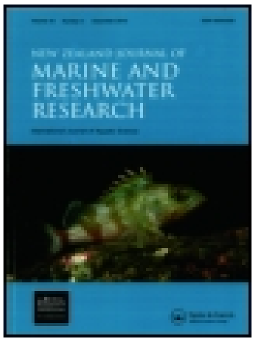

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REMOVAL OF INTERTIDAL ALGAE BY HERBIVORES IN EXPERIMENTAL FRAMES AND ON SHORES NEAR AUCKLAND

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ABSTRACT

When grazing animals are excluded from any intertidal area algae grow unchecked. In screened frames on the shore where predation experiments are in progress such growth is undesirable. A number of shore herbivores were tested for their ability to remove such algal growth and prevent its reformation without interfering with the main experiments. Only the browsing species *Lunella smaragda* and *Melagraphia aethiops* were capable of removing large algal growths, and these species were acceptable food for some of the predatory species. The complex inter-relationship between grazing species and shore zonation at several places near Auckland is discussed.

INTRODUCTION

The absence of grazing animals from a shore, whether prior to the recolonisation of experimentally or naturally denuded shores, colonisation of newly immersed surfaces, or following oil spills and detergent treatment, results in an upsurge of algal growth. However, once grazing animals become established the algal cover is usually reduced, until finally a relatively stable zonation pattern similar to that on nearbv shores emerges.

During 1962–63 during a study of the repopulation of artificially cleared rocky shores near Auckland (Luckens unpublished 1964), observations were made on the inter-relations of algae and grazing animals.

In the following years (1964–66) screened concrete frames were used for a series of experiments on the role of predation and competition in barnacle zonation (Luckens unpublished 1966, 1970). The study area was dominated by barnacles. Algae were abundant only in pools and below low water neap level (*see* Fig. 1). A few weeks after the frames were attached, the algal growth in and around them contrasted strongly with the barnacle-covered reef surface. Even at the highest level there was some macroscopic growth, but at both the lowest two levels it was quite common to find frames packed full of algae, particularly *Ulva,* after 2–3 months. Some of these plants became detached from the rock surface, but were held in by the screening.

The problem was to find suitable grazing species for inclusion in the experimental frames. The grazing ability of a wide range of species was therefore tested so that the species most efficient at grazing, but least harmful and least palatable to the other experimental animals, could be selected. Comparisons could then be made with results obtained in other areas, and with situations occurring naturally on the shore.

AREAS AND METHODS

GOAT ISLAND BAY, LEIGH

The main study area was on the seaward side of a reef at Goat Island Bay (36° 16′ S, 174° 48′ E), on the east coast some 96 km (60 miles) north of Auckland. Concrete frames 20 cm (8 in.) square internally and 5 cm (2 in.) deep were cemented to the shore and covered with fibreglass screening at four experimental levels. Although the reef is on the open coast, it is slightly protected from wave action by Goat Island to the north and by another reef to the east, and it rises almost 3 m to the approximate level of high water of spring tides.

The four levels where the frames were attached were (Fig. 1):

A. Highest level – in the *Chamaesipho brunnea* (barnacle) zone at the top of the reef about 0.5 m above high water neaps.
B. Upper middle level – at the top of the *Elminius plicatus* (barnacle) zone at about the level of high water neaps.
C. Lower middle level – in the *Chamaesipho columna* (barnacle) zone about 0.3 m above the top of the brown algal zone; and
D. Lowest level – about 0.3 m below the top of the brown algal zone between low water neap level and extreme low water spring tide level.

Except in and below the brown algal zone and in pools, algae are not a noticeable feature of the reef. Pools at the top of the reef contain *Corallina* paint, *Enteromorpha, Pylaiella* and a few *Ulva* tufts. Occasional plants of *Porphyra* occur within the upper parts of the *Chamaesipho brunnea* zone on open rock surfaces. There are various small blue-green algae in any damp places, such as crevices or seepage areas among barnacles. *Ulva, Hormosira,* and *Corallina* paint are the commonest algae in pools at low levels, with scattered plants of *Bryopsis* or finely branched rhodophyceans ('*Polysiphonia*'). A brown algal zone of *Carpophyllum maschalocarpum* and *Xiphophora chondrophylla* overlies a variety of small mixed algae whose abundance, variety, and extent is related to wave exposure and to the density of the sea urchin *Evechinus chloroticus*.

