

BEHAVIOURAL MECHANISMS OF POPULATION REGULATION IN
THE LIMPET, ACMAEA DIGITALIS

by

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ABSTRACT

Two hypotheses that described possible mechanisms of population regulation in Acmaea digitalis were examined in this study.

The first hypothesis stated that local populations could be regulated by means of changes in the homing behaviour of individual limpets. These changes would occur as a result of feedback from density changes. Results from experiments which tested this hypothesis were inconclusive.

The second hypothesis stated that local populations could be regulated by means of upward migration of limpets if such migration were density dependent; and that mortality during summer would also act in a density dependent way. This hypothesis was substantiated experimentally, although it was not shown that the mechanism does indeed regulate local populations.

Possible explanations of homing and migration behaviour are presented and discussed.

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GENERAL INTRODUCTION

A problem of general interest to ecologists concerns regulation of the number of animals within a population. Eisenberg (1966) defined such regulation as "the maintenance of the numbers of animals in a natural population within a certain range, around some level that is determined by the whole of the environment, and which is brought about as a result of feedback from population density."

Feedback from population density has been supposed to occur in a number of ways. Nicholson (1933) discussed several factors that might vary with population density in their effect on individuals. Birth rates (Ricker, 1954) and mortality (Lack, 1966) have each been suggested as density dependent factors which might regulate populations.

Feedback from population density may also occur through the behaviour of individuals that affects dispersal. Huffaker, Shea and Herman (1963) showed that a predator species and a prey species formed a more stable system when the laboratory environment was made more complex. The more complex "universe" allowed the prey to disperse more widely, and hence the predator did not over-exploit the prey in the whole system, as it was previously able to do within a smaller, less complex system. Wellington (1964) showed that differences in dispersing behaviour among adult and larval tent caterpillars resulted in a complex distribution within a mixed environment. The patterns of behaviour and distribution ensured that food resources were never over-exploited, and that the species was able to survive unfavourable weather conditions. Dispersal can thus be extremely important to the stability of a population.

Regulation of populations by means of dispersal has been widely considered. Territories may be required by individuals for breeding (Watson and Jenkins, 1968) or feeding (Connell, 1963). Emigration from areas of high

density was suggested as an important factor in controlling the population of Microtus, a small rodent (Krebs, et al., 1969). Such emigration was thought to be brought about by changes in aggressive behaviour which accompanied changes in density (Krebs, 1970). Studies such as these indicate the need for recognition of individual differences in behaviour when populations of animals are being examined.

The purpose of this study was to examine behavioural mechanisms of dispersal in the limpet Acmaea digitalis. Although territorial behaviour has been reported in at least one species of limpet (Stimson, 1970), it has not been demonstrated in this limpet, and it appears unlikely that aggressive behaviour occurs (Galbraith, 1965). The two major types of dispersing behaviour appear to be homing (Wells, 1917) and seasonal migration (Frank, 1965).

Frank suggested that regulation of local populations could occur through changes in homing behaviour. This hypothesis is discussed in a section below, and was tested in this study. A second hypothesis, describing a way in which local populations might be regulated by seasonal migration, was developed from studies published by Frank (1965) and Lewis (1954). This hypothesis was also examined in this study, and is discussed below. Possible explanations of the two types of behaviour are also considered.

EXPERIMENTAL METHODS

Introduction

Special techniques, such as marking and fencing, were developed and employed in this study. To avoid repetition and disruption of continuity in the sections dealing with experiments, the general techniques are presented in this section. Procedures peculiar to one experiment are presented in the appropriate section dealing with the experiment.

Determination of tidal heights

The tidal heights at specific locations on the beach were determined in May, 1970, in conjunction with a mapping survey conducted by several members of the University of British Columbia. The relative heights of points were determined with a surveyor's level. The height of one point was determined by observing the time at which it was reached by the tide, then calculating the height of the tide at that time using tide tables. This was repeated eleven times, and the calculated heights were averaged. The heights of points on the beach were then determined by comparison with the known point.

Marking

Limpets were marked individually with adhesive plastic wire markers made by the W. H. Brady Company. These small numbers were available from 0 through 99. To obtain a higher number a small piece of adhesive coloured plastic, made by the same company, was placed with the number. The number was then coated with two coats of plastic cement ('Dekophane'). Marking mortality was never higher than five per cent and appeared to be caused chiefly by cement coming in contact with the mantle.

Groups of limpets were marked with fast-drying paint lacquer or acrylic artist's paint. Unlike the individual markings, which remained on the animals for periods in excess of a year, paint markings lasted no longer

than four months after application.

A requisite for marking was that the shell of the limpet be quite dry. For this reason marking could be done only in summer. Drying wet shells of the animals with alcohol or acetone was attempted without success. Marking of wet shells with acrylic putty, alcohol marking pens, oil pastel crayons, epoxy putty and acrylic paint were all unsuccessful. Filing marks into the shells proved to be impractical because the limpets migrated away from the place where they were marked, apparently in response to the disturbance caused by filing.

Enclosures

Limpets were contained in areas or restricted in movement by means of fences attached to the rock. Fences were constructed from 7cm wide strips of a plastic mesh sold as 'Vexar', which is manufactured for use in produce sections of supermarkets. The strips were folded and attached to the rock by means of rock nails or metal screws and screw anchors, depending on the hardness of the rock. The upper edge of the folded strip was held above the lower edge by means of a rubber tap washer inserted onto the nail or screw between the two edges (Figure 1). Limpets were able to move easily on the mesh itself but were unable to cross the sharp upper edge of the fence.

It was necessary to seal the lower edge of fences to the rock. This was done by using a mixture of fibreglas resin, sand and catalytic hardener, which formed a sort of fibreglas concrete. Ordinary concrete was used once successfully, but this required a much longer setting time and more work. Acrylic modelling putty and an acetic acid based cement were both tested for the purpose and found to be inadequate.

Displacement of limpets

Limpets were removed to experimental sites in several experiments.

