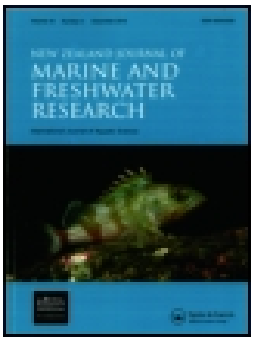

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POPULATION VARIATIONS IN THE GRAZING TURBINID *LUNELLA SMARAGDA* (MOLLUSCA: GASTROPODA)

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ABSTRACT

The grazing turbinid gastropod *Lunella smaragda* was sampled regularly over 3.5 y from precise sites of different microtopography and height on the platform shore at Goat Island Beach near Leigh, Northland, New Zealand. Growth is linear for over 3 y, and the year-classes distinct. The position of the different size-classes is related to both the shelter afforded by the microtopography, and to the height on the shore. The populations in the mid-eulittoral turf flats, low eulittoral bare rock areas, and the sublittoral fringe are distinct, and there is a general movement down the shore with age and size. Wave action apparently dislodges the animals from higher areas when they grow to a critical size and transports them to sites lower on the shore, where wave disturbance is less. Field experiments with marked animals and laboratory studies with a wave tank confirm that the wave-effected distribution is size related. However measurements showed that the ratio of foot attachment area to the shell area presented to the wave does not vary with animal size. The possible benefits of wave dislodgment and wave-effected distribution are considered.

INTRODUCTION

The distribution of different mobile gastropods on bedrock shores and their attachment abilities may be size related. However, these generalisations remain untested because of the difficulty of interspecific comparisons. Different species have a number of different characters, any one of which might affect distribution, and it is difficult therefore to test the theory that size is a most important factor. This paper describes the distribution of a single species, *Lunella smaragda*, on hard shores in relation to the animals' size and the shelter afforded by the microtopography. This species is distributed through the eulittoral and is found in a fairly wide range of wave exposure conditions. Evidence is presented for distribution being size related and also that wave transport is important in distribution after wave dislodgment: wave dislodgment need not lead to the elimination of an individual, but rather may facilitate transport to a more tolerable site.

The growth rate and age class distribution of the grazing turbinid *Lunella smaragda* was established by studying a population on the "Echinoderm Flat" of Goat Island Bay, near Leigh, New Zealand (36° 16′ S, 174° 48′ E). This is adjacent to the University of Auckland's

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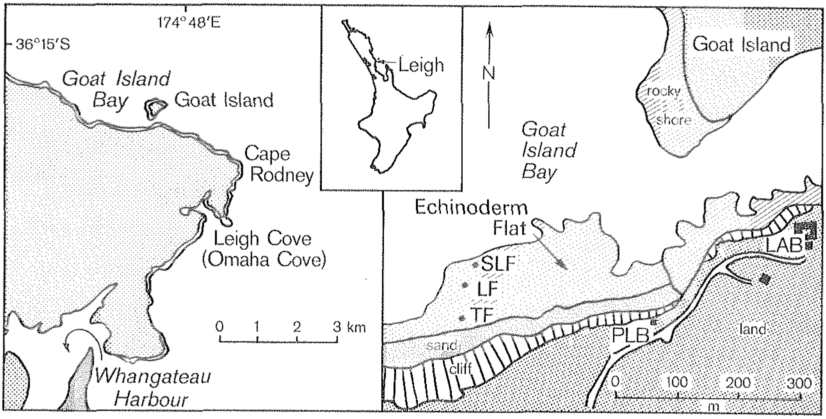

FIG. 1—Sketch maps of (*middle*) the location of the principle study area, (*left*) the coastline around Leigh, showing Goat Island Bay and subsidiary study areas, (*right*) part of Goat Island Bay showing the Echinoderm Flat and the precise positions of the Top (TF), Low (LF), and SLF Flat (SLF) sampling areas for *Lunella smaragda* (PLB = public lavatory block, LAB = Leigh Marine Laboratory).

Marine Research Laboratory, on the east coast of Northland, some 50 km north of Auckland. Reference was also made to populations of other shores in Auckland and Northland. The population structure at three sites on a transect down the Echinoderm Flat shore (Fig. 1), were followed for over 3.5 y, and the patterns of distribution effected by wave action rather than by the animals' own motility were noted.

Echinoderm Flat is a gently sloping shore of intermediate exposure, constructed of Waitemata sandstone flysch and formed into terraces, some of them backwardly sloping. The back of the shore is fringed from mid- to upper eulittoral by a narrow mobile beach of coarse-grained sand. In places the terraces have a litter of boulders and elsewhere are clean flat surfaces, clear of interruptions to the forward rush of breaking waves. The upper platforms (mid-eulittoral) are characterised by their very extensive cover of coralline turf (over 85%); other macroalgae are rare. The lower platforms (low eulittoral) have substantial but very patchy coralline turf (15–35% surface cover). Between these patches the open rock surface has a partial cover of coralline paint (10–30%) and a scattering of individual plants of the fucoid *Hormosira banksii*. A disorderly succession of other macroalgae also occur here; *Liogora harveyana*, *Colpomenia sinuosa*, *Laurencia botrychoides*, and *Leathesia difformis*. All of these may develop into substantial clumps but seldom more than about 5 cm high, and each species may bloom between storms, to cover as much as 50% of the surface. In the sublittoral fringe, there is an extensive cover (over 75%) of coralline paint, and large brown algae, particularly *Carpophyllum maschalocarpum*, form a canopy over the rock surface. Other important brown algae here are *Carpophyllum plumosum*, *Xiphophora chondrophylla*, and *Cystophora torulosa*.

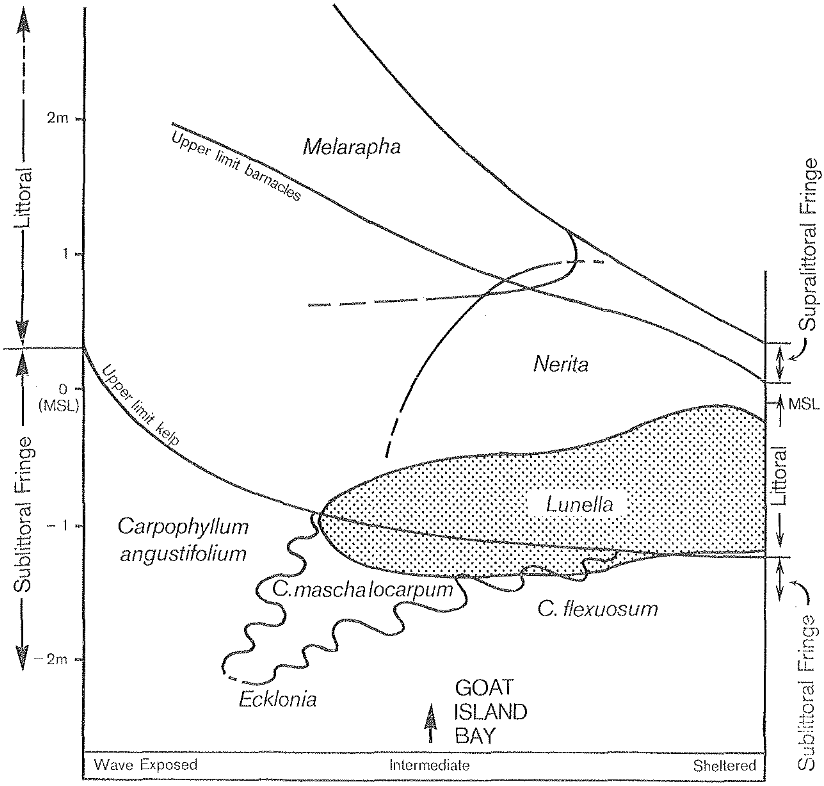

FIG. 2—Distribution of *Lunella smaragda* on Northland shores in relation to wave exposure and height on the shore, and to the grazing gastropods *Melarapha* and *Nerita* and the algae *Carpophyllum* spp. and *Ecklonia*. After Smith (unpublished 1969).

Lunella reaches its highest density in the lower regions of sheltered and semi-exposed shores, where it is also the dominant grazer (Smith unpublished 1969). Characteristically, it is found associated with *Corallina* sp. in the lower and mid-eulittoral, above *Carpophyllum*. As wave exposure increases (Fig. 2), the abundance of *Lunella* drops away abruptly implying that the mechanical effects of waves and the problems of attachment limit the distribution. *Lunella* extends only into moderate exposure in the lower shore, and in the absence of turfing algae in these places, small individuals (less than 5 mm diameter) are found only in cracks and crevices and are not common. In sheltered beaches, *Lunella's* range extends into the upper eulittoral. On shores of intermediate exposure its upper limit is in the mid eulittoral, and on the most exposed shores on which it occurs, it is not found above low eulittoral. "*L. smaragda* apparently is very tolerant of desiccation" (Rasmussen unpublished 1965) and so this vertical shift seems primarily related to wave tolerance. The examples described here clearly demonstrate the effect of wave action on distribution and the importance of animal size in relation to microtopography.