On the open shore the highest of the molluscan grazers is *Littorina* (*Austrolittorina*) *unifasciata antipoda,* most numerous in the *Chamaesipho brunnea* zone, but with small specimens in particular extending below mid tide. *Nerita melanotragus* and *Melagraphia aethiops* are common on barnacle-covered or bare rock surfaces from the upper middle experimental level down to the brown algal zone, and are joined in the lower half of this range, and in pools, by the cat's eye *Lunella*

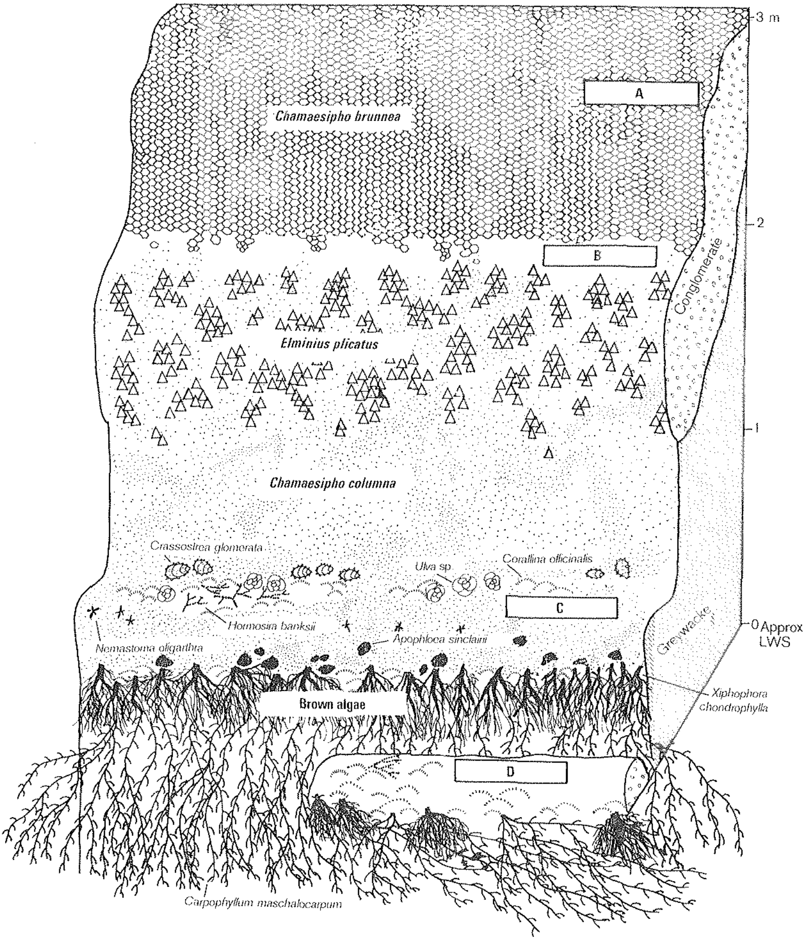

FIG. 1—The experimental reef at Goat Island Bay, Leigh, showing the four experimental levels (A, B, C, D). The main zoning organisms and the substrate of conglomerate over greywacke are also shown.

smaragda. The chiton *Sypharochiton pelliserpentis*, and the limpets *Cellana ornata*, *C. radians*, and *Siphonaria zelandica* range from pools at the top of the reef and from open rock at the upper experimental level down to the top of the brown algal zone. Although some grazing species may move slightly down the shore or into cooler or damper areas during hot weather, there is no marked seasonal migration up or down the shore by any species. The reef is dominated by barnacles and by grazing molluscs down to the brown algal zone. Zonation at Goat Island Bay is described in more detail in Morton & Chapman (1968).

TABLE 1—Molluscan species used in the grazing experiments, with the numbers and total weights used in each frame at Goat Island Bay

Species	Number	Total Weight (g)
Littorina (Austrolittorina) unifasciata antipoda	50	12.5
Littorina (Austrolittorina) cincta	18	12.5
Nerita melanotragus	30	50
Melagraphia aethiops	30	50
Lunella smaragda	30	50
Sypharochiton pelliserpentis	12	30

The species used in the grazing experiments are noted in Table 1. All specimens in one sample were of a similar size. Comments on the grazing ability of some other species which, although common in the area, were less suited to the experimental frames have been included in this paper. Since limpets failed to re-attach successfully in the frames, they were not used in the regular experiments. Chitons would reattach only if they were held against the floor of the frame until they had taken a firm grip.

To test the grazing ability of these species, two series of experiments were carried out. In the first series, a certain number and weight of grazing molluscs were placed in a frame free of all algal growth at each of the four levels. Only one species was present in each frame, and where possible the same number and weight of each species was used. The frames were inspected at intervals, when the number of animals present and the extent and type of algal growth were noted. The second series of experiments was similar to the first, except that the grazing animals were placed in frames which already contained a growth of algae. The results of the experiments and pertinent shore observations are discussed later for each species.

Unless otherwise noted grazing animals used in experiments were collected from nearby reefs. In the first series of experiments, the grazing species were added straight after the clearance, or attachment and screening of the frames. In the second series the frames were screened and left for 2 to 3 weeks while an algal cover developed before the grazers were added. Grazing ability (or the lack of it) became apparent within 3 weeks, although most of the experiments were continued for periods ranging from 6 weeks to 6 months or longer.