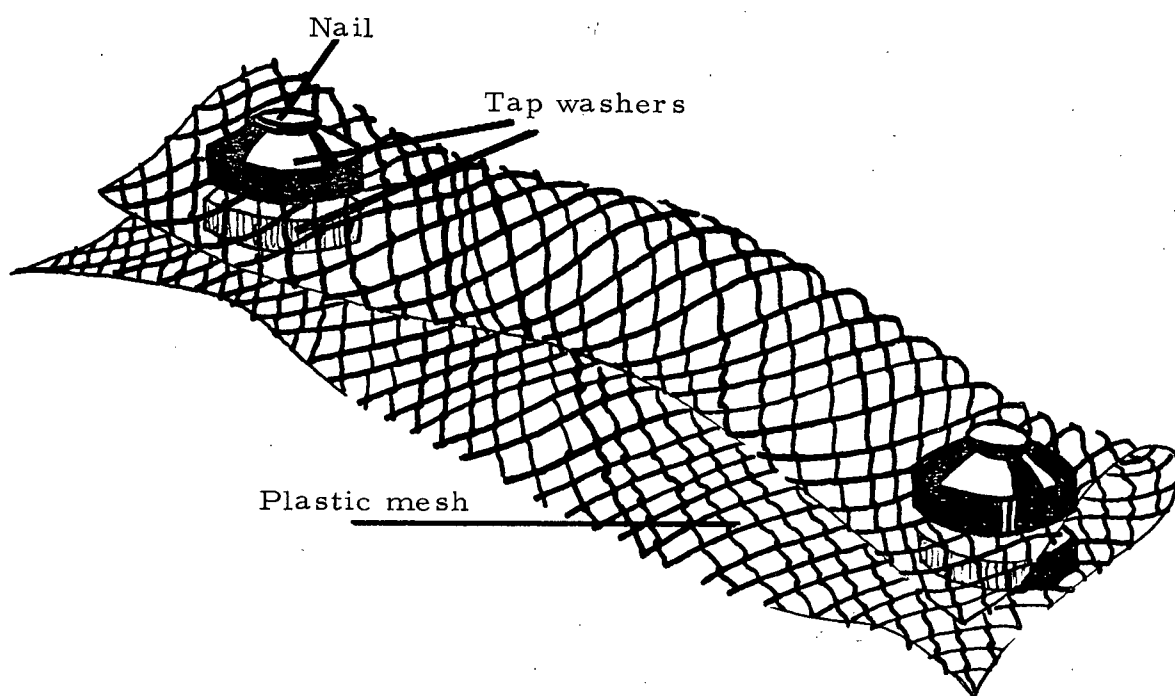


Figure 1. Detail of enclosure construction.

To minimize mortality, the following procedure was used. A limpet was removed by the insertion of a dull blade under the shell margin, followed by gentle lifting. Limpets were placed in fresh sea water for a period of five to ten minutes prior to replacement. The replacement area was wetted with sea water, then the limpets were placed on the area and, if necessary, held until they had taken hold. After all limpets had been replaced, the area was wetted again with sea water. It was necessary to allow at least thirty minutes between the time of replacement and the arrival of the tide.

Measurement of limpets

Limpets were measured in situ so that disturbances caused by removal would not be introduced into experiments. Because the animals were often packed closely together or found in narrow cracks in the rock, it was not possible to use vernier calipers. Measurements were made by closing a drawing compass until it touched both ends of the shell and drawing the arc in a field book. The length of the arc was later measured with vernier calipers to .01cm.

A standard length was defined as the distance from the most anterior portion of the shell to the longer of the two ribs at the posterior margin.

DESCRIPTION OF THE STUDY AREA

Location

This study was carried out on the west coast of Vancouver Island near Port Renfrew. The section of shore on which the study was done is known locally as Botanical Beach, in reference to the Seaside Station maintained there by the University of Minnesota from 1900 to 1910. Although Botanical Beach is accessible by road, it is remote from human habitation and seldom visited by people except during the summer. The area was thus largely undisturbed. Living and research facilities, which were constructed near the old Station site by members of the University of British Columbia, were used during visits to the study area.

Physical factors

Botanical Beach consists of a broad, rocky shelf of varying width and slope. The intertidal zone is 100 metres wide in some places when exposed. The shelf, composed of sandstone intruded by hard metamorphics, has been carved into a complex array of pools, prominences and benches. The microtopography varies from very flat, smooth sandstone to the extremely rough, pitted surfaces of some metamorphic projections. The beach is bounded at both ends by upturned shale beds, which were not studied. Detailed geological description has been given by Hall (1906).

Although the shore bounds the outer reaches of the Strait of Juan de Fuca, it is an exposed coast. Pacific storms and seas have unrestricted access to the beach from the west and northwest. The tides are mixed semi-diurnal, with two unequal high tides and low tides every 25 hours. The range of the tide varies from 6.1 to 12.6 feet.

In summer, the lower low tide occurs between dawn and noon at spring tides, and the higher high tide occurs at night. During the winter, lower low

tide occurs between sunset and midnight at spring tides, while the higher high tide occurs in the late morning. Thus the upper intertidal is exposed for longer periods to sunlight during summer than winter. Shifts of the seasonal tide patterns occur in September and March.

Periods of drying during the summer, which are brought about by tide patterns as well as warmer weather, are further exaggerated by sea conditions. Large swells occur almost constantly during the colder months, and at any time they wash the rocks at levels far above the tide level. The summer sea is much calmer; swells are rarely greater than two feet high, and the rocks are washed only to the actual tide height. If the weather is calm and dry during neap tides, the rocks above the 11 foot level may be dry for up to 20 days.

Rainfall occurs mostly in the colder months. During the summers of 1969 and 1970, campfire permits were suspended for lack of rain in the nearby forest. The weather was sunny except for periods of sea-fog, which did not dampen the rocks.

During the one winter (1969-1970) included in this study, no ice, such as that observed by Frank (1965), occurred. Frank reported that floating masses of ice ground limpets from the substrate. The only adverse conditions for intertidal organisms observed during winter were large amounts of fresh water from rain and runoff, and heavy seas, which often carried large pieces of driftwood and logs across the beach. The winter observed may have been atypical; during the preceding winter freezing conditions at Vancouver persisted for several weeks and large amounts of intertidal ice were observed.

Distribution of Acmaea digitalis

In May, 1969, limpets were counted and sampled along a line that was run down a gently sloping part of the shore. Intervals of 1m along the line were marked on the rock with chalk. Limpets within 10cm on either side of

the line were counted within every interval, and samples consisting of every limpet within five counting areas were taken. The lengths of limpets in the samples were measured later. The tidal heights of points along the transect were determined in May, 1970. (tidal height refers to the elevation of a point above chart datum, 0.0 tidal feet).

A. digitalis was found from 6.0 to 10.0 tidal feet where the transect was made. At another portion of the shore that was steeper and more directly exposed to surf, the species was found from 9.0 to 14.0 tidal feet. Corresponding differences in the distribution of algae species were also observed between the two areas. The difference appeared to be caused by the difference in exposure to surf, and demonstrates that tidal height is only a relative measure which must be modified by consideration of local factors.

Figure 2 shows the number of limpets per unit area at different heights on the transect. Density increases rapidly from 6.0 to 7.25 feet, then declines. A series of very shallow tidepools, in which A. digitalis were not found, occurred on the transect from 8.0 to 8.75 tidal feet. This accounts for the low value of density at 8.25 feet. A section of uniform substrate would probably show a continuous decline in density from 7.25 to 10.0 feet.

The relative abundance of each size class at different tide levels is shown in Figure 3. The modal size class increases with tidal height. This observation is consistent with those reported by Frank (1965) for A. digitalis and Lewis (1954) for the ecologically similar Patella vulgata. Both found largest limpets at the upper part of the shore, and smaller ones lower on the shore. Frank suggested that this differential distribution of size classes was caused by migration. The limpets he studied showed net upward movement during the fall and winter, and a lesser net downward movement in spring. Thus the larger limpets at the upper end of the vertical distribution are those which have made several migrations from the place where they originally settled.