SAMPLING METHODS

Lunella was sampled approximately monthly over 3.5 y from May 1970 to December 1973 from three specific sites on a transect down the shore of the Echinoderm Flat. One site was chosen in each of the three general areas detailed below:

a) A turf covered flat at the top of the mid-eulittoral with no boulders, called the "Top Flat", positioned 300 m on a bearing of 271° T from the public lavatory block at Goat Island Beach:

b) A flat in the low eulittoral with patches of coralline turf and *Hormosira* separated by bare rock areas with coralline paint, called the "Low Flat", positioned 302 m on a bearing of 280° T from the public lavatory block.

c) A flat step in the sublittoral fringe (SLF) covered with coralline paint and with a canopy of large brown algae, called the "SLF Flat" and positioned 293 m on a bearing of 287° T from the public lavatory block.

From each site, samples of about 300 *Lunella* were collected, a number large enough to give meaningful size-class histograms. Approximately 2 m^2 yielded this number at each site. The samples were taken to the laboratory nearby where details were recorded. The animals were then stored in running seawater and returned to the site from which they had been taken at the next convenient low tide. All measurements were normally completed within 1.5 h of collecting the animals. Rapid and accurate measurement of length (the longest measurement across the shell, see histogram ordinate in Fig. 3) to the nearest 0.25 mm was made with a "V" board, and the *Lunella* were separated to the nearest 0.5 mm division into a multicompartmented tray. The numbers of each 0.5 mm size class were plotted.

SUMMARY OF DISTRIBUTION

Figure 3 is a diagrammatic representation of the Echinoderm Flat shore (with the coarse sand beach at the top, turf flats below the sand, falling away to terraces with boulder litter, through to flats in the low eulittoral, and short steps in the sublittoral fringe characterised by *Carpophyllum* sp.; below this fringe the shore falls away quite sharply into the sublittoral, and the dominant kelp here is the laminarian *Ecklonia radiata*). The insets diagrammatically represent the *Lunella* and associated algal cover and the histograms represent typical distribution of size-classes for *Lunella* at the three sites in the spring (October 1970).

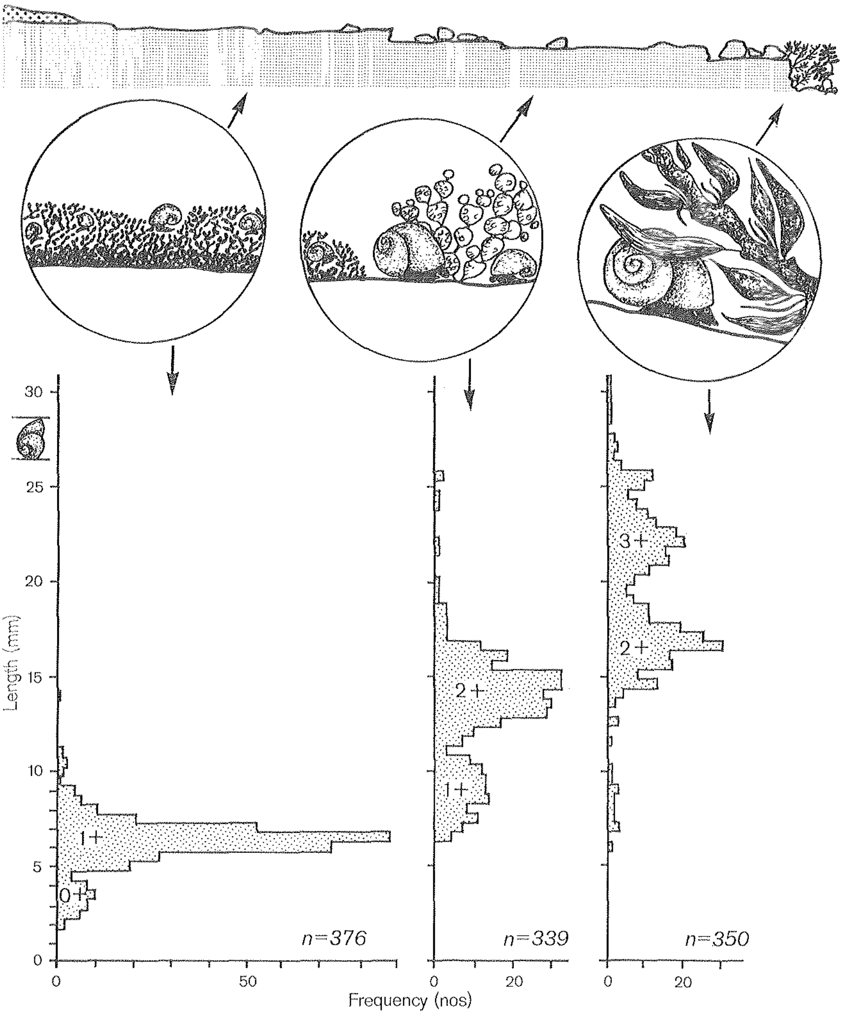

FIG. 3—Age and size-class distribution of *Lunella smaragda* at Goat Island Bay: (*upper*): form of the platform shore; (*middle*): Diagrammatic microtopography of the three sample areas with their major plant associations; and (*lower*): Size-frequency histograms for each successive area for 15 October 1970. Numbers in histograms normalised to 350.

The Top Flat has an almost total cover of coralline turf, with small *Lunella* only amongst the turf. The Low Flat has small *Lunella* in the isolated patches of coralline turf and larger individuals, up to about 17 mm, on the open rock between the turf patches and the erect macro-algae. On the SLF Flat small individuals are few, and there is a range of other sizes of *Lunella*, up to about 35 mm, which occur mostly on the smooth paint-covered rock, with some on the fronds of the over-cover of *Carpophyllum*. As shown in the histograms of Fig. 3, animals beyond a certain size do not occur on the Top Flat and the numbers of juveniles in the Low and SLF Flats are insufficient to account for the large numbers of older individuals. It would appear therefore, that recruitment occurs from the Top Flat to both the Low and SLF Flats.

CHANGES IN THE TOP FLAT POPULATION

Typical Top Flat population changes are shown in Fig. 4. Only one size-class peak is found from May to the beginning of September (an example is shown in Fig. 4, *middle*). In late September the largest of the 0+ year-group are first found and are distinct as a separate year-class in October or November (Fig. 4, *lower*). The sample numbers of this year class are low because the very smallest animals are very difficult to find and consequently samples of the animals up to 1 y old are biased downwards. Young *Lunella* shells are a similar colour to the coralline turf and its contained debris, and at low tide occur well down in the turf, often almost completely buried. Normally about an hour was spent searching a metre square during Top Flat sampling.

By January the juveniles are nearly one year old, and they constitute the main part of the Top Flat sample as they become easier to find and the 1+ year-group is lost from the flats (Fig. 4, *upper*). This loss commences when the animals reach about 7 mm, and some negative skewness in the histograms is seen as early as July (Fig. 4, *middle*) when some of the fast growing 1+ had been lost from the flat. The skewness becomes more extreme later in the year (Fig. 4, *lower*) as the mean size of the population grows beyond 7 mm and by the next January most of this size-class has been lost.

The initial appearance of the young *Lunella* in these turf flats has not been recorded. The Top Flat population consists entirely of sexually immature juveniles. *Lunella* has separate sexes and maturity is not reached until the animals are about 15 mm diameter. The majority of animals of this size and above occur lower on the shore at Goat Island Beach. The gonads appear to be in a ripe state from as early as September, but spawning probably does not occur until January or February. That large numbers of juveniles appear in the coralline turf flats remote from the sexually mature population implies a larval stage pelagic for at least a short time. Portions of the turf scraped from the rock were sorted under a binocular microscope and by this means a few juveniles as small as 1 mm were found by June. However, during the regular sampling, these very young individuals (0+ year-class) were not detected until late September.

Grange (1976) induced *Lunella* to spawn in February. The pelagic larvae resulting settled after about 48 h. He observed the main spawning in the field during storms in the same month; males and females release

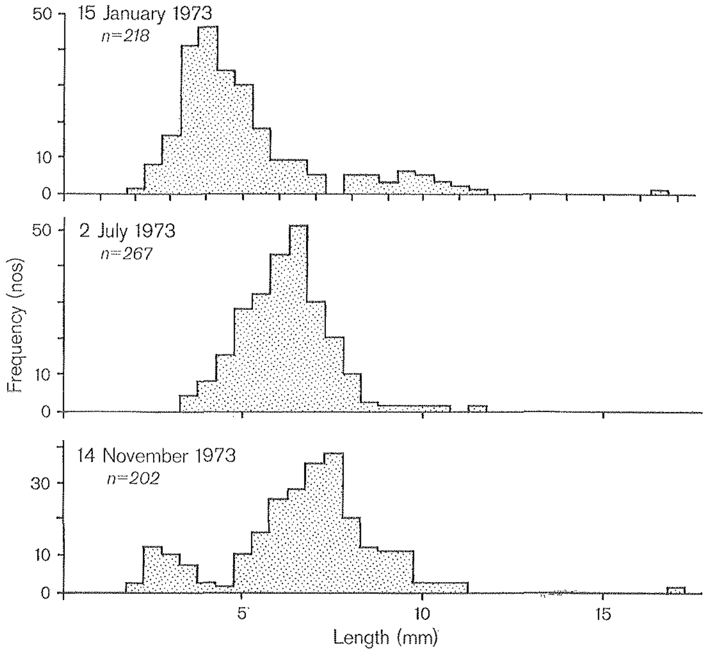

FIG. 4—Changes of the *Lunella smaragda* population of the Top Flat through a year, January–November 1973. Numbers in histograms normalised to 250.

spawn into the sea water simultaneously, and the trigger for this activity is apparently rough seas. Subsequent lesser spawnings, also coincident with rough seas, may occur up to early April.