AUCKLAND HARBOUR

Cages similar to those used by Castenholz (1961) were attached to sandstone reefs at both St Leonard's Point (36° 48′ S 174° 47′ E) and West Tamaki Head (36° 51′ S, 174° 43′ E), but these were damaged by members of the public to such an extent that their use had to be discontinued. At St Leonards Point the sandstone reef is partly covered by a hard iron compound; before clearance, the vertical sandstone face is covered with the tubeworm *Pomatoceros cariniferus* and the bryozoan *Watersipora cucullata*, with numerous specimens of the naked pulmonate slug *Onchidella* and of the chiton *Sypharochiton pelliserpentis*. Adjacent to a sewage outfall, much of the reef surface is covered with a mat of short green algae, mostly *Ulva* and *Enteromorpha*, which partly obscure the sessile tubeworms and bryozoans.

At West Tamaki Head the reef surface is almost horizontal and during most of the year the surface is covered with the barnacle *Elminius modestus* and a light growth of green algae. The common grazing species is the chiton *Sypharochiton pelliserpentis*, usually to be found along the cracks between the sandstone blocks, where the surface is often devoid of both barnacles and algae.

In April 1963 two rectangular areas (0.3×0.5 m) were chosen away from all cracks and crevices. Both were covered with *Elminius modestus* and had a light growth of green algae. Half of each area was cleared completely, and all grazing animals removed from the surrounding rocks. After one month one area had a cover of small green algae with a few *E. modestus*. There was evidence that fish had grazed the algae in several places leaving bare areas with tooth marks. The second area was settled by scattered *E. modestus* with some fine filaments of brown algae. In June, 24 *Sypharochiton* were placed on this area.

RESULTS

ALGAL GROWTH AT GOAT ISLAND BAY

Concrete frames without grazing animals at the highest level (A) sometimes contained small macroscopic algae, but usually had a green or brown stained appearance.

At the upper middle level (B) algal growth usually consisted of an open turf of *Ulva* 1–2 cm deep, with a few patches of filamentous brown algae in the ungrazed frames. There was a slight tendency for brown algae to be more prominent than *Ulva* in some of the frames with grazing species, particularly those with *Sypharochiton* and *Littorina*.

Algal growth was most abundant at the lower middle level (C) and consisted of a mixture of *Ulva, Petalonia, Bryopsis, Colpomenia,* and *Scytosiphon*. These algae appeared to flourish in the control frames even when small *Littorina* and limpets could not be excluded completely. The control frames were often filled with algae including detached plants of *Ulva*. A certain amount of silt tended to accumulate at the base of the algae, and specimens of the protozoan *Gromia* became common. At times fish eggs were found among the algae next to the screening.

In contrast, algal growth at the lowest level (D) was not as abundant. This may be partly related to light reduction both by the screening itself and by diatom blooms which settled on the screening soon after the start of the experiments. After the diatoms had gone, there was settlement of *Ulva* both within and adjacent to the frames. Other algae found in the frames at this level included filamentous '*Polysiphonia*' and *Corallina* paint and turf regenerated from small pieces left when the rock surface was cleared for the cementing of the frames. *Colpomenia* settled during the experiments.

Although there were slight seasonal variations in the amount of algae settling, these appeared to have little effect on the frames, with the exception of the heavy growth of diatoms at the lowest level in April 1965.

GRAZING AT GOAT ISLAND BAY (Table 2)

Small specimens of *Littorina* (*Austrolittorina*) *unifasciata antipoda* were able to crawl through or under the screening, so only the largest specimens with their typical blue and white striped shells were used in the experiments. On the shore, small specimens are more numerous than large ones, and their total density is greater than that used in the experiments. The few small specimens that entered the frames did not affect the results, and occurred in the control (ungrazed) frames as well.

These snails are thought to feed on algal and lichen sporelings (Foster 1966), and to scrape up wave-stranded particles, diatoms, and algal filaments (Murray unpublished 1965). However, macroscopic sporelings are not eaten by *Littorina*.

At the highest experimental levels in the study area, the *Littorina* were dispersed thoughout the frame, but at the two lowest levels they showed a tendency to aggregate around the sides and upper corners of the frames. Where the *Littorina* were grouped around the sides of the frame, these were the only parts grazed, and even there control of the algal growth was incomplete. They appeared to be easily dislodged by wave movements. At the three lowest levels many suffered chipped and abraded shells and later died.

A larger species with a more southern distribution *Littorina* (*Austrolittorina*) *cincta* is found occasionally on Goat Island, Leigh, but the specimens used in the experiments were collected from Piha (36° 57′ S, 174° 28′ E) on the west coast at Auckland at the top and slightly above the *Chamaesipho brunnea* barnacle zone.