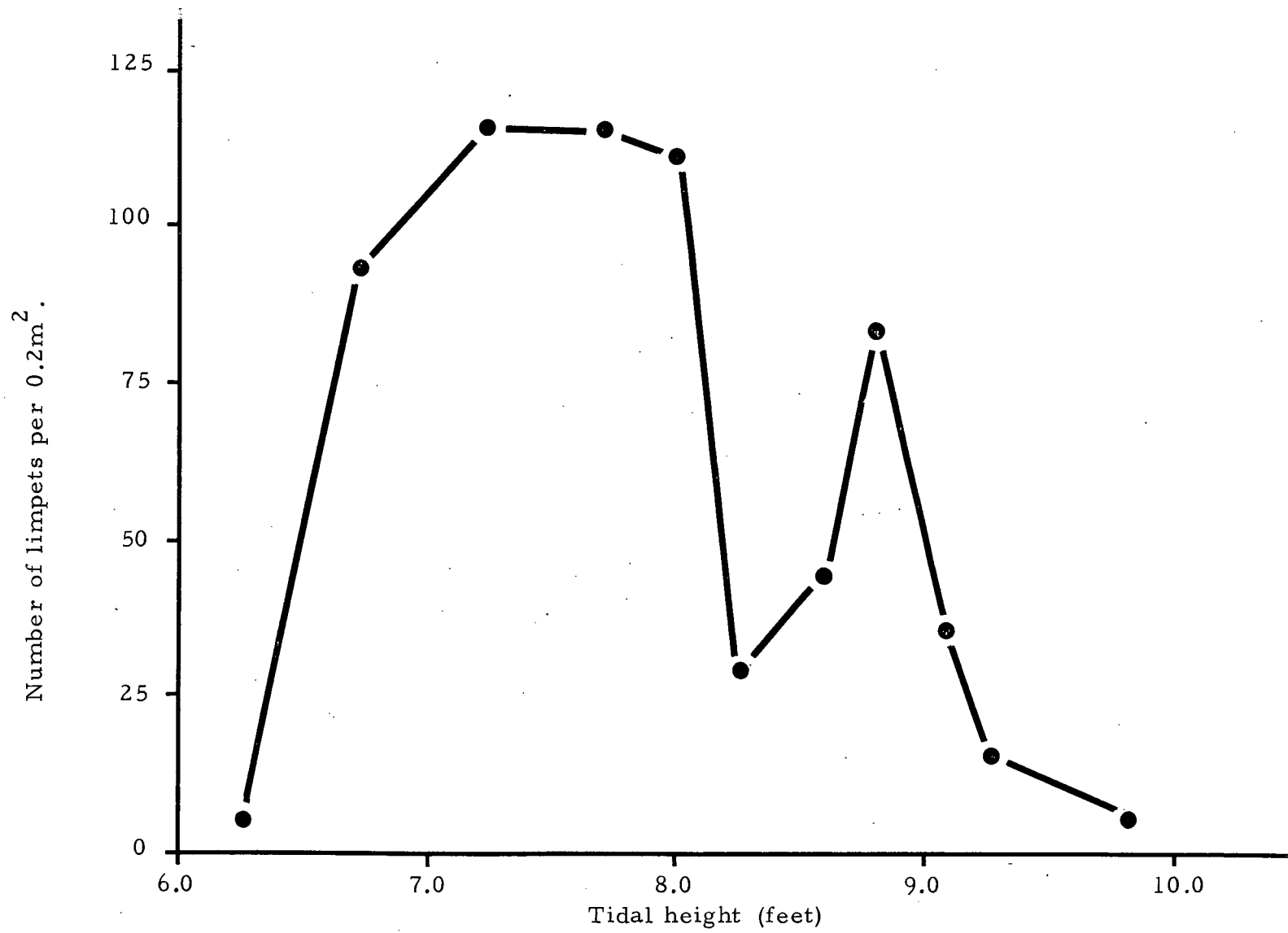


Figure 2. Density of limpets against tidal height.

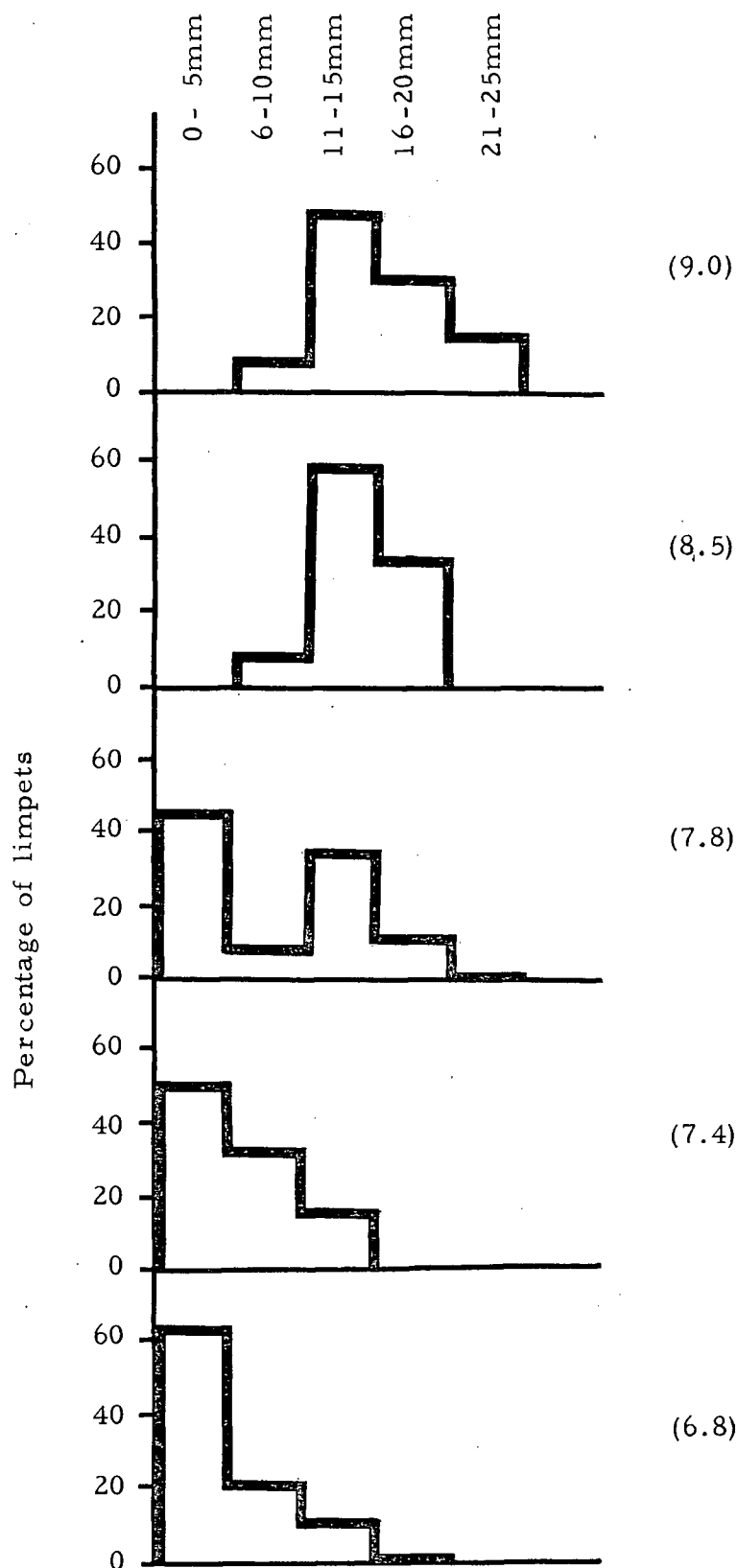


Figure 3. Percentage of limpets in each size class at different tidal heights. The tidal height of each sample is given in parentheses.