The two peaks in the Top Flat population in November therefore represent 0+ and 1+ year-groups. The 0+ individuals settle as larvae early in the year and grow to about 4.5 mm diameter (average) over 10 to 11 months, and the 1+ are steadily lost from this mid-eulittoral flat as they approach 2 y old. Also present in the samples are odd individuals of older age-classes which wander on to the turf and are normally found in natural depressions or crevices.

The variations in numbers, conditions, and growth rates followed over nearly 4 y showed that the timing of the 1+ year-group's movement from the Top Flat is related to size. The 1+ year-class of 1972 was fast growing, and at the end of August 1972 the peak was at about 7.5 mm. In Fig. 5 (*upper*). The regular monthly sample of 28 August 1972 showed a marked step-down at 8 mm diameter in the near-normal distribution of the plotted histogram. After returning the animals the next day to the sample site in the middle of the turf-covered Top Flat, a second sample of 1 m^2 was taken at the bottom (seaward) edge of

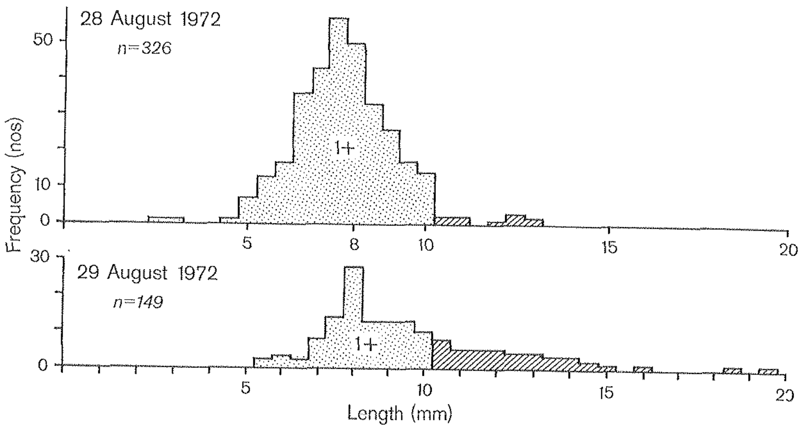

FIG. 5—Histograms of samples of *Lunella smaragda* from the Top Flat, demonstrating the loss of larger individuals from the centre and recruitment seaward at the edge: (*upper*) sample from the routine sampling area in the centre of the flat; and (*lower*) sample from the seaward edge of the same flat. Hatched areas show the proportion of larger animals in each sample.

that flat. Although this area was similarly turf covered, the population composition differed markedly, (Fig. 5, *lower*). In the middle of the flat only 3% of the total were greater than 10.25 mm diameter, whereas towards the edge of the flat 29% were over this size, and the 1+ population peak was higher (above 8 mm). The larger individuals in this area were probably composed of animals which had crawled up on to the platform edge from the shelter of the step below (having previously been removed from the main body of the flat by wave action), and also larger specimens from the main body of the Top Flat (which were for the first time being transported down the beach by wave action).

CHANGES IN THE LOW FLAT POPULATION

The Low Flat, with bare rock broken up by turf patches, has a population structure as distinctive as the Top Flat, but subject to greater variations. These changes are associated with annual growth to another critical size and also with variations in the micro-shelter afforded by seasonal or opportunistic growth of macroalgae, which may delay dispersal or allow temporary colonisation by larger individuals. The histograms of Fig. 3 show that the population here is composed mainly of the 2+ year-class, although lesser numbers of older and younger year groups are also present. Sampling of the Low Flat population was consistantly accurate only for the 2+ year-class and older animals, because around the solstices or when atmospheric pressure was low, the flat was not completely uncovered at low tide, and samples had to be

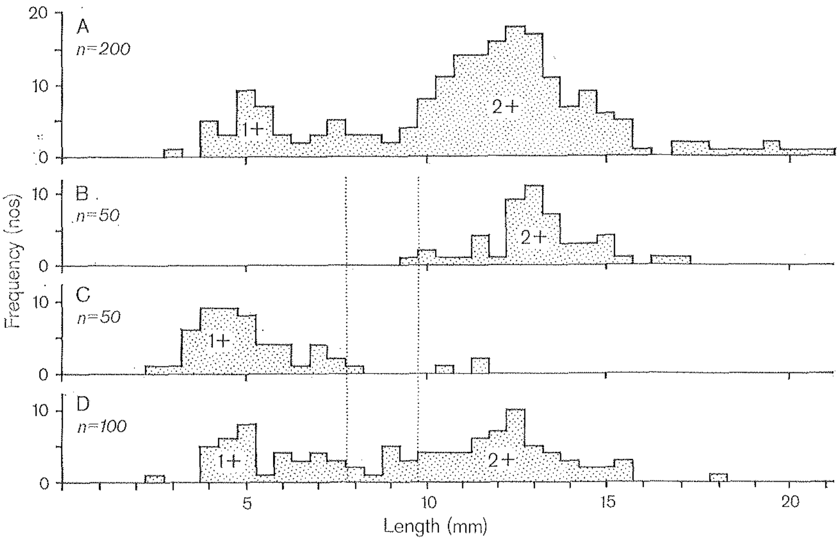

FIG. 6—Histograms showing the distribution of size-classes of *Lunella smaragda* on the Low Flat, 2 May 1973 (dotted lines separate out a transitional size range between turf and bare rock fractions of the population). (A) routine sample from regular transect; (B) sample from bare rock only, at least 1 cm remote from coralline turf; (C) sample from coralline turf only, at least 1 cm remote from bare rock; (D) sample from turf/bare rock margin taken as a 2 cm strip around turf patches and consisting of 1 cm bare rock and 1 cm turf.

collected from under water. Under these conditions, sampling of the 1+ population amongst the turf was difficult, although the larger sizes were easily found.

The Low Flat population is divided between the two microhabitats (bare rock and turf) present. Figure 6 shows the frequency histograms for the flat sampled in four ways as follows:

Fig. 6A shows the distribution in the regular sample across the flat. A strip 0.5 m wide was sampled, along the regular sampling transect, until 200 animals had been collected. The histogram shows two peaks of distribution corresponding to the 1+ and 2+ year-groups.

Fig. 6B shows the distribution, along a continuation of the same strip, of animals found only on bare rock surfaces at least 1 cm remote from any turf. The population consists almost entirely of 2+ individuals, with a few older specimens but no young *Lunella*. About 50 animals were sampled.

Fig. 6C shows the distribution in the middle of the coralline turf patches of the same area, with sampling restricted to turf at least 1 cm from bare rock. About 50 animals were sampled. This sample consists almost

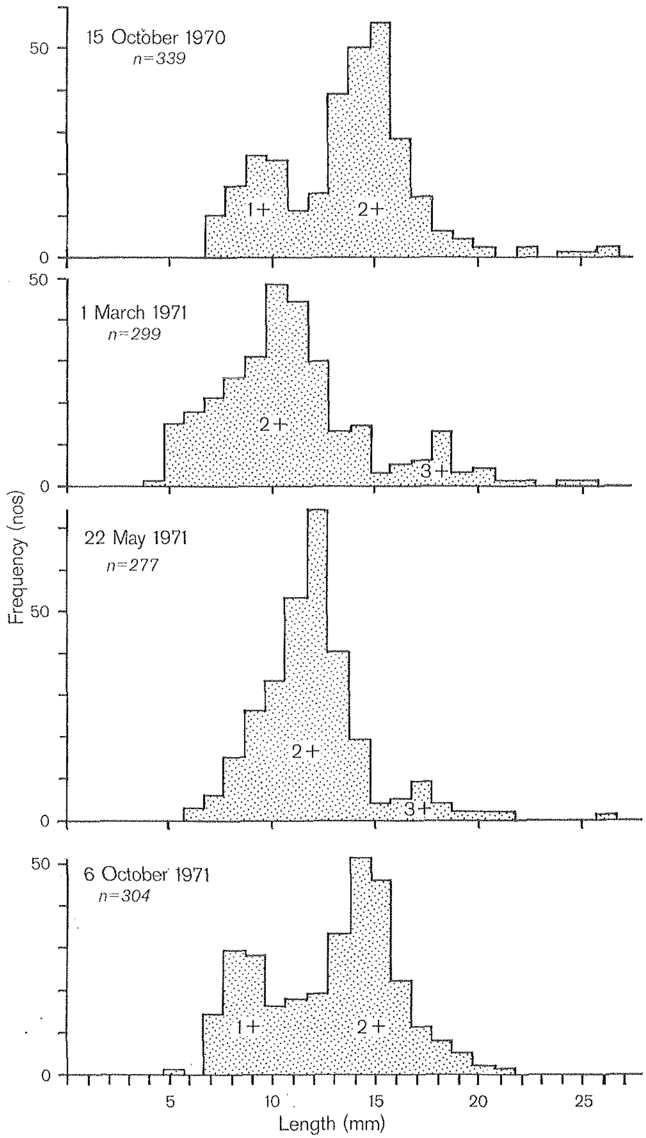

FIG. 7—Changes of the Low Flat population of *Lunella smaragda* through a year, 1970–71. Numbers in histograms normalised to 300.

entirely of 1+ year-group individuals, with a few older beasts, but presumably also contained very small 0+ animals (not found in the sampling).