During the experiments the specimens tended to rest on the highest parts of the frame, or on the screening during low tide. When the frames remained damp while the tide was out at the lowest two levels, these animals rested with the foot extended. If disturbed by the removal of the screening they crawled up the sides and out of the frames.

Feeding was irregular over the frame, and at the lower experimental levels it was restricted to the walls of the frame. The animals did not maintain a definite cleared area, although some parts of the frame were more heavily grazed than others.

Nerita melanotragus, the northern New Zealand member of the warm water family Neritidae, is often found aggregated in large groups in depressions on the gently sloping or boulder shores near the experimental reef at Goat Island Bay, Leigh. This aggregating behaviour persisted at all levels during the experiments and, at the two lowest levels the *Nerita* tended to assemble in the highest part of the frame.

At the highest two levels, *Nerita* kept part of the frame clear of macroscopic algae, but at the lowest two levels, during March 1965, they were unable to maintain cleared areas; perhaps their tendency to move upwards affected their grazing behaviour adversely. In contrast, when 15, 30, and 60 *Nerita* were added to bare frames at the two lower levels in April 1965, there was no macroscopic growth in any of the frames 5 weeks later.

At the highest level some specimens of *Melagraphia aethiops* died, probably from some factor related to reduced submergence; at the upper middle level it was only partially successful as a grazer, and at the lowest two levels it was unable to maintain distinct bare areas. It did not show aggregating behaviour either naturally on the shore or in the frames, and was very similar in grazing ability to *Nerita,* but was less resistant to desiccation at the highest level.

Lunella smaragda, a common browsing mollusc of the lower shore, was more numerous on the bare or *Corallina*-covered, low level flats and pools at Goal Island Bay, Leigh. At the higest level, where some deaths occurred, it congregated in the lowest part of the frame, in contrast to its behaviour at lower levels, where it was always dispersed. The density of animals used was sufficient to browse a heavy growth of algae from a frame in a short time, and to prevent its redevelopment. In fact, at the upper middle level, 12 specimens were sufficient for this purpose. It was the most efficient grazing gastropod of all those used in the experiments.

In April 1965 when the screening on the frames at level (D) was generally covered by patches of diatoms, that frame containing *Lunella* was free of diatoms except on the edges of the screening above the concrete frame itself. The *Lunella* had apparently been able to scrape the algae from the upper surface of the screening.

Sypharochiton pelliserpentis tend to 'home' on the upper shore but to be more free-ranging on the lower shore. They showed a characteristic feeding pattern of cleared feeding areas and untouched patches of algae. At the upper middle level, six specimens kept all the frame, except their own plates, clear of macroscopic algae

At Goat Island Bay, the sea urchin *Evechinus chloroticus* is abundant at and below low water. Small specimens (less than 5 mm diameter) occasionally settled naturally in frames at the lowest level, and grew well. When diatoms had settled densely on the screening, the *Evechinus,* in grazing on them, ate large holes in the screening, but remained in the open frames, even when only the outside strip on top of the concrete was left.

TABLE 2—Behaviour and grazing ability of the molluscan and echinoderm species used in the experimental frames at four levels at Goat Island Bay, Leigh 1964–66 (*=many times the experimental number; N.A.=not applicable)

Species	Level	Behaviour in Frame	*N*	Total Weight (g)	Feeding Area		No. to Keep Frame Bare	Resistance to		
					Maintenance	Extension		Desiccation	Predation	Wave Action
Littorina (Austrolittorina) unifasciata antipoda	A	Dispersed	50	12.5	No	No	*	Good	Good	Poor
	B	Dispersed	50	12.5	No	No	*	Good	Good	Poor
	C	Aggregated upwards	50	12.5	No	No	*	Good	Good	Poor
	D	Aggregated upwards	50	12.5	No	No	*	Good	Good	Poor
Littorina (Austrolittorina) cincta	A	Dispersed upwards	18	12.5	Partial	No	*	Good	Good	Fair
	B	Dispersed upwards	18	12.5	Partial	No	*	Good	Good	Fair
	C	Dispersed upwards	18	12.5	Partial	No	*	Good	Good	Good
	D	Dispersed upwards	18	12.5	Partial	No	*	Good	Good	Good
Nerita melanotragus	A	Aggregated	30	50	Yes	No	30	Good	Good	Good
	B	Aggregated	30	50	Yes	No	30	Good	Good	Good
	C	Aggregated upwards	30	50	Partial	No	60 (March)	Good	Good	Good
	D	Aggregated upwards	30	50	Partial	No	15 (April) (varies seasonally)	Good	Good	Good