Very small limpets began to appear in April and May, 1970. They were not found above approximately 8.0 feet on the transect line. Doty (1946) suggests that critical tide levels may define the upper limit of distribution of species in the intertidal zone. The upper limit of distribution of newly settled limpets, 8.0 feet, corresponds with the lowest level of lower high tide (LHT). This is the high tide which occurs during the day in summer, and parts of the shore which are not covered by LHT are exposed for most of the day. There is a large difference in the maximum length of daytime exposure between parts of the shore above and below LHT. That young limpets settle below 8.0 feet may indicate they are not able to withstand the long periods of desiccation encountered above that level, whereas larger limpets can. Davies (1969) has shown that smaller Patella lose water at a greater rate than larger ones. The ability of small limpets to survive at levels above 8.0 tidal feet was not tested in this study because it was impossible to remove and replace the very small limpets without damaging them. If it is true that a critical tide level exists for very small limpets, then upward migration in fall and winter would be partly explained in terms of adaptation to physical factors. The upward migration will be discussed more fully in later sections.

A. digitalis occurs on exposed rock rather than in pools. Pools located within the range of A. digitalis were inhabited by A. paradigitalis (Fritchman, 1960) and A. pelta. A. testudinalis began to appear in pools toward the lower limit of distribution and was found below the lower limit of A. digitalis. There was no apparent competition between A. digitalis and other limpets, for either food or shelter space, because A. digitalis almost always occurred separately.

Possible competitors for food were the littorines Littorina scutulata and L. sitkana. Both species occurred within the vertical range of A. digitalis and frequently occupied the same shelter sites at low tide. However, competition for shelter space did not seem to exist because littorines occupied either shelter sites without limpets or the interstices between clumped limpets. On one falling tide littorines were observed feeding after the limpets

had already become immobile and ceased feeding later to shelter in the limpet clumps.

Distribution and abundance of food species

The substrate on which A. digitalis was found supported no macroscopic algae in summer above 9.0 feet. Below that level, in the zone in which this limpet was found, only tufts of Gelidium sp. were found, which limpets did not appear to eat. The substrate was very thinly coated with microscopic plants. In June, 1969, a small fence was constructed to prevent limpets and littorines from grazing the area within; after two weeks the thickened algal covering was sampled. It was found to consist entirely of several species of colonial diatoms, which were not identified further.

In early October, 1969, the diatom film above 8.0 tidal feet on all parts of the shore became a thick mat, composed of strands up to 3cm long. A similar thickening of the algal mat in fall was noted by Castenholz (1961), who suggested that it was caused by decreases in littorine density. However, the thick cover appeared on the study beach in an area where littorines were never observed; consequently, this explanation seems unlikely. Appearance of the thick mat followed the change from summer tide patterns to winter patterns and may have been related to the increased dampness of the inter-tidal zone at this time.

Soon after it appeared, the mat disappeared around depressions that contained limpets or littorines, apparently having been grazed down. The mat declined gradually during the next four months, after which it had been nearly reduced to its summer level. The thick mat remained in the area which contained no grazers for two months after it had disappeared elsewhere. It appears likely that grazing action was partly responsible for the decline. In November, the zone between 8.0 and 15.0 feet became covered with Prophyra sp. By the time these plants reached 5cm in length, they had virtually disappeared in the zone below 12.0 feet, where most limpets occurred;

but they remained above that level until late February when they began to dis-colour and die.

Fucus sp. occurred in a few shaded places where limpets were found, but such places were not common. One plant was found in an area with some marked limpets and remained there throughout the study. Limpets do not appear to eat large Fucus plants.

Ulva sp. and Enteromorpha sp. began to appear during winter, but were located above the upper limit of A. digitalis. That they did not appear in the region inhabited by limpets may indicate that these plants are eaten by limpets as soon as they settle.

Colonial diatoms, present throughout the year but most abundant in early winter, thus appear to be the major food species of A. digitalis. The limpets may also graze macroscopic plants such as Porphyra, Ulva and Enteromorpha. Since these are not present with limpets except in the winter, and are then quickly grazed away, they must form only a small part of the diet of A. digitalis. The limpets may help to determine the vertical distribution of some macroscopic algae, such as Porphyra.

Summary

Physical conditions observed at the study area, including tides, weather and sea conditions, appeared to be more favourable for limpets during the winter of 1969-1970 than during the summers of those years. During winter heavy seas, driftwood and fresh water were the only possible adverse factors observed. During the summers, low tides occurred during the day, combining with hot, dry weather and low seas to produce long periods of desiccation. The winter observed may have been atypical.

A. digitalis was found to be distributed from just above mid-tide level nearly to the high tide level. The density decreased with increasing tidal height, and the modal length increased with increasing height. It was con-

cluded that competition with other species of limpets does not occur, although competition with littorines for food may occur.

Food for the limpets, which was found to consist mainly of colonial diatoms, was present throughout the year but became most abundant from October through January. Other species of algae were observed, and it was concluded that they were not a substantial part of the limpets' diet. A. digitalis may affect the distribution of algae between tide-marks.

STUDIES OF HOMING BEHAVIOUR

Introduction

Limpets that are exposed to air during part of the tidal cycle are usually immobile during that period. In several species of Acmaea, limpets are reported to return to a home site, in which they remain during low tide (Wells, 1917). Such behaviour may assure the limpet of being protected in a suitable place from desiccation. Limpets are thought to utilize local topography rather than chemical stimuli to return to the home site (Jessee, 1968; Galbraith, 1965).

At low tide A. digitalis remain inactive in cracks and depressions in the substrate, which provide shade and moisture. Aggregations of limpets (termed clumps), which may contain up to several hundred animals, are often seen in such places. The clump may increase protection from desiccation (Millard, 1968), and may also provide protection from predators. A limpet within large, tightly packed clumps might be less vulnerable to predation than a single limpet, much as a fish in a school is less likely to be selected by a predator than a solitary fish (Brock and Riffenburgh, 1960).

Frank (1965) and Millard (1968) found that some individuals were repeatedly observed in the same clump, even though the clump changed position on the rock. Frank (1965) reports that homing to a specific home site does not occur, but rather the limpets remain within a "home range" (Frank, 1964). However, Miller (1968) found that 25 per cent of a group of marked limpets returned to the site at which they were marked over nine days. Galbraith (1965) reported 54 per cent homing within a grid system over seven days. Different techniques were used by the various authors to study homing; this might account for discrepancies among their findings.

It was of interest that some limpets in the studies reported above showed homing behaviour while others did not. Frank (1965) suggests that

when environmental conditions are favourable, limpets tend to remain within a home range. When conditions deteriorate, limpets begin to migrate from their home range. In this way local population density could be self-regulated in the sense of Eisenberg (1966). Because A. digitalis have pelagic larvae, which drift about in the plankton for an unknown length of time, it is difficult to define a "population" of these animals. After settlement, however, the limpets do not usually move more than a few metres (Frank, 1965). A "local population", in which self-regulation might occur, could thus be defined as those limpets within a few square metres of rock surface area, from which only a small proportion of the total number of limpets normally emigrate.