Fig. 6D is the distribution in a sample taken around the edges of the turf patches as a 2 cm strip consisting of 1 cm turf and 1 cm bare rock. In the 100 animal sample, all size classes are represented, as in sample A, with similar peaks for 1+ and 2+ year-groups.

The sampling treatment used here demonstrates the result of movement from the turf substrate to the bare rock with increase in size. Analysis of the three area-specific samples (B, C, & D) indicates that there is a transitional size that lives in the marginal areas. In both the bare rock (B) and the turf (C) samples, only 2% of each sample falls within the size range 7.75–9.75 mm, whilst in the turf/bare rock margin sample (D), 11% fall within this range. This size is the same as that at which young *Lunella* are lost from the Top Flat population, and thus a relationship is demonstrated between the nature of the turf habitat and the size of *Lunella* it can accommodate.

Population changes in the Low Flat over a full year are shown in the histograms of Fig. 7. The two October samples show the similarity of growth rates for 1970 and 1971. In October, 1+ and 2+ year-groups are present in the sample. Towards the end of the year the mean for the 2+ year class reaches about 16 mm and animals over 15 mm start to be lost from the flat. The sample for March shows that nearly all of this size class (now just over 3 y old) have been lost from the flat. The new 2+ year-group is now the major size class in the sample; it grows at nearly 0.6 mm length per month and remains on the Low Flat until the maximum size for *Lunella* in that area is again reached. In both of the October samples there was already some loss of the larger sizes from the 2+ distribution; most of the faster growing individuals had been removed from the population after they attained 15 mm.

CHANGES DURING A MACROALGAL BLOOM

The October and May histograms of Figs 3 & 7 show the typical situation, in which most of the sample are less than 17 mm in diameter, but, if there is an increase in microshelter, the numbers of larger *Lunella* increase correspondingly.

Figure 8 follows the monthly changes in the population through an extremely profuse bloom of the alga *Colpomenia sinuosa* and shows that wave action and shelter are involved in the limitation of size of individuals in the population. *Colpomenia* grows in the form of hollow, irregularly lobed, thin walled vesicles. These vesicles start as small "bubbles" and not uncommonly grow to 5 cm in diameter, but during this particular bloom at Goat Island Beach, the alga formed massive, somewhat flattened, bladders up to 20 cm in diameter.

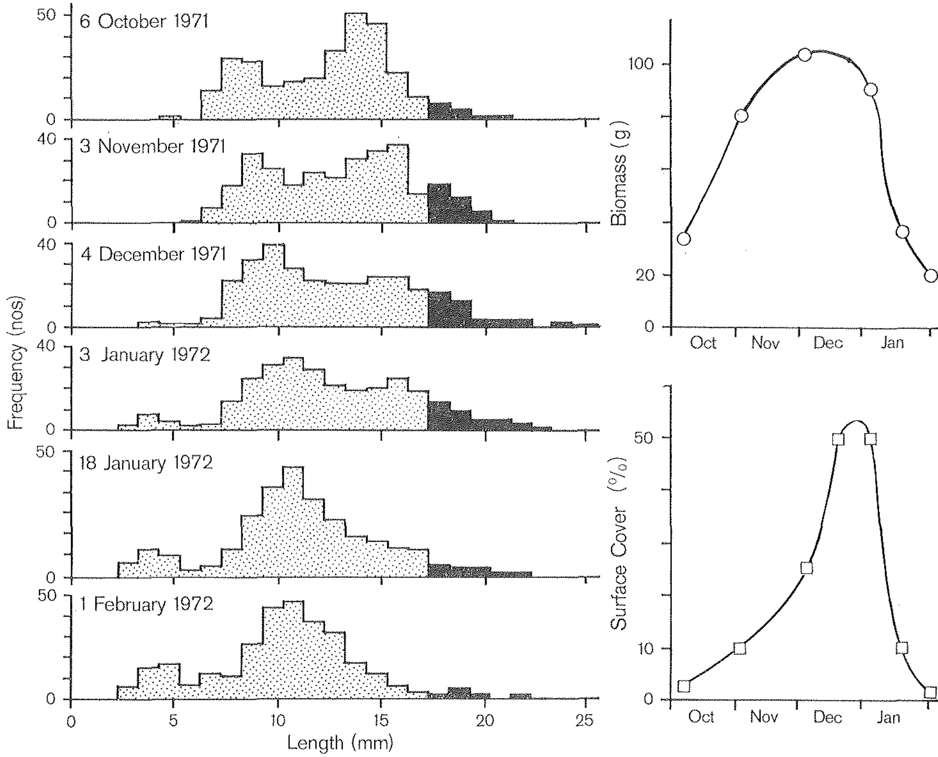

FIG. 8—Changes of the *Lunella smaragda* population of the Low Flat associated with a bloom of the alga *Colpomenia sinuosa* in late 1971: (*left*) histograms of the Low Flat population of *Lunella*, 1971–72; emphasising the change in numbers of the large individuals (solid portions of histograms) through the period of the bloom; (*upper right*) changes in the biomass of large *Lunella* (those greater than 17.25 mm diameter) over the period of the bloom; and (*lower right*) changes in the percentage surface cover of the alga *Colpomenia sinuosa* on the Low Flat.

At the peak of the bloom about 50% of the Low Flat surface was covered, and in some areas of 0.5 m² the surface cover was greater than 80%. *Lunella* were still able to move about the rock surface below and between the *Colpomenia*, and the shelter it afforded allowed large *Lunella* to colonise the flat. The peak of the bloom was reached towards the end of December. From 29 December 1971 until 2 January 1972 there was a storm, and on 3 January, although there had been no removal of whole plants, nearly all were markedly damaged. A heavy infestation of the plants by small rissoid snails then developed, and the vesicle walls became further eroded. Although an extended period of moderate to calm seas followed, the *Colpomenia* steadily declined, and by 18 January covered only about 10% of the surface (Fig. 8, *lower right*); the numbers of the large *Lunella* dropped correspondingly (Fig. 8, *left* and *upper right*).

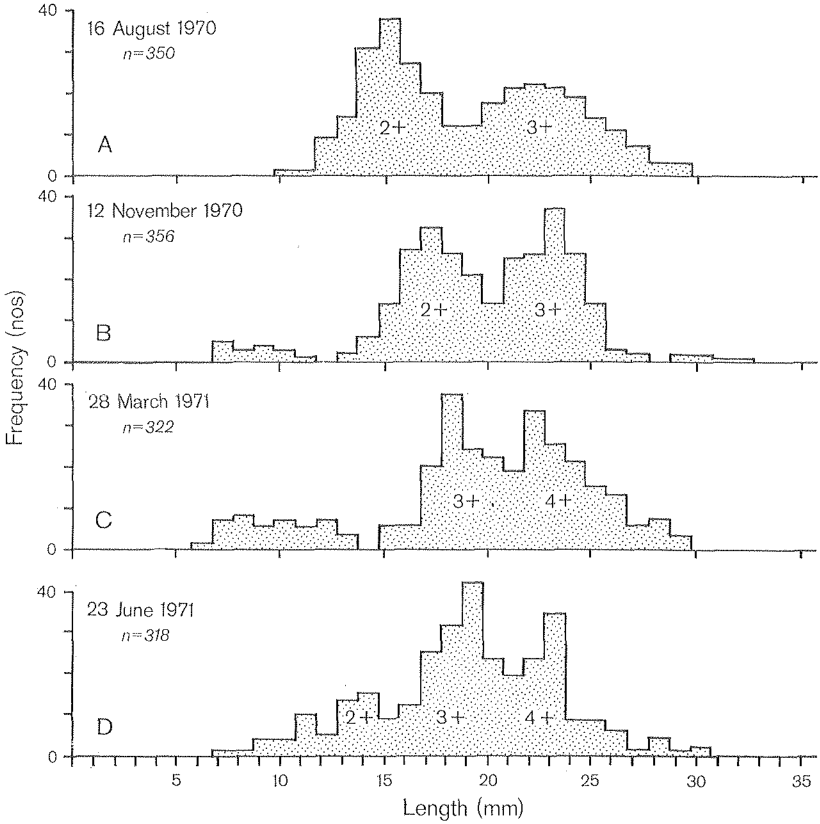

FIG. 9—Changes in the SLF Flat population of *Lunella smaragda* through a year 1970–71, showing the loss of the 4+ year-group and the recruitment of 2+ individuals.