Melagraphia aethiops	A	Dispersed	30	50	No	No	*	Poor	Poor	Poor
	B	Dispersed	30	50	No	No	30–50	Fair	Poor	Poor
	C	Dispersed	30	50	Partial	No	30–50	Good	Poor	Fair
	D	Dispersed	30	50	No	No	30–50	Good	Poor	Good
Lunella smaragda	A	Aggregated downwards	30	50	Yes	Yes	<30	Poor	Fair–poor	Fair
	B	Dispersed	30	50	Yes	Yes	12	Good	Fair–poor	Good
	C	Dispersed	30	50	Yes	Yes	<30	Good	Fair–poor	Good
	D	Dispersed	30	50	Yes	Yes	<30	Good	Fair–poor	Good
Sypharochiton pelliserpentis	A	Dispersed	12	30	No survival		N.A.	Poor	Good	Poor
	B	Dispersed	12	30	Yes	Yes	6	Good	Good	Good
	C	Dispersed	12	30	Yes	Yes	9	Good	Good	Good
	D	Dispersed	12	30	Yes	Yes	*	Good	Good	Good
Evechinus chloroticus	A	Dispersed	Few	2–4 cm diameter	No survival		N.A.	Poor	N.A.	Poor
	B	Dispersed	Few	2–4 cm diameter	No survival		N.A.	Poor	N.A.	Poor
	C	Dispersed	10 & 7	2–4 cm & <5 mm diameter	Yes	Yes	6 larger	Poor	Good	Poor
	D	Dispersed	10 & 7	2–4 cm & <5 mm diameter	Yes	Yes	3 larger	N.A.	Good	N.A.

At the lowest experimental level, in frames which remained damp during low tide, *Evechinus* survived throughout the year. Two specimens with a body diameter of 2–4 cm kept 80% of the frame clear of algal growth, and at this density, where food supply was not limiting, the screening was little damaged. Specimens placed at the lower-middle level in mid-June all survived until early October, after which time they became detached, despined, and died. At the upper-middle level one specimen survived only 10 days in June, while another specimen had grazed about 26% of the frame before dying in mid-August.

Towards the end of October 1965 7 newly settled and 10 small (2–4 cm diameter) *Evechinus* were placed in two frames at the lowest level. All these were alive and healthy, the smaller set having reached a test diameter of 22 mm, when observations were concluded in mid January of the following year.

GRAZING AT AUCKLAND HARBOUR SITES

In grazing experiments at Oregon, Castenholz (1961) used stainless steel mesh to enclose *Littorina scutulata* and *Acmaea* spp. in shallow artificial pools or on rock faces. When a few animals were introduced into a sterilised pool, they were unable to keep the whole area grazed. Each individual or group of animals concentrated on keeping one small area clear, and preventing the appearance of macroscopic algae on this area. Animals introduced into a pool which already contained an algal cover started by forming their own bare areas and working outwards from these. Even without cages at St Leonards Point and West Tamaki Head, Auckland, it was apparent that the grazing animals were behaving similarly to those at Oregon. At St Leonards Point when the gently sloping rock surface was cleared of vegetation and animals, the cover after 2–4 weeks consisted of a mat of green algae. Limpets and chitons from surrounding areas began to graze the algae, starting at the edges and gradually working inwards. The adjacent vertical sandstone face was settled by algae and then grazed in the same way. *Cellana*, *Sypharochiton* and *Onchidella* start grazing at the edge of a patch of algae, and maintain an area of increasing size free of macroscopic algal growth. *Sypharochiton* is an indiscriminate rasping form, and the gut contents include algae, rock particles, crushed barnacle shell and the remains of small crustaceans (Murray unpublished 1965).

The 24 *Sypharochiton* placed on the experimental area at West Tamaki Head in June kept two small patches free of algae and settling barnacles, but did not harm the older barnacles. The chitons tended to avoid patches of barnacles, but they grazed the shells of solitary specimens within the feeding area. While the tide was out the chitons remained near the edges of the feeding area, and appeared to 'home' on to the same places. Several of these were just outside the cleared area where the rock surface was uneven By 9 June only 10 remained, but when a further 14 were added only 19 were found on the area on the following day. On 21 August, 19 chitons remained. Except for the replacement of lost chitons these areas were not touched.

TYPES OF GRAZERS

After investigating the radula of grazing gastropods in relation to the size and texture of the food, Murray (unpublished 1965) placed the molluscs below in the following groups:

- Heavy rasping forms, i.e., indiscriminate feeders
  - *Sypharochiton pelliserpentis*
- Browsing forms, which cut off fragments of algal thallus
  - *Lunella smaragda*
  - *Melagraphia aethiops* (scrapes also)
- Scraping forms, which scrape up water-stranded particles, diatoms, and algal filaments.
  - *Nerita melanotragus*
  - *Littorina* (*Austrolittorina*) *unifasciata antipoda*
  - *L.* (*A.*) *cincta*