Frank also suggested that the threshold of tolerance to local conditions varies among limpets; consequently, this mechanism of regulation would operate at a wide range of densities and local conditions. If Frank's hypothesis is correct, then at any density some limpets are tolerant of local conditions and remain within a home range, while others are intolerant and have no home range. When local density increases, local conditions deteriorate, and a greater proportion of the population becomes intolerant and thus does not display homing behaviour. These limpets tend to migrate from the area, and local conditions tend to improve.

A similar hypothesis was suggested by Lomnicki (1969), who reported that land snails (Helix pomatia) demonstrated two behavioural types. Some snails tended to remain beneath the surface of the ground in a small area, while others migrated about on the surface. Lomnicki suggests that more mobile snails are the excess of the population, and that local density is regulated by migration. Neither author tested his hypothesis.

The hypothesis was examined in several stages. Small groups of A. digitalis were studied to determine whether homing behaviour was demonstrated. Larger groups were marked to determine whether the two types of behaviour predicted from the hypothesis could be identified. The proportion

of limpets of each behavioural type was measured over a range of densities in an enclosed area to determine whether the proportion of non-homing individuals increased as the density increased. Finally, environmental conditions around groups of limpets were made unfavourable by direct manipulation, to determine whether changes in homing behaviour would occur.

Occurrence of homing

Forty limpets were marked individually in May, 1969, and their positions were recorded on eleven subsequent days at low tide. Twenty-six were seen in the original position at every recorded observation, five changed position once, and ten changed position more than once. Limpets which did not change position were known to have moved, presumably in feeding, because twenty-two were in small clumps of up to ten animals, and the relative positions of limpets within the clumps were seen to change. The position of each clump remained constant.

A second group of nine limpets was marked in August, 1969. These were very large A. digitalis (more than 3.5cm) in an area of low density. The position of each limpet was marked by drilling a hole immediately beside the limpet. After one month, five were still in place, two had changed position and two were missing. After nearly a year, three were still in place, three had changed position and three were missing. The three still in place had been frequently observed, as they were beside the path normally taken onto the main beach. They were never observed away from the original point of marking.

It is shown later that removal of limpets from the rock affects homing, even when they are replaced where they were found. Thus, homing could not be studied by displacing limpets and observing whether they return to their original sites. It was concluded from the evidence above, however, that homing behaviour is demonstrated by some individual limpets. Homing to a specific site and homing to a clump were both observed.

Identification of two behavioural types

To determine whether homing limpets and non-homing limpets could be distinguished, as predicted from the hypothesis, the individuals in two larger samples were marked. The first sample occurred on a vertical rock outcropping, on which a permanent grid containing 28 squares was laid by drilling holes 20 cm apart. Columns and rows of the grid were given numbers and letters respectively, and were used to describe the position of each individual.

Observations were made on six consecutive days, from June 5 through June 10, 1969. Each day's observation included the square in which each limpet was found and the number of limpets with which it was clumped. A clump was defined as four or more limpets grouped such that no limpet was more than 1 cm from another limpet. The observations from each limpet were recorded across a sheet of data paper so that at the end of six days the number of changes of position could be seen.

To avoid confusion between changes in shelter position, as seen between successive low tides, and feeding movements, the term "migration" was adopted to describe the former. Thus, if a limpet moved from its shelter site to feed and then returned to the same site, it had not migrated. If, after feeding, it adopted a new shelter site, it had migrated. A migration could occur in two ways: a limpet could migrate to a new square; or it could migrate from within a clump in a square to a position outside the clump in the same square.

The second sample of limpets was located on a projection of smooth soft sandstone in which there were 30 small, hollow depressions. These depressions, in which the limpets tended to form clumps, were numbered and used in place of the grid system to describe positions of limpets. All other procedures were the same as those described for the first sample. This sample was observed from August 11 through August 16, 1969.

The number of migrations made by each limpet was determined and a distribution of migration frequencies compiled. These are seen in Tables I and II. In both samples, there were more limpets which did not migrate at all than in any other category, and there were progressively fewer limpets in each category of higher migration frequency.

If all limpets were equally likely to migrate on a given night, and if the probability of any limpet migrating were not modified by whether it had migrated on previous nights, then the distribution of migration frequencies would follow a Poisson distribution. This situation might be found if migrations were produced by local disturbances affecting limpets randomly, or by an innate tendency of the limpets to migrate at random intervals. In such a situation the migration frequency pattern would have little importance with respect to regulation of local density. By comparing the observed migration frequencies with the Poisson distribution, calculated using the mean number of migrations per limpet, one can test whether the migrations are indeed distributed among the limpets randomly and independently. If the observations are not in accord with the Poisson distribution, it indicates either that migrations are not distributed randomly among the limpets, in that all limpets are not equally likely to migrate; or that migrations are not distributed independently, in that the probability of a limpet migrating is affected by whether or not it has previously migrated. A combination of both factors could also be responsible for deviation from the Poisson distribution.

The observations were compared with the calculated Poisson by means of the Chi-squared test of goodness of fit. These comparisons are shown in Tables I and II. Both sets of observations were significantly different from the Poisson. Both samples differed from the Poisson in that more limpets than expected did not migrate at all, fewer migrated only once, and more migrated more than once. In 1970, observation of the first sample was continued in association with an experiment to be discussed below. Five sets of observations were obtained (Tables III, IV, V, VI and VII). All show a

TABLE 1. The number of limpets which occurred in each category of migration frequency. The data were collected from the first marked sample of limpets, from June 5 through June 10, 1969. The observed distribution of migration frequencies was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last four categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	56	49.28
1	19	28.53
2	8	8.26
3	4	1.59
4	1	0.23
5	0	0.03
Total	88	87.92

Chi-squared = 4.94,

Significant at $\alpha^* = .05$,

d.f. = 1.

* Throughout this study, the level of rejection (α) was .05. Where the null hypothesis could have been rejected at a lower value of α , the lower value is given instead of .05.

TABLE II. The number of limpets which occurred in each category of migration frequency. The data were collected from the second marked sample of limpets, from August 11 through August 16, 1969. The observed distribution of migration frequencies was compared with the Poisson distribution calculated from the mean number of migration frequencies per limpet. The last four categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	173	145.45
1	24	61.49
2	16	13.02
3	2	1.82
4	4	0.19
5	3	0.02
Total	222	221.99

Chi-squared = 15.22,

Significant at Alpha = .001,

d.f. = 1.

TABLE III. The number of limpets which occurred in each category of migration frequency. The data were collected from February 15 through February 19, 1970. The observed distribution was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last three categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	35	30.65
1	9	15.60
2	5	3.97
3	1	0.67
4	1	0.09
Total	51	50.98

Chi-squared = 4.50,

Significant at alpha = .05,

d.f. = 1.

TABLE IV. The number of limpets which occurred in each category of migration frequency. The data were collected from April 29 through May 2, 1970. The observed distribution was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last two categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	72	64.40
1	15	28.34
2	10	6.23
3	3	0.91
Total	100	99.88

Chi-squared = 12.05,

Significant at alpha = .001,

d.f. = 1.