CHANGES IN THE SLF FLAT POPULATION

Large *Lunella* are the dominant grazers of the sublittoral fringe below the turf flats. Throughout the year the samples were composed mainly of animals over 17 mm diameter; on average, 68% of the animals sampled were over this size (maximum 75%, minimum 53%). By comparison the numbers over 17 mm diameter in the Low Flat population were always very small: even during macroalgal blooms their percentage went up to only 15%, and during periods of no bloom the average was about 4%. As there is no turf in the sublittoral fringe, only a few juvenile *Lunella* were found, and these were usually in crevices and depressions.

The histograms of Fig. 9 show that in the last half of the year the large *Lunella* consist mainly of the 2+ and 3+ year-groups, with some

4+ distinguishable as a separate size-class. From February these become 3+, 4+, and 5+ respectively. In the early half of the year the 3+ and 4+ year-groups remain numerically dominant in the samples, although the new 2+ may be clearly distinguished (Fig. 9C). From late June obvious recruitment occurs from the Low Flat, the faster growing 2+ being washed down into the sublittoral fringe by wave action as they attain the critical size. At the same time a marked decrease in the 4+ year group occurs on the SLF Flat (Fig. 9D); by the end of July their frequency is very reduced, and the population then again consists mainly of 2+ and 3+ year-groups.

EXPERIMENTS ON WAVE-EFFECTED DISTRIBUTION

Wave-effected distribution of different sizes of *Lunella* within a turf flat was investigated by daily recording the positions of marked animals. Fifteen animals of five size-classes (8 mm, 13 mm, 18 mm, 23 mm, and 28 mm) were selected from samples freshly collected from the shore.

Individuals were painted with a size-class identifying mark. Red nail-varnish was found to show up well and to adhere for at least a fortnight if the shell was first dried with absorbant paper and then allowed to air dry for 15 min. before application of the varnish. The varnish dried in a few minutes, and the animals were then placed in running sea water overnight, before being transferred to the field.

Each animal was placed aperture down at a selected starting point on the turf of one of the extensive top flats, approximately 0.5 h before tidal immersion. About a litre of seawater was gently poured over the marked animals to wet the turf and to encourage attachment. The weather chosen was reasonably calm. Every day, the area surrounding the starting point was examined carefully on a 1 m^2 grid pattern; the new positions of the marked animals were recorded as numbers of each size-class in each grid area.

Most individuals of the two largest size-classes (23 mm and 28 mm) were quickly lost from the immediate vicinity of the starting point. After two tides, all that could be found nearby were some broken shell fragments of one 28 mm *Lunella*; another 28 mm animal was found 100 m along the beach, still alive, close to the sand/rock boundary. This animal had probably been washed from the turf flat and carried along the sandy part of the shore on the rising tide and left on another part of the rocky shore on the falling tide: it could not itself have crawled so far in a single day.

The smaller size-classes became distributed mainly up and down the shore. A 4 m^2 area, with the starting point (S) at its centre, was termed the "home square" (Fig. 10). Animals moved in this area both by their own locomotion and by wave action. Distribution outside the home square was more or less confined to a 2-m-wide strip running up and down the shore; movement into these zones was mainly by wave

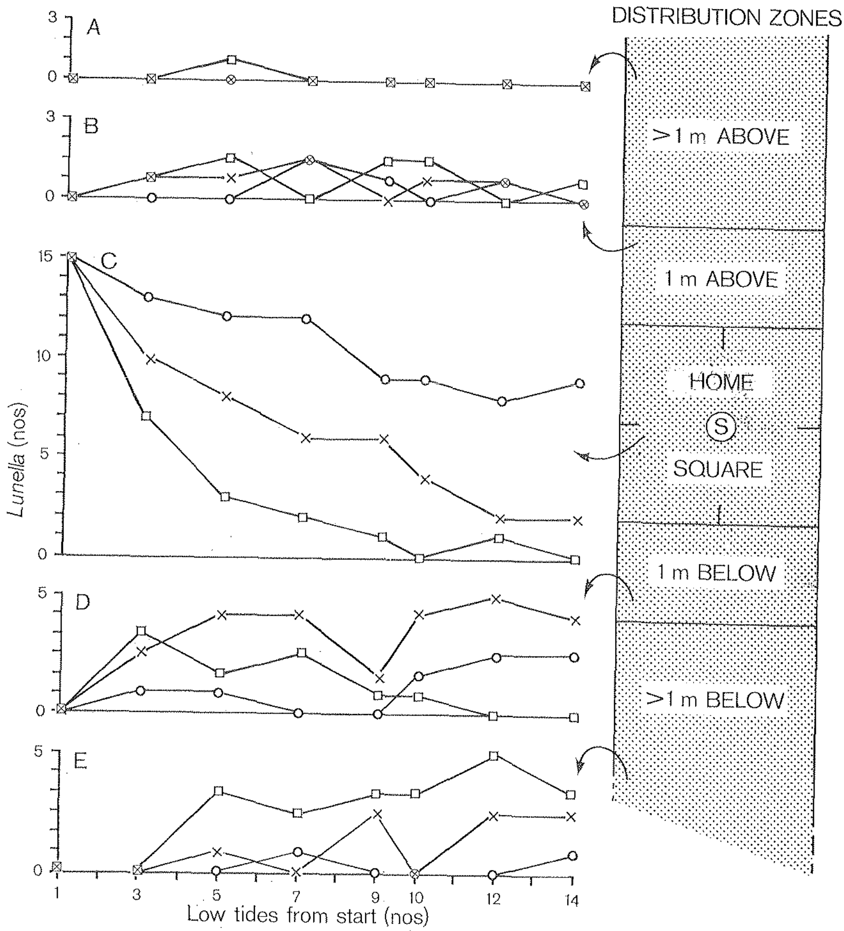

FIG. 10—Graphs showing the distribution on a turf flat, from a starting point "S" of 3 lots of 15 marked *Lunella smaragda* in three-length-classes: 8 mm (open circles), 13 mm (crosses), and 18 mm (open squares). Graph C (*middle*) shows the decline in numbers of each class from the "home square" (= 4 m² about the starting point); graphs B & D show recruitment and loss in areas up to 1 m above and below the Home Square respectively; and graphs A & E show movements into areas further above and below respectively.

action. Numbers in the Home Square declined with time, and the rate of decline varies directly with increase in animal size (Fig. 10C). Over half of the 18 mm size-class were lost from the Home Square after 2 tides (one day), and all had been lost after 10 tides, but less than half of the smallest size-class had been lost after 14 tides. After one day, the individual of the three smallest size-classes most distant from the starting point (S) was at 2 m, and on the following days the distances were 7 m, 9 m, 11 m, 16 m, and 17 m down the beach. There was some movement up into the zones above the home square (Fig. 10A & B) and a marked movement into the seaward zones (Fig. 10D & E). The progressive movement of the 18 mm size-class down the beach can be followed in Fig. 10C, D & E: the initial loss of animals from the home square corresponds to an increase in numbers of that size-class in the zone immediately below. Later, the numbers in this zone also decline (Fig. 10D) and there is a corresponding increase in the numbers of the next zone down the shore (Fig. 10E). A similar pattern of distribution down the shore can be followed for the 13 mm size-class, but the rate of distribution is slower.

In this experiment the movements up and down the shore are much greater than movements across it. Movement up was approximately twice the lateral movement, and movement down approximately five times. The absolute values varied from trial to trial according to the conditions, but the effect remained obvious.

REATTACHMENT EXPERIMENTS

Survival after dislodgment depends on the animal's reattachment abilities. Field and laboratory observations show that *Lunella* does not reattach quickly; after being dislodged, the animal must be moved to a sheltered site (pool or crevice) before it can reattach. *Lunella* are dislodged by waves when they grow beyond a critical size for the available shelter, and when they move in calm conditions into an area where wave disturbance is not normally tolerable. (For example, small pools scattered about the mid-eulittoral turf flats accommodate a few large *Lunella*. If these *Lunella* wander up on to the turf, they are washed off, either back into the wave shelter of a pool or down the shore into deeper water).

In the experiments, two conditions of detachment were considered: the animal detached with the foot wholly or partially retracted, but with the shell the normal way up (i.e., with the aperture facing the substrate), and the animal rolled over (i.e., with the aperture uppermost).

Reattachment rates are related to the wave frequency for the area. Analysis of data for wave frequency on the shore (recorded daily) showed the average period to be about 9 s (15 s maximum, 5 s minimum, average waves per minute in 1971 = 6.53).