From the experimental results, the only species capable of removing large algal growth were the heavy rasping and browsing forms. *Evechinus* should be included here, as it is capable of removing almost all algal cover. At Goat Island, Leigh, *Evechinus* has been responsible for extensive removal of algae at and below low tide level, and for depredation of *Ecklonia radiata* beds leaving only a bare rock surface or a cover of *Lithothamnia* in the sublittoral (Dromgoole 1964, Chapman 1966). On the grazed areas in the frames containing *Evechinus*, the only organisms left were *Corallina* paint, specimens of the barnacle *Balanus trigonus*, and a single specimen of a solitary hydroid (probably *Myriothela* sp.). Although Dromgoole reported this heavy grazing as confined to the lower sublittoral there were areas on Goat Island in 1966 where grazing had continued to the top of the brown algal zone. This resulted in a cover of *Corallina* paint or *Lithothamnia* extending from the barnacle zone well into the subtidal area and is comparable with Californian kelp bed depredation (Leighton *et al.* 1967).

Frames at the upper middle level containing *Littorina* spp. were peculiar in that the dominant algae in them were *Petalonia* and *Colpomenia*. The control frame in contrast contained *Ulva*, as did the frame with *Nerita*. It is possible that the *Littorina* discriminate between different species of algae as they feed, or was there some slight difference between the frames initially? Certainly in the frames with *Littorina*, any algae which grew, grew well and apparently were not touched, the animals simply scraping the rock or concrete and avoiding the plants. Frames at the lower-middle level contained some fine individual specimens of *Ulva*, finely branched red algae ("*Polysiphonia*") and *Petalonia*. If grazing molluscs were absent at the three lower levels, *Ulva* was usually the dominant genus.

The characteristic feeding pattern noted here particularly with *Sypharochiton*, *Cellana*, and *Siphonaria* but also seen with *Nerita*, *Melagraphia*, and to a lesser extent with *Littorina*, appears to be more typical of rasping or scraping forms than of browsing forms which can attack standing algae from above. Indeed, when the scraping and rasping forms enlarge their feeding area into an area of standing algae, such as *Ulva*, it is questionable whether the whole algal thallus is eaten, or whether the thallus is merely rasped through near the base with the loss of the main portion. If the main part of the thallus is simply detached, this would account for the large detached plants found in many of the frames. *Evechinus* apparently rasps through the base of *Ecklonia* stipes, which then drift away. Both *Lunella* and *Evechinus* ate large detached pieces of algae both in the frames and under natural conditions, as observed by Dix (1970). *Lunella* was observed cropping large pieces of alga off both *Corallina* and *Ulva* plants, and Murray (unpublished 1965) reports similar behaviour in *Melagraphia*. However, *Melagraphia* can also apply its radula more closely to the substrate than *Lunella* and thus can scrape off small algae, sporelings, detritus and inorganic matter.

SURVIVAL OF GRAZERS

At the highest two experimental levels there was a reduction in grazing capabilities due to the adverse effects of increased emersion. This was worst at the highest level, where varying numbers of grazing molluscs died during the experiments. Survival was related not only to the normal shore height of the species, but also to its powers of attachment and resistance to abrasion. Once detached, a specimen is not only liable to shell damage while being washed around in the frame, but can also detach further specimens.

Certain investigators have shown that the degree of tolerance to desiccation is greater among high level species than it is among low level species, e.g., Brockhuysen (1941) for some South African molluscs, and Clark (unpublished 1957) for three species of New Zealand gastropods. Others (Evans 1948) found no such correspondence.

At Leigh there was some correspondence between desiccation resistance and shore height, but it was complicated by the behaviour of the various species and the effects of confinement in the frames.

Littorina (Austrolittorina) cincta showed the best survival in the frames at all levels, but particularly at the highest level. Not only is it a high-level species, but it is able to survive strong wave action, usually without becoming detached, and if detached, its shell is stout enough to withstand the subsequent abrasion until it can re-attach.

Littorina (Austrolittorina) unifasciata antipoda, also a high level species, suffered severely from the effects of dislodgement and abrasion and it was probably this, rather than the effects of altered submersion times that resulted in its poor survival in the frames. Dislodgement by wave action has been advanced as a likely source of mortality among all size groups (Foster 1966). Of unmarked specimens displaced by him to the bottom of the barnacle zone at Mangawhai, 26 km (16 miles) north of Leigh, only 20% had returned to their original location 2 m above, while 60% of those removed to high tide level had returned after climbing 1.5 m in the same 24-hour period. When unconfined on the shore, dislodged specimens are probably able to re-attach in calmer, deeper water, but those confined in frames are rolled around until the surge zone has passed that level.

Nerita melanotragus, a thick-shelled, high-level, northern species, was resistant to desiccation, predation and abrasion, and survived well at all levels.