TABLE V. The number of limpets which occurred in each category of migration frequency. The data were collected from June 1 through June 5, 1970. The observed distribution was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last three categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	63	51.25
1	6	25.92
2	11	6.55
3	5	1.11
4	0	0.14
Total	85	84.97

Chi-squared = 26.63,

Significant at alpha = .001,

d.f. = 1.

TABLE VI. The number of limpets which occurred in each category of migration frequency. The data were collected from June 16 through June 19, 1970. The observed distribution was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last three categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	73	60.39
1	6	27.35
2	11	6.20
3	5	0.94
4	0	0.11
Total	95	94.99

Chi-squared = 29.91,

Significant at alpha = .001,

d.f. = 1.

TABLE VII. The number of limpets which occurred in each category of migration frequency. The data were collected from July 23 through July 27, 1970. The observed distribution calculated from the mean number of migrations per limpet. The last three categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	76	62.75
1	19	37.43
2	12	11.17
3	7	2.22
4	0	0.33
Total	114	113.90

Chi-squared = 13.90,

Significant at alpha = .001,

d.f. - 1.

similar pattern of deviation from the Poisson.

If migrations were not distributed randomly among the limpets, this might be explained by differences in behaviour patterns associated with size among the limpets or with the sizes of the clumps in which the limpets occurred. If the migration pattern of smaller limpets differed from that of larger limpets, or if limpets in smaller clumps behaved differently from those in larger clumps, a distribution of migration frequencies which differed from the Poisson would be observed. Checks were made to determine whether limpet size or clump size could account for the type of distribution which was observed. The effect of size was discounted immediately because all the limpets on the first area were approximately the same size, between 1.50 and 2.00 cm. To check whether clump size affected the migration behaviour, the following test was performed in both samples of marked limpets. An arbitrary division between "large" and "small" clumps was made so that roughly half the limpets fell into each group, and the data were divided according to the initial clump in which each limpet was found. The distributions of migration frequencies from the large and small clumps were then compared by means of the Chi-squared test for independence of samples (contingency tables). These comparisons are shown in Tables VIII and IX. In neither sample was there a significant difference between the migration frequencies from the two types of clumps.

The deviations from the expected Poisson distribution might also have resulted from using short periods of observation. The probability that a limpet would migrate might be affected by whether or not it had migrated in the previous few days; but such bursts of migration activity could be independent of activity made a month previously. If this were the case, migrations could be considered to be independent over the longer term and the deviation from the Poisson would have little importance. This possibility was tested by examining data collected over six months. Four sets of observations of the same limpets, made at various times during the six months and presented

TABLE VIII. A comparison between the migration frequency distributions of limpets initially found in large and small clumps. A small clump was defined as that containing less than ten limpets; a large clump as that containing ten or more limpets. The data were collected from the first sample of marked limpets, from July 23 through July 27, 1970. The last two migration frequency categories were grouped to meet the requirements of the Chi-squared test for independence of samples.

Number of migrations	small clumps		large clumps	
	No. limpets observed	No. limpets expected	No. limpets observed	No. limpets expected
0	38	42.67	38	33.33
1	12	10.67	7	8.33
2	8	6.74	4	5.26
3	6	3.93	1	3.07
Total	64	64.01	50	49.99

Chi-squared = 3.73,

Not significant at alpha = .05,

d.f. = 1.

TABLE IX. A comparison between the migration frequency distributions of limpets initially found in large and small clumps. A small clump was defined as that containing less than fifteen limpets; a large clump as that containing fifteen or more limpets. The data were collected from the second sample of marked limpets, from August 11 through August 16, 1969. The last three migration frequency categories were grouped to meet the requirements of the Chi-squared test for independence of samples.

Number of migrations	small clumps		large clumps	
	No. limpets observed	No. limpets expected	No. limpets observed	No. limpets expected
0	61	61.56	112	111.44
1	8	8.54	16	15.46
2	6	5.70	10	10.31
3	1	0.71	1	1.29
4	2	1.42	2	1.93
5	1	1.07	2	1.93
Total	79	79.00	143	142.36

Chi-squared = 0.39,

Not significant at alpha = .05,

d.f. = 1.

above in Tables III, IV, V and VI, were combined. The resulting distribution of migration frequencies contained fifteen possible migration categories. Only observations made on consecutive days were included; migrations of limpets between sets of observations were ignored. Comparison of the combined observations with the calculated Poisson distribution (Table X) indicated that the observations were not in accord with the expected Poisson. The pattern of deviation from the Poisson was the same as that observed in the component sets of observations.

Thus there appeared to be two behavioural types. More limpets did not migrate, fewer migrated only once and more migrated many times than would be expected from the mean number of migrations per individual. Such behaviour persisted for long periods of time, and could not be explained by differences in behaviour associated with clump size. It is possible that the observed behaviour pattern resulted from a stimulus distributed randomly in space; because the limpets are not distributed randomly in space and thus would not be affected randomly by such a stimulus. This situation was considered unlikely, however; and it was concluded that two behavioural types of limpets, homing and non-homing, had been detected.

Relation between density and homing behaviour

An experiment was performed to determine whether the percentage of non-homing limpets would increase as the density increased. The reasoning was that an increase in density in an enclosed area would result in less favourable local conditions, with a consequent increase in the number of limpets intolerant to local conditions and thus non-homing.

In February, 1970, the area containing the first sample of limpets described in the preceding section was enclosed by means of a plastic mesh fence. All A. digitalis within the enclosure were marked or remarked. Two sets of observations were made on the migration behaviour at natural density. Then limpets from elsewhere were added to the enclosed area, increasing the

TABLE X. The number of limpets which occurred in each category of migration frequency. The data are combined from Tables III, IV, V, and VI. The combined distribution was compared with the Poisson distribution calculated from the mean number of migrations per limpet. The last four categories were grouped to meet the requirements of the Chi-squared test for goodness of fit.

Number of migrations	Number of limpets observed	Number of limpets expected
0	16	6.95
1	8	12.18
2	3	10.65
3	2	6.22
4	4	2.72
5	3	0.95
6	2	0.28
7	2	0.07
Total	40	40.02

Chi-squared = 33.69,

Significant at alpha = .001,

d.f. = 3.

density to twice the previous level, and two further sets of observations were made. More limpets were added to increase density to four times the density in February, and one further set of observations was made.

The percentage of limpets that migrated and the mean number of migrations per limpet per day were calculated for each set of observations, and are seen in Table XI. The correlation between relative density and per cent migrating was $r = .349$. The correlation between relative density and the mean number of migrations per limpet per day was $r = .242$. Neither was statistically significant. This indicated that there was no relation between relative density and percentage of limpets that migrated; nor between relative density and the mean number of migrations per limpet per day, at least within the experimental range of densities.

A possible criticism of this experiment is that homing behaviour was observed in one group of limpets over time, rather than in several groups of limpets at the same time. The weather changed during the course of the experiment, and it might be argued that the weather caused changes in either the homing behaviour or the local conditions in the experimental area. Such changes could have compensated for changes in behaviour caused by increased density in the experimental area, with the result that no change in homing behaviour was observed.