EQUIPMENT

The response to wave strike and the reattachment rates of detached *Lunella* of different sizes were studied in a wave tank (Fig. 11). The floor and end walls were made of reinforced concrete, which gave a rock-like substrate. The side walls were clear acrylic sheet, screwed to

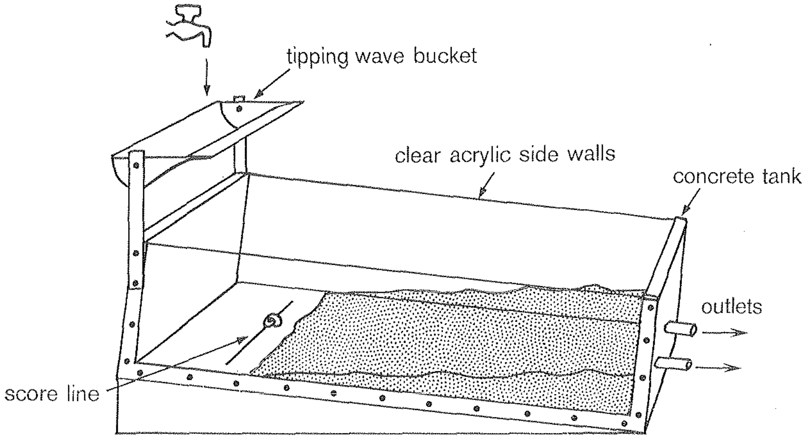

FIG. 11—Wave tank apparatus used for subjecting *Lunella smaragda* to a standard wave force during reattachment experiments.

the concrete and sealed with non-setting aquarium putty. The transparent walls permitted observation of the animals during wave splash and allowed almost full illumination of the tank for natural algal growth on the concrete substrate. The tank was set at a 6° slope to the horizontal. The internal dimensions were 90 cm long, 31 cm wide, and 25 cm deep. The wave-washed but non-submerged part of the tank floor was 24 cm long and the water depth at the outlets 7 cm. In operation, water ran into the PVC 'wave bucket'; this bucket tipped over when full and was balanced so that it returned to the horizontal position for refilling when empty. The capacity of the wave bucket was 1080 cm^3, and its pivot was 40 cm above the tank floor. On the non-submerged part of the floor there was a substantial covering of a leathery encrusting brown alga, *Ralfsia verrucosa*, and in the submerged part there was some *Hildenbrantia* sp. and a little coralline paint. These coverings and the bare "rock" offered a natural surface for attachment by the *Lunella*.

If the *Lunella* moved to the site of greatest wave force, they were not dislodged by the breaking wave, although the force was sufficient to cause the animals to retract against the surface and to stop all feeding activity and locomotion until the wave had passed over. Normal wave frequency in the tank was about two per minute. Thus the artificial waves of the apparatus were not powerful enough to dislodge, but forceful enough to visibly disturb the animals.

'APERTURE-DOWN' EXPERIMENT

From each of seven size-classes (5 mm, 10 mm, 15 mm, 20 mm, 25 mm, 30 mm, and 35 mm) five individuals freshly collected from the shore were each placed aperture down on a score line marked across the tank 5 cm from where the wave broke, at the point that it gained its maximum horizontal velocity. As they were placed on the line, a stop watch was started and after a set time the filled wave bucket was allowed to tip, causing the standard wave to break over the animal. If the animal was not moved by the wave it was said to have satisfactorily reattached. Each animal was tested in sequence for each set time, and between tests each animal had a rest and recovery period in a calm seawater tank.

The graphs of Fig. 12 show the number of each group which achieved reattachment for each set time before the wave broke, and thereby indicate the reattachment time for each size-class of *Lunella* tested. This was greater for the larger size-classes, because of the longer time required to fully extend the large foot from the shell: some reattachment was generally achieved within 15 s, but the foot had not fully extended to smoothly and completely contact the surface by this time, and the animals were dragged off the surface by the wave.

Of the seven size-classes tested, the 5 mm and 10 mm correspond to the Top Flat population, the 10 mm, 15 mm and 20 mm to the Low Flat population, and the 20 mm, 25 mm, 30 mm and 35 mm to the SLF Flat population. The ability to reattach increases with size up to 20 mm, but subsequently falls away. Small *Lunella* completed reattachment rapidly once it commenced, but commencement was generally very slow.

'APERTURE-UP' EXPERIMENT

The same *Lunella* used in the 'aperture-down' experiment were tested in the aperture-up position. They were first placed on the score line, out of the water but on wet rock, and reattachment was observed while the waves were stopped. The experiment was repeated lower down the tank with the animals submerged. In another series of trials the animals were placed aperture up on the score line, the waves started and reattachment observed.

Of 10 trials with the waves stopped, using the 7 size-classes, no *Lunella* attached within 1 min., and only 10 out of 70 reattachments were made within 30 min. In the experiment with the animals submerged, no attachments were made within 1 min. and only 12 were made within 30 min.

When the animals were placed on the score line and the waves started, they were all moved down the tank by the water rush. About 90% were turned over to the aperture-down position by the first wave, and generally all of the remainder by the next wave. The animal's shape and centre of balance therefore made the aperture-down position the most stable one and the tendency to turn to this position facilitated more rapid attachment.

FOOT ATTACHMENT AND SHELL AREAS

Accurate measurements of foot area contacting the substrate and of the area of the shell exposed to the wave were made by close-up photography. For the measurement of the foot area, the animals were photo-

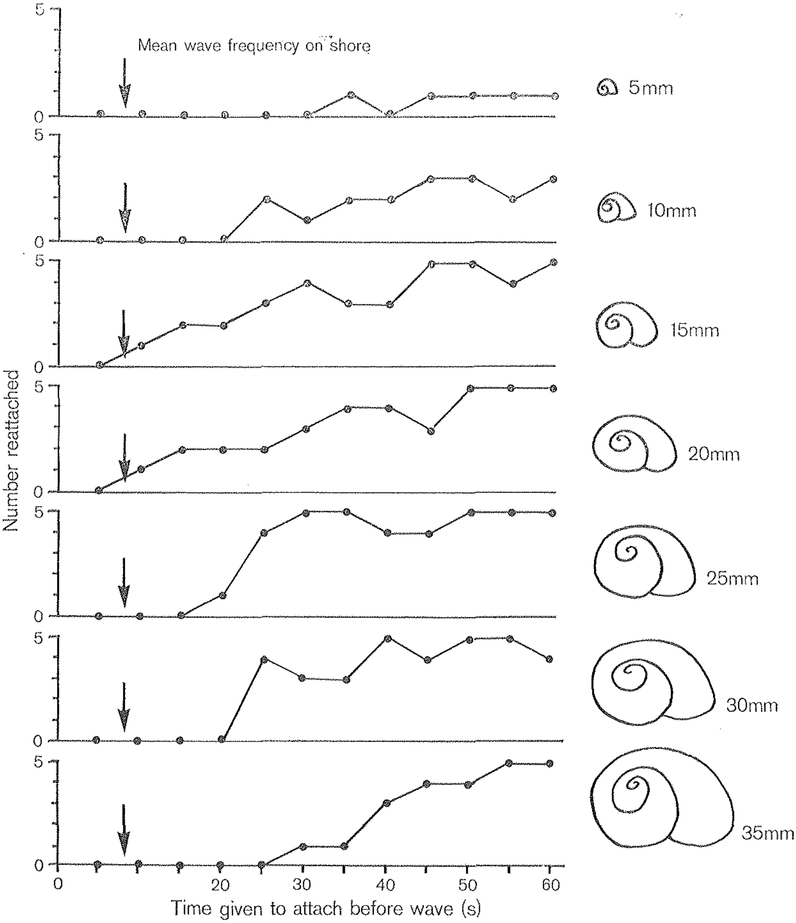

FIG. 12—Graphs showing the relative reattachment abilities of *Lunella smaragda* of different lengths subjected to a standard wave force. Each graph shows the number of animals which reattached in each of a sequence of trials in which the time given for reattachment before wave strike was increased by 5 s per trial ($n = 5$ in all groups).

graphed from below through a wetted clear acrylic plate to which the animals were attached. The plate had a grid (1 cm^2 units) scored into the surface. By projecting an enlarged image on to graph paper with a 1 mm^2 grid, accurate measurements of the foot area could be made. The grid squares covered on the graph paper were counted and divided by the enlargement factor known from the fit of the plate grid image to the graph paper grid. The area of the shell exposed to the wave was measured by the same method: the photographs of the animals were taken from a common aspect, and each included a scale. Fig. 13 shows

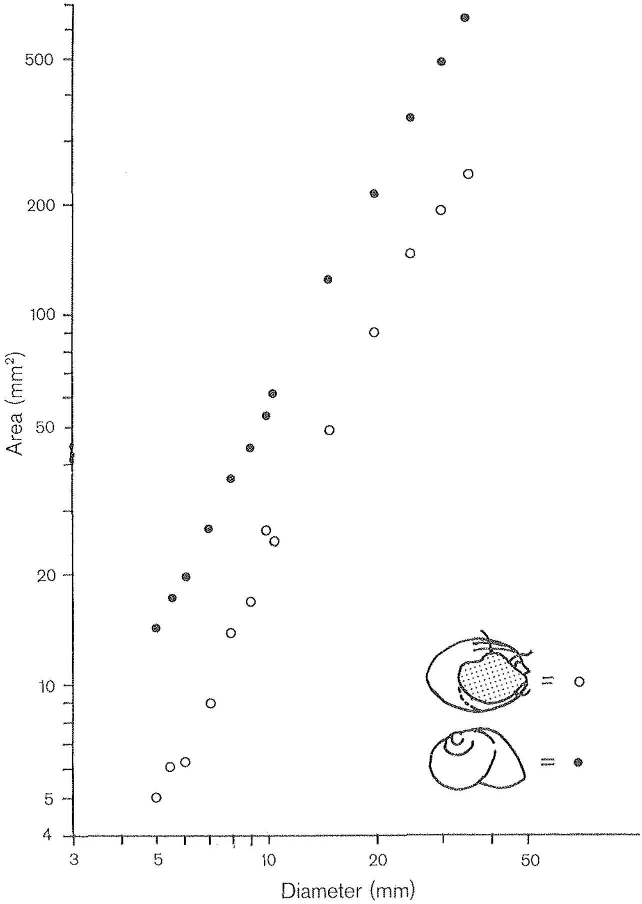

FIG. 13—Relationships of foot area (open circles) and shell area presented to the wave (solid circles) against shell diameter in *Lunella smaragda* (log scales).

that both the area of the foot attached and the area of the shell presented to the waves have a constant ratio to the diameter.