Different samples of *Melagraphia aethiops* varied in their resistance to desiccation, but were more susceptible than *Nerita* or *Littorina* spp. Even at the highest level *Melagraphia* remained scattered throughout the frame, unlike *Lunella* at the highest level and *Nerita* at the lowest two levels.

At Kaikoura, experiments on the resistance to desiccation of *Littorina* spp., *Melagraphia aethiops,* and *Lunella smaragda* showed that the resistance to desiccation was not in the same order as their positions on the shore (Rasmussen unpublished 1965). The *Littorina* species were both the highest species and the most resistant to desiccation. However, *M. aethiops,* which occurred higher on the beach than *L. smaragda,* was considerably more susceptible to heat and drying. Rasmussen concluded that some modifying factor may influence the upper limits of *M. aethiops.* After testing the desiccation resistance of several size groups of *L. smaragda* and *M. aethiops* he found that the largest and oldest specimens were most resistant to desiccation. Surprisingly, the smallest and least resistant specimens of *L. smaragda* are found within the intertidal zone, while the largest specimens are mainly sublittoral.

When *Lunella* of three sizes were confined in a frame at the highest level at Leigh all survived the first 6 weeks, but after 10 weeks only 20% of the total were alive; all were in the smallest size group. A parallel series of *Melagraphia* showed a better survival rate with 57% alive after 10 weeks.

The restriction of such a browsing form as *Lunella* to the lower parts of the shore, to pools, and especially the restriction at Kaikoura of the large specimens to subtidal levels, may simply be a reflection of the large amounts of food needed by such animals. Only at these low levels is there sufficient food and feeding time to sustain these large specimens. From the results of the experiments at lower levels *Lunella* ate much greater quantities of algae than *Melagraphia.*

At higher levels shelter from desiccation is easier to find for small specimens which can seek shelter between barnacles or in small depression. Thus the upper shore may be effectively 'damper' for small specimens than for larger ones. At the highest level *Melagraphia* would seem to be better equipped to feed on what was available, and to require less food to support the same weight of animal than *Lunella.* This decrease of size of *Lunella* in an upshore direction accords well with pattern (2) of Vermeij (1972) for species of low intertidal levels.

At the highest level the *Sypharochiton* tended to become detached and die after rolling around in the frame and having much of their girdle abraded away. No specimen survived as long as 2 months at the highest level. At the lowest two levels, they survived well in the frames, although some crawled out under the screening and grazed areas of algae growing on the concrete beside the frames.

SUSCEPTIBILITY OF GRAZERS TO PREDATION

Although grazing species were necessary for algal control in frames where predation experiments were in progress, there were times when the grazing molluscs were eaten in preference to the experimental prey provided. *Melagraphia*, with its comparatively thin shell and horny operculum, was fairly readily eaten by the muricid gastropod *Haustrum haustorium*, and to a lesser extent by the related *Lepsiella scobina* and *Neothais scalaris*. These latter species fed primarily on barnacles and bivalves, although gastropods were eaten in the absence of other suitably sized food. On the shore at Leigh, *Haustrum* fed on gastropods, particularly the pulmonate limpet *Siphonaria zelandica*.

Predation of grazers did not affect the grazing experiments since predators were excluded, but was a source of error in the predation experiments. The ideal grazing species for predation experiments was one that did not interfere with either the predator or the prey, was capable of removing all algae and maintaining the frame free of algae, and neither died of emersion nor was eaten by the predator. *Lunella* satisfied all these conditions except the last, at all but the highest level. However, because of its thick and calcified operculum, the predators all bored through the shell, and thus specimens eaten by a predator could be easily distinguished from those which died from other causes.

DISCUSSION

The effect of grazing molluscs on the zonation of any shore is exceedingly complex. The type and number present may well determine whether algae or barnacles are to be dominant.

A cover of barnacles, by restricting grazing of the larger limpets and chitons, and by increasing the dampness of the shore at low tide, can encourage dense growths of algae which may finally kill the barnacles. However, at Narrow Neck (Auckland Harbour, 36° 49′S, 174° 48′E) it was noted that, in the barnacle zone, many of the *Cellana radians* maintained a barnacle-free area beside their 'homes' and at West Tamaki Head the chitons were able to keep an area grazed down, and either prevent barnacles settling on it, or remove any that settled in the course of their grazing. Once the barnacles had reached a diameter of several millimetres the chitons graze over their shells without harming them. Although both limpets and chitons feed mainly on the cleared grazing areas, they could also feed at the edge of the algal mat to increase the size of their grazing areas. This was noted by Stephenson & Searles (1960) for the chiton *Acanthozostera gemmata*.

It appears that the barnacles protect the algae from grazing animals, but once an area has been cleared and colonised by algae, the barnacles are prevented from settling. This gives rise to the mosaic of patches of barnacles with green algae, separated by bare strips usually adjacent to cracks where the *Sypharochiton* 'home'.