It is unlikely that weather had this effect on local conditions. Since weather became progressively warmer and drier as density in the experiment was increased, any effect of weather on homing behaviour would have been in the same direction as that of increased density. It is possible, however, that warmer and drier weather decreased the tendency for limpets to migrate, even though local conditions affected by density were deteriorating.

The effect of weather could be eliminated by observing limpets at different densities within a short period, or by observing several groups of limpets at the same time. There was no time available in which this experi-

TABLE XI. Comparison between relative density and percentage of limpets that migrated during the period of observation, and between density and the mean number of migrations per limpet per day. Relative density was calculated by dividing the number of limpets by the number in the enclosure on February 15. Correlation coefficients for both comparisons were calculated.

Period of observation		Total number limpets	Total number marked limpets	Relative density	Percentage marked limpets migrating	Mean number migrations/limpet/day
Feb.	15-	133	51	1.00	31.4	0.127
Feb.	19					
Apr.	29-	125	100	0.94	28.0	0.146
May	2					
June	1 -	290	95	2.18	23.2	0.113
June	5					
June	16-	283	117	2.13	28.2	0.162
June	19					
July	23-	561	114	4.22	33.3	0.149
July	27					

For the correlation between relative density and percentage migrating,
 $r = 0.349$.

For the correlation between relative density and the mean number
 migrations per limpet per day, $r = 0.242$.

Neither is significant at $\alpha = .05$.

ment could have been repeated.

Relation between homing and local environmental conditions

The previous experiment examined homing behaviour with respect to density, in an attempt to determine whether the proportion of homing limpets decreased as density increased. It was assumed that increased density would cause reduction of some resources used by the limpets, such as food and shelter space. This section deals with experiments in which local environmental conditions were manipulated directly. The same hypothesis was tested; that, if local conditions are made unfavourable for limpets, a smaller proportion of the limpets show homing behaviour.

Two experiments, one in 1969 and one in 1970, were performed to test whether a decrease in food availability results in a decrease in the proportion of homing limpets. In these experiments, the algae on the rock surrounding a clump of marked limpets was removed. The number of marked limpets which subsequently emigrated from the clump was used as a measure of non-homing, and was compared with the number of emigrants from a control clump around which the algae had not been removed.

In each of the two experiments, the experimental and control clumps of limpets contained similar numbers of limpets of similar size. The two clumps were located in areas of similar topography with the distance between them just great enough so that limpets would not be likely to move from one to the other. The algae was removed from the rock, by scrubbing the rock with a wire brush, up to 0.6m around the experimental clump. This method of removing algae had a possible disadvantage in that it slightly altered the surface of the rock, but it was the best of any method tried. Alcohol, spread on the rock with a brush to kill the algae, tended to run into the limpet clump and kill the limpets. Burning the algae with a propane gas torch was too slow and inefficient to be practical.

For each group, the number of limpets remaining in the clump, the

number of emigrants and the distances they travelled were subsequently recorded. The results of the 1969 and 1960 experiments are presented in Tables XII and XIII respectively. In the former experiment, the number of limpets which emigrated from the experimental group was only slightly higher than the number which emigrated from the control group. However, the emigrants from the experimental group tended to migrate much farther than those from the control. In the 1970 experiment, the rate of emigration was much higher in the experimental group than the control, although the distances travelled by the emigrants were similar.

The 1969 and 1970 experiments were carried out in similar locations on different parts of the shore. One difference between the experiments was that the limpets tested in 1970 were smaller than those used in 1969. Larger limpets may have a greater tendency to remain at the home site.

It was concluded that decreased food availability results in a decrease in the proportion of limpets which return to their home sites. This conclusion must be modified by taking into consideration the possibility that larger limpets are less likely to migrate from the home site even during unfavourable local conditions. The possible relation between size and tendency to migrate should be investigated further.

Another factor which might affect the proportion of homing limpets was thought to be crowding on areas where limpets feed. Increases in local density would increase crowding on the feeding area; under the hypothesis being tested the proportion of homing limpets would be expected to decrease.

This prediction was tested in the following way. All limpets found in a clump were marked, then an equal number of limpets from elsewhere were added to the clump. It was reasoned that these added limpets would increase the degree of crowding on the feeding area during the first night, but would not decrease the availability of food in that time. If the proportion of marked limpets that returned to the original clump by the following day was smaller

TABLE XII. The number of limpets remaining, the number of emigrants and the median distance travelled by emigrants in the experimental (E) and control (C) groups of an experiment designed to measure response of limpets to reduced food levels. Algae was removed from around the experimental group on July 30, August 2, 10, 15 and September 1, 1969.

Date	Number marked limpets remaining		Number emigrant limpets		Median distance travelled (cm)	
	<u>E</u>	<u>C</u>	<u>E</u>	<u>C</u>	<u>E</u>	<u>C</u>
July 20	84	77	-	-	-	-
August 2	83	74	1	3	20.0	16.7
August 10	66	71	6	4	60.0	50.0
August 15	62	62	16	10	105.5	38.0
September 1	59	58	16	14	160.0	92.1

TABLE XIII. The number of limpets remaining, the number of emigrants and the median distance travelled by emigrants in the experimental (E) and control (C) groups of an experiment designed to measure the response of limpets to reduced food levels. Algae was removed from around the experimental group on June 4 and 5, 1970.

Date	Number marked limpets remaining		Number emigrant limpets		Median distance travelled (cm)	
	<u>E</u>	<u>C</u>	<u>E</u>	<u>C</u>	<u>E</u>	<u>C</u>
June 4	93	111	0	0	0	0
June 5	84	109	6	0	42.5	0
June 16	46	90	43	18	54.5	45.0

than that of a similar control clump, then the prediction made from the hypothesis would be confirmed.

In June, 1969, four similar clumps of limpets were marked. Two were designated as control groups and two were designated as experimental groups. Limpets removed from elsewhere were added to double the number of limpets in the experimental clumps. In addition, the effect of removal and replacement on those limpets that were added to the experimental groups was tested. All the original limpets in one experimental group and one control group were removed from the rock and replaced at the same time.

The position of each marked limpet was recorded the following day. The numbers remaining in each clump are presented in Table XIV. Few limpets remained in the control and experimental clumps that were removed and replaced, while a higher percentage remained in the two clumps that were not removed and replaced. This indicated that removal and replacement caused a high proportion of limpets to migrate from their home sites. In addition, each experimental group had fewer limpets remaining than the appropriate control group. This indicated that crowding caused a slight decrease in the proportion of homing limpets.

The experiment was repeated in 1970 with three pairs of experimental and control groups. This experiment was inconclusive for the following reason. Limpets were added to the experimental groups on the morning of a very hot day. Because limpets that are placed down on an area do not move about to find shelter sites, and thus are unable to resist desiccation as well as undisturbed limpets, all groups of limpets were splashed with seawater throughout the day to reduce desiccation. During the following high tide, virtually all limpets moved away from their original positions, in the control groups as well as the experimental groups. This was thought to result from the disturbance caused by splashing the groups throughout the day. This unexpected effect made the results completely inconclusive. The experiment was not

TABLE XIV. The initial number of limpets in each of four treatment groups of an experiment designed to measure response of limpets to crowding, and the number that remained in each group after one day. Limpets removed from elsewhere were added to the experimental groups; disturbed groups were removed from the rock and replaced at the same site.