CONCLUSIONS

Lunella of intermediate size have superior reattachment abilities for both behavioural and physical reasons. The differing reattachment abilities can be related to the different sites where each size-class occurs. The smallest sizes are found protected from frequent disturbance amongst the coralline turf and are possibly only rarely detached. The largest animals are not generally found above the sublittoral fringe,

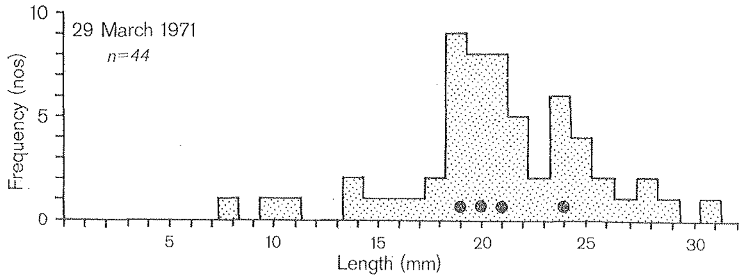

FIG. 14—Size frequency histogram of whole shells of *Lunella smaragda* found in the drift line at Goat Island Bay; solid circles show sizes of shells containing whole but moribund animals.

although some are found in pools where wave action is less than on open rock surfaces.

The reality of redistribution by wave action has been demonstrated by field and laboratory experiments. Most dislodgments are followed by reattachment in a place where wave stress is less. If a dislodged *Lunella* is wave transported to a place similar to that from which it was dislodged, then it will probably be moved again by the next wave. This is because the wave frequency is shorter than the fastest complete reattachment times. Wave transport will continue until the animal is finally put down in a sheltered site where it can reattach, or until the shell is broken, or the animal is left stranded in the drift above the highest satisfactory site.

MORTALITY

Twenty collections of whole shells from the drift line were made to establish some of the causes of mortality. Because of wave sorting, and also probably erosion factors, the drift shells consisted mainly of medium to large shells typical of the SLF Flat population and the larger members of the Low Flat population.

Figure 14 shows a fairly typical size-class distribution of the whole shells found in the drift at the top of the shore. This sample atypically included three shells containing whole *Lunella* and one containing a very damaged beast; in samples of about this number (44), one shell still containing an animal may be expected.

Entire animals found in the drift and placed in circulating sea water generally did not recover, about 25% did. Those which did not may have been already debilitated in some way, but more probably they had been slowly dying in the drift for a number of days.

Large numbers of very small shells were sometimes found amongst gravel in shallow pools adjacent to the turf flats, particularly in summer. Such mass mortality of juveniles in the turf flats may be related to regular daily exposure for up to a week to the very high temperatures of interstitial water in the turf. Low spring tides occur at about midday in the Auckland region, and in midsummer turf water temperatures over 30°c were commonly recorded. Whilst occasional exposure to such temperatures may be tolerable, exposure for three or more hours for up to six successive days may not be. Spencer Davis (1969) reports the build up of a desiccation deficit under similar conditions in the limpet *Patella vulgata*, and something similar may apply to juvenile *Lunella*.

GROWTH RATES

The size-frequency histograms of the regular samples (Figs 4, 7, & 9) show distinct peaks for at least 4 y of growth. However, wave-effected distribution and other effects bias the data.

As the 0+ year-class starts to appear in the samples, the distributions are biased by the absence of the very small individuals not found. This bias continues until about half way through the second year (1+). Towards the end of the second year a negative skewness occurs in the 1+ Top Flat population, because of the loss of the larger individuals to the Low Flat. At about the same time the 1+ Low Flat population shows some positive skewness caused by recruitment. Therefore the peak in the Top Flat for 1+ is artificially low and that for the Low Flat is elevated. There is a similar relationship between the Low Flat and the SLF Flat for the 2+ size-class when wave-effected redistribution of the larger animals occurs. The numbers of the very oldest year groups of the SLF Flat population are also progressively reduced, affecting the peaks in that area. *Lunella* occur only rarely in the sublittoral and even then are found close to the sublittoral fringe; the population found in the SLF Flat therefore represents the climax at Goat Island Bay, although older and larger animals are found in populations at other, more sheltered beaches nearby (see below).

Because of these biases, detailed statistical treatment by the normal methods has little value, and a more generalised "by eye" approach was adopted; the accuracy of this approach was aided by the large sample numbers and the extended sampling programme. For each month, the peak of distribution for each size-class was estimated for each site in which that peak was distinct. In some months, peaks for one size-class were clear in two populations, and both were included in an averaging analysis. Thereby the effects of bias, usually positive in the sample from one flat and negative in the other, are to some extent balanced: the resulting growth rate diagram, Fig. 15, shows a close fit to a smooth curve. Growth is approximately linear for the 3.5 y that *Lunella* are present in abundance on the Goat Island Bay shore.

For the North American turbinid *Tegula funebralis*, Frank (1965) found that the growth was also linear for the first 3 y. Rates for *Lunella* (5.9 $mm.y^{-1}$) are slightly faster than for *Tegula* (4.7 $mm.y^{-1}$). After 4 y

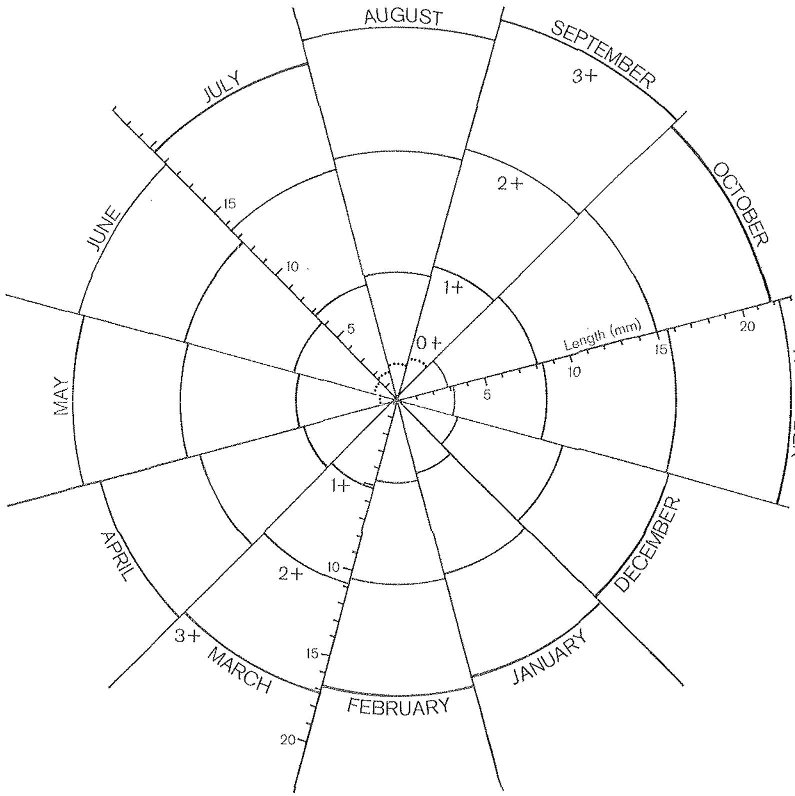

FIG. 15—Polar plot of growth curve for *Lunella smaragda* from analysis of samples from three collecting sites on Echinoderm Flat, Goat Island Bay, over 3.5 y, 1970–73. Lines for each month show the average length for each year-class.

the growth rate falls off rapidly for *Tegula*, but in the present sampling programme the growth rate of *Lunella* could not be followed beyond this age. Larger individuals do occur on the Echinoderm Flat shore, but they are sparsely distributed, and a different approach would be necessary to follow their growth. For older *Tegula funebralis*, individual marking discs cemented to the shells have been used (Darby 1964), but recovery was very low over 2–3 y. The technique may, however, be useful for some of the distinct populations of larger *Lunella* mentioned below, in which the animals are in various ways limited to specific areas.

LARGE *Lunella*

In Northland, large *Lunella* up to 50 mm long may be found in reasonable numbers on sheltered shady shores in a variety of places.

