenced and Open areas in Fig. 3). Grazers were at sufficient densities in open areas to eliminate all spores and sporelings of foliose algae. The encrusting algae, notably *H. prototypus* (although the same was true for *Lithophyllum,* but it occupied less than 10% of all surfaces and detailed data are not presented here), escapes grazing because of its tough thallus. Scrapes of radulae of a number of species of molluscs can be seen on the alga, but grazers have vitually no effect and are mostly removing microflora from the underlying *Hildenbrandia.* To become established in cleared areas, *H. prototypus* has two advantages over the foliose algae. The first, vegetative lateral growth, enables it to occupy a great deal of space from established thallus outside a cleared area. Second, an individual starting to grow from tiny cracks and pits in the rock can occupy a lot of substratum by vegetative growth (Fig. 4). For most of the other algae, this is not possible. Individual *Ulva, Enteromorpha, Chaetomorpha,* etc., only occupy a minute amount of primary substratum. To occupy a significant amount of space, numerous individuals must escape from grazers and start to grow too large to be eaten. In non-shaded areas of the mid-shore at Cape Banks, this cannot happen and all individuals are eaten by molluscs. Comparable effects of the advantages of vegetative encrusting growth have been described. Cheney and Mathieson (1978) cited *Chondrus crispus* as a perennial alga which has extensive vegetative reproduction from the holdfast system and early sporeling stages which are resistant to grazing. Similarly, the holdfast system of *Gigartina papillata* allows this alga to retain much primary space in high intertidal locations on the west coast of the U.S. and *Gigartina* can rapidly recolonize areas after disturbance, by vegetative growth (Dayton 1971).

The fate of foliose algae which became established in the absence of grazers indicates that physical factors are responsible for the death of mature thalli. The turf in fences was removed by grazers after they were allowed in to, or when they invaded experimental areas. Macroalgal grazers such as *Siphonaria denticulata* migrated into these areas, but were never seen in experimental plots where no foliose algae grew (i.e., Open and Roofed treatments). Creese (1978) has described changes in local dispersion of siphonarian limpets in response to seasonal growths of foliose algae at lower levels on the shore. Clearly, an established growth of foliose algae at mid-tidal levels on this shore could only persist whilst grazers remained absent. Under such circumstances, indirect effects of the absence of grazers could prevent settlement of other organisms such as the barnacle *Tesseropora rosea,* which does not settle amongst algae (Denley and Underwood 1979) but this did not occur in the site studied, where there was no settlement of barnacles at all.

The effect of grazing molluscs at mid-tidal levels on this shore is to remove all spores of foliose macroalgae of a number of species, thus causing the upper limit of distribution of these algae. That all spores are removed at a density of about 5 animals per plot supports the conclusion that experimentally increased densities of grazers suffer from a shortage of food (Underwood 1978). In contrast to some other studies, grazing does not influence the process of colonization of primary substratum, because there were no long-term effects of competitive interactions between foliose and encrusting perennial algae.

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