On most of the barnacle-dominated shores the grazing animals are numerous and various enough to prevent the establishment of algae during most of the year. Particularly in spring and autumn, an increase in the abundance of algal spores may result in a temporary upsurge of algal growth. At Piha (36° 57′S 174° 28′ E) in the late winter and early spring on shaded south-facing slopes from mid tide level to at least 2 m above high tide, a mixture of algae, including *Ulva* and *Porphyra,* formed a cover over the rock surface. Grazing and increased insolation later removed this within a few weeks. Calcareous turfing algae such as *Corallina* can exclude limpets and chitons, but not forms such as *Lunella,* which graze the top of the turf.

After clearance of the rock surface at St Leonards Point, algae settled densely. Grazing species moved into the area but it was noticed that tubeworms *Pomatoceros* and *Spirorbis* and the bryozoan *Watersipora* were common among the algae of the ungrazed area and absent from the grazed portions. This suggests that grazing removes or dislodges settling or newly-settled animals. Under cover of the algae they are temporarily safe from grazing, and by the time the area is grazed, the animals may be too large to be damaged. Thus the algae may benefit the serpulids by providing them with shelter from grazing animals. They also prevent certain animals, such as barnacles, from settling and competing with the tubeworms.

In experimental work carried out by Stephenson & Searles (1960) at Heron Island, fish were regarded as the most important modifier of vegetation on the reef flat, although grazing molluscs were found there. Grazing by fish was of greater importance on the reef flat than on the more dissected parts of the reef. At West Tamaki Head grazing by fish also removed barnacles from the experimental areas; it was commonest on those cleared areas with a cover of green algae, but was also observed on slates attached on the lower part of the reef. Removal of algae by fish was common on vertical plates suspended from the Naval Base paint raft at Devonport (Auckland Harbour, 36° 57′ S, 174° 28′ E). At West Tamaki Head grazing by fish often delayed or decreased the settlement of barnacles, but it was not consistent enough to keep all barnacles removed, and eventually these became large enough to discourage further grazing.

Whenever an area of intertidal rock is cleared of all animals and plants, algae will probably become more abundant on it than on surrounding areas, until the influx of grazing animals reaches a density sufficient to cope with the algal growth. The experiments of Jones (1948) and Southward (1956) at Isle of Man, Castenholz (1961) at Oregon, Rasmussen (unpublished 1965) at Kaikoura, Luckens (unpublished 1964) at Piha, Narrow Neck, West Tamaki Head, and Leigh, and others are all examples of this interaction. Since so many of these grazing molluscs have planktonic larvae few if any areas remain free of them for long.

At one stage an attempt was made to remove all the grazing animals from a flat patch of rock about 1 m × 2 m below the *Crassostrea* at Goat Island Bay. This was mainly bare rock but there were areas of *Corallina officianalis* paint, and some *Corallina* turf in a few small depressions. During 3–4 weeks, several thousands molluscs were removed from the area and a good growth of *Enteromorpha* resulted. The greenness of the patch could be seen from some distance. When removal of grazing animals ceased, the area rapidly returned to its former condition.

On the open shore, grazing is far more intense than in the frames, and the different types of grazing animals complement each other. Except low on the shore, in places where algae are favoured by lack of grazing animals, and where the algae are unpalatable or simply too large, the grazing animals will ensure that few of the millions of spores stranded there survive. In the control frames at the middle levels, i.e., those where grazers were excluded experimentally, large numbers of small limpets and *Littorina* (*Austrolittorina*) *unifasciata antipoda* were present, but appeared to be having little or no effect on the algae. Presumably they ate wave-stranded spores and detritus and not the algal thallus.

CONCLUSION

The only species capable of removing large algal growths in frames at Goat Island Bay are the sea-urchin *Evechinus chloroticus* and the gastropod *Lunella smaragda.* The chiton *Sypharochiton pelliserpentis,* an indiscriminate rasping feeder, can enlarge its feeding area into algal turf. The scraping gastropods *Melagraphia aethiops, Nerita melanotragus, Littorina* (*Austrolittorina*) *unifasciata antipoda* and *L.* (*A.*) *cincta* are only occasionally able to maintain clear areas and rarely eat standing algae. At St Leonards Point, Auckland Harbour, *Cellana* species, *Sypharochiton pelliserpentis* and *Onchidella* all start grazing at the edge of a patch of algae, maintaining a small feeding area free of algal growth.

Survival of grazers is related to their normal shore height, powers of attachment, and resistance to abrasion. Desiccation resistance is related to size, shore height and food requirements in *L. smaragda* and *M. aethiops.*

Barnacle-dominated or bare shores may be maintained by high densities of grazing molluscs, but the balance is delicate, and removal of grazing species usually results in a temporary or persistent increase in algal cover.

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