The east–west aligned inlet, Leigh Cove (see Fig. 1), has rocky shores with *Lunella* on both north and south sides. The north side is overhung with trees including pohutakawa, *Metrosideros excelsa,* which stretch out over the shore, in places to below high water mark, giving considerable shade. On the shaded side of the cove only, very large *Lunella* are found high on the shore in the upper eulittoral. They are separated from the smaller sizes of *Lunella* found lower on the shore in their normal association with coralline turf and *Hormosira*. These large animals are mostly between 30 mm and 40 mm long, although some larger and a few as small as 25 mm are also found.

A similar situation is found on the pohutakawa-shaded shore of the sheltered side of High Island (35° 50′ S, 174° 31′ E) inside Whangarei Heads. Here again separate populations occur, with the large animals (up to 50 mm) high on the shore. Three of these large *Lunella* from a very shaded site were found to be living without an operculum.

"Large specimens of the catseye *Lunella smaragda,* as big as plums", are seen "among mangroves, in shaded places, though never on the outer flats": Morton & Miller (1968), referring to Northland harbours and enclosed shores. In the mangroves of the Whangateau Harbour, near Leigh (see Fig. 1) another separate population of large *Lunella* occurs with individuals up to 45 mm long; no small ones have been found, and over 90% were over 30 mm.

At this site there is no local coralline turf or similar substrate to support the juvenile year-groups which are the source of the larger animals of the earlier examples. The mangrove populations examined were at least 0.5 km from any hard shore with *Lunella*. The mangroves could possibly support a juvenile population, but perhaps only a few animals are recruited from the plankton. However, survival here would be very good, because the three most important causes of mortality are not operating; wave action, predation, and the lethal effects of summer temperatures.

No animal would be broken by wave action, as the shore is so sheltered and the substrate so soft. The shells are uneroded and in good condition; they frequently carry large epizooites such as *Saccostrea glomerata,* which are never found on *Lunella* on rougher shores.

The important predators, especially the thaids *Neothais scalaris* (predator on juvenile *Lunella*) and *Haustrum haustorium* (predator on older *Lunella*), are absent.

Mortality amongst juveniles associated with high temperatures in the turf flats during summer could not occur as the mangrove trees shade the shore, and the mangrove mud has a high water content. Nevertheless, over the period of this study, a juvenile population was not found. Although mature animals are present, possibly they do not spawn, if the rough water trigger for spawning is critical (Grange 1976). If there is no local spawning, possibly only a very small number of larvae reach the mangroves from the remote breeding areas, as the pelagic larval period is short (Grange 1976). Survival of these would be high, but the small animals could remain concealed amongst fallen branches and in the oyster clumps on the mangrove trunks and pneumatophores. If *Lunella* has a similar growth curve to that of *Tegula funebralis* (Frank 1965) in which the growth rate falls off with age, then the large animals may represent many years of settlement. Alternatively, most of the large *Lunella* population here could belong to the settlement of a single year, perhaps some 10 y ago, in which unusual wave and tide conditions permitted a spatfall in the mangrove regions.

Large *Lunella* are also found on moderately exposed coasts, but only in the shade and shelter of deep pools. Such pools may support a population from juveniles through to animals up to 40 mm long. Commonly, such pools are rimmed by a collar of coralline turf which accommodates the juveniles. Larger animals are found well below this, and presumably it is difficult for them to escape from the pool: they must first cross the unstable turf collar, from which they are easily washed back into the shelter of the pool. Good examples of such pools are found from Goat Island Beach to Cape Rodney near Leigh (see Fig. 1) and also on the seaward side of Lion Rock at Piha on the North Island west coast (36° 57′ S, 174° 28′ E). Piha is very exposed, and *Lunella* are never found there on open rock surfaces, but are restricted to these large pools.

GENERAL DISCUSSION

That the distribution of many intertidal plants and sessile animals is limited in part by wave exposure (Ballantine 1961, Lewis 1964) is now accepted. The relative abundances of indicator species on a given shore can be used to establish a position for that shore on a wave-exposure scale (Ballantine, *et al.* 1973). However, it is difficult to fit mobile animals like *Lunella* into such a scheme, especially if waves sort their different sizes, although their distributions may show how exposure can vary within a shore. Thus, at Goat Island Bay, *Lunella* is "abundant" in both the mid-eulittoral turf flats and also in the sublittoral fringe. However, at each site the size-classes typical of the other site are only "rare" to "occasional" on the Ballantine *et al.* (1973) scale, because wave exposure becomes greater higher on the shore and moves the larger *Lunella* down the shore; a similar size to shore-position relationship occurs in *Tegula funebralis* (Wara & Wright 1964).

Vertical zonation on the shore is associated in part with desiccation factors, and in this study with tolerance to wave action also, producing zonation within a species according to size. What happens when a littoral gastropod is hit by a breaking wave will depend on the force of the wave, the form of the animal, and the tenacity of its attachment. Only recently has Miller (1974) paid detailed attention to how animals maintain their position and move with control in the wave-swept marine littoral: the size and form of both shell and foot, the type of locomotion used, the substrate type, and the wave exposure position are all inter-related for each species. She also considered sheer stresses compared with pulls perpendicular to the substrate: it is sheer tenacity that is particularly important on the plaform shore, where waves breaking over the steps accelerate across the flats.

If there is no offshore protection from reef or stack on a shore of intermediate exposure, the smooth platform will have only a surface-encrusting algal cover, e.g., coralline paint or *Hildenbrantia* sp., and, at best, only the most streamlined grazers such as chitons and low-spired limpets. If there is a little surface confusion seaward of the flat, such as a small boulder field, coralline turf is then able to establish, and it accommodates a very rich microfauna, including young *Lunella smaragda* feeding mainly on filamentous algae epiphytic on the *Corallina.* The turf is, nevertheless, a poor substrate for foot attachment, and is therefore only a satisfactory habitat so long as the *Lunella* can shelter within it or in the natural depressions in the turf surface.

The effects of waves striking an animal and exerting sheer forces are graded in proportion to the wave force and the shell area presented. For an animal of given size, extremely heavy waves will wash it off; extremely gentle waves will have no visible affect, and waves of inter-mediate forces will cause a graded restriction on feeding and locomotion according to intensity. An actively grazing *Lunella* may stop feeding, or stop moving and feeding, or may clamp its shell to the substrate as the wave passes over. As the animal grows in the same wave milieu, it will be disturbed more frequently and therefore must spend less time in feeding and more time and effort in maintaining its position. Eventu-ally, the animal grows large enough for dislodgement to be a possible advantage, should it be wave-transported to a site where the general level of wave disturbance is less, provided it can survive the transport hazards. It would then benefit from reduced disturbance by intermediate waves and from increased time available for feeding.

The dislodging of animals by wave action is often regarded as a final event, and sometimes this is true. In this study, paint-marked broken shell fragments were found during the field experiments on wave-effected distribution; also most animals are lost from the Goat Island Bay pop-ulation by the time that they attain 23 mm, which corresponds closely to the peak size of *Lunella* shells in the drift. However, grazers like *Lunella* have rounded, thick shells, well adapted to being rolled by waves on a rocky shore; the stability of the size-classes found at each of the three sites during 4 y of sampling clearly indicates that wave transport to more tolerable conditions occurs regularly.

The life cycle of *Lunella smaragda* commences in February, when the mature adults spawn. Larvae probably settle all over the shore, but only those that find shelter in coralline turf or fine crevices in the rock survive. Most juveniles develop in the turf, where they remain for 1.5–2.0 y, feeding on the more delicate algae epiphytic on the *Corallina* and on some coralline segments. The young *Lunella* first become a distinct portion of the routine sample in September, and they remain in the turf until they are 7–10 mm long, when they are washed off the flat.

The precise time at which animals are washed off probably depends on such considerations as animal size, turf length, wave characteristics, and position of the animal in the turf at the moment of dislodgment. Possibly, wash-off may also depend on orientation of animal to the wave and the attachment ability of the individual (which may vary slightly between animals).

The very fastest growing animals may reach wash-off size when only a little over a year old. However, up till nearly 2 y old, over 70% fall within one standard deviation of the mean size, and over 90% within two standard deviations. Therefore, less than 10% of the year class will be over 7 mm in May, but by August, the number of animals lost increases markedly, and by January most have been removed.

The 2+ year-group develops on the low flats. They become sexually mature when they reach about 15 mm diameter; probably only a few have reached maturity at 2 y, although most of the population are sexually mature at 3 y. The threshold size for wave dislodgment from the Low Flat is about 15 mm, and few animals over 17.5 mm are found except during macroalgal blooms, when some larger individuals colonise for the duration of the bloom. On the Low Flat, some animals are small enough to get down into the turf, and some cannot. The latter must survive on the bare rock surface, gaining whatever shelter they can in the lee of upstanding turf patches (these patches sometimes form "hedges" around the grazing areas).

Animals washed from the low flats in their third year survive in the sublittoral fringe for nearly two more years. Then their numbers suddenly decline, probably as they reach another critical size related to wave conditions. Animals washed from this site probably do not survive at Goat Island Bay; a sublittoral population of *Lunella* does not exist there.

ACKNOWLEDGMENTS

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