Group	June 7, 1969	June 8, 1969	Percentage remaining
	Initial number of limpets	Number of initial limpets remaining	
undisturbed experimental	47	39	82.97
undisturbed control	51	50	98.03
disturbed experimental	52	3	5.76
disturbed control	52	7	13.46

repeated again because of lack of time.

It was thus not conclusively demonstrated that crowding causes a decrease in the proportion of homing limpets. It is apparent, however, that artificial disturbances, such as splashing the limpets during the day with sea water or removing and replacing the limpets, result in a large decrease in the proportion of homing limpets.

An experiment was designed to measure the amount of disturbance caused by crowding and low levels of food. Such disturbances were thought to occur naturally as a result of local increases in density. The amount of disturbance was measured by placing limpets in a partial enclosure that was open at one end, and observing the number which remained within the enclosure on the following day.

In July, 1970, two sets of four adjoining partial enclosures were constructed with plastic mesh fences. Each partial enclosure was bounded on three sides, each 30cm long, by the fence. The fourth side was left open. The two factors to be tested were low food availability and crowding. Response of the limpets to low food availability was tested by placing twenty limpets within a partial enclosure from which the algae had been removed. The number of limpets remaining in the enclosure on the following day could be compared with a control, in which twenty limpets were placed in an enclosure from which the algae had not been removed.

The effect of crowding was determined in the remaining two partial enclosures. In one of these, forty limpets were placed. This was called the high density treatment. In the other, twenty empty limpet shells were glued and then twenty limpets were placed (shell treatment). By comparing each of these treatments with the control, a measure of the effect of crowding on migration could be determined. In addition, the high density and shell treatments could be compared with each other. If the number remaining in the shell treatment were greater than the number remaining in the high density

treatment, this would indicate that stationary limpets do not cause as much disturbance to other limpets as limpets which move about.

Four replicates were obtained; one from each set of enclosures on two successive days. Completely different limpets were used on the second trial. The results are shown in Table XV. There was little difference between the control mean and the means of the low food and high density treatments, but the shell treatment mean was higher than the control. Limpets used the shells as shelter sites, while in the other treatments they sheltered along the sides of the enclosures or moved out.

Because of the high variability among replicates of single treatments, it was not shown that low food or crowding cause disturbances resulting in high emigration from the enclosures. The experiment could not be continued because of lack of time and because of problems with the enclosures. It could be concluded, however, that limpets in search of a place to shelter stop when they encounter a stationary limpet. This may partly explain how large clumps of limpets form in an area.

When food availability is suddenly reduced around a clump of limpets, it appears that the proportion of limpets which home to the clump decreases. This result is in agreement with that predicted by the hypothesis.

Experiments that examined the effect of crowding on homing were inconclusive. An interesting result incidental to the experiments was that limpets respond to artificial disturbances, such as removal and replacement or being splashed, by moving away from their home site. This response is similar to that predicted from the hypothesis when deterioration of local environmental conditions occurs.

Conclusion

An hypothesis describing local regulation of density by means of changes

TABLE XV. The number of limpets that remained in each of four treatment groups after one day. (See text for explanation.) The number remaining in the high density treatment has been divided by 2, so that results can be directly compared. The first two replicates were obtained from July 23 to 24; the second two from July 24 to 25, 1970.

Replicate	Treatment			
	Control	Low food	High density	Shell
1	17	12	15.5	18
2	15	8	7.5	14
3	11	15	13.0	13
4	4	12	7.0	15
Mean	11.75	11.75	10.75	15.0

in homing behaviour was examined. The hypothesis states that homing occurs as a response to favourable local conditions, and that non-homing occurs as a response to unfavourable conditions. It further states that thresholds of tolerance vary among limpets, so at a given density both types of behaviour are found.

Homing behaviour was observed in individual A. digitalis. Limpets were observed to home to both home sites and home clumps. There appeared to be two behavioural types, homing and non-homing, as predicted from the hypothesis.

When density was increased in an enclosed area, the proportion of non-homing limpets did not increase. This result contradicted the response predicted from the hypothesis. When local conditions were made unfavourable by artificial means, however, apparent decreases in the proportion of homing limpets were observed.

It is not possible to state conclusively whether changes in homing behaviour occur as a result of changes in local conditions in the limpets' environment. Further work should be carried out to test this hypothesis.

STUDIES OF SEASONAL MIGRATION BEHAVIOUR

Introduction

Frank (1965) reported that A. digitalis tend to migrate upward in fall and winter. He observed that migration occurred at all levels of the shore where the limpets were found, and that in winter limpets could be found in areas where they were not present during the summer. A downward migration, which was not as great as the upward migration, occurred in spring. Frank suggests that the differential distribution of size classes, with larger limpets at the upper end of the shore and smaller ones lower, is caused by the upward migration in fall and winter.

A similar pattern of distribution was observed by Lewis (1954) in the ecologically similar limpet, Patella vulgata. Lewis also reported vertical migration in the colder months and a lesser downward migration in spring. Both authors noted that a combination of hot, dry weather, neap tides and calm seas produced long periods of desiccation at the upper regions of the shore. Lewis found dead and dying limpets at the upper levels of his study area in June, and Frank observed a mouse removing and eating limpets which were weakened by desiccation.

Although Frank recognized the importance of the upward migration in terms of the vertical distribution of A. digitalis, he did not investigate its potential importance in regulation of numbers. If the upward migration is density dependent, so that at low densities only a small proportion of limpets migrate and at higher densities a higher proportion migrate, mortality during summer is also density dependent. After a large upward migration in fall and winter, many limpets would be found in the uppermost zone of the shore, in which mortality is reported to be highest in summer (Frank, 1965). A smaller proportion of limpets would be exposed to such mortality if the upward migration were small. In this way migration, combined with subsequent summer mortality, could have a regulatory effect on the numbers in local populations

of limpets.

This hypothesis was tested in three stages at Botanical Beach. Marked limpets were observed during the fall, winter and spring to determine whether vertical migration occurred during those periods. The possible relation between density and the proportion of limpets that migrated upward was examined experimentally. Finally, mortality was studied during the summer of 1970 to determine whether it was highest at the upper levels of the shore.

Occurrence of seasonal migration

Two large samples of limpets, which had been individually marked for the study of homing behaviour, demonstrated an upward migration during the period September 1, 1969, to February 16, 1970. Figures 4 and 5 show the number of marked limpets remaining on the reference areas and the number seen outside the reference areas during this time. The decline in number inside the areas during late fall coincides with an increase in number seen outside the areas. The upward tendency of this migration is seen in Figures 6 and 7, in which the number of animals which migrated in each direction is plotted for two groups.

The spring migration involved fewer limpets. The downward tendency of the migration from February 16 to June 5, 1970, can be seen in Figure 8 in one group of marked limpets. (Fewer data were collected during the spring migration because the subsequent movements of animals that had migrated from reference areas could not be followed accurately.) No limpet that migrated from its original position was observed to return to that position. These observations of seasonal migrations are consistent with those of Frank (1965).

Limpets that immigrated in winter to areas in which limpets had previously been marked appeared to be smaller than the marked limpets. This was substantiated in one area by comparing the mean lengths of the two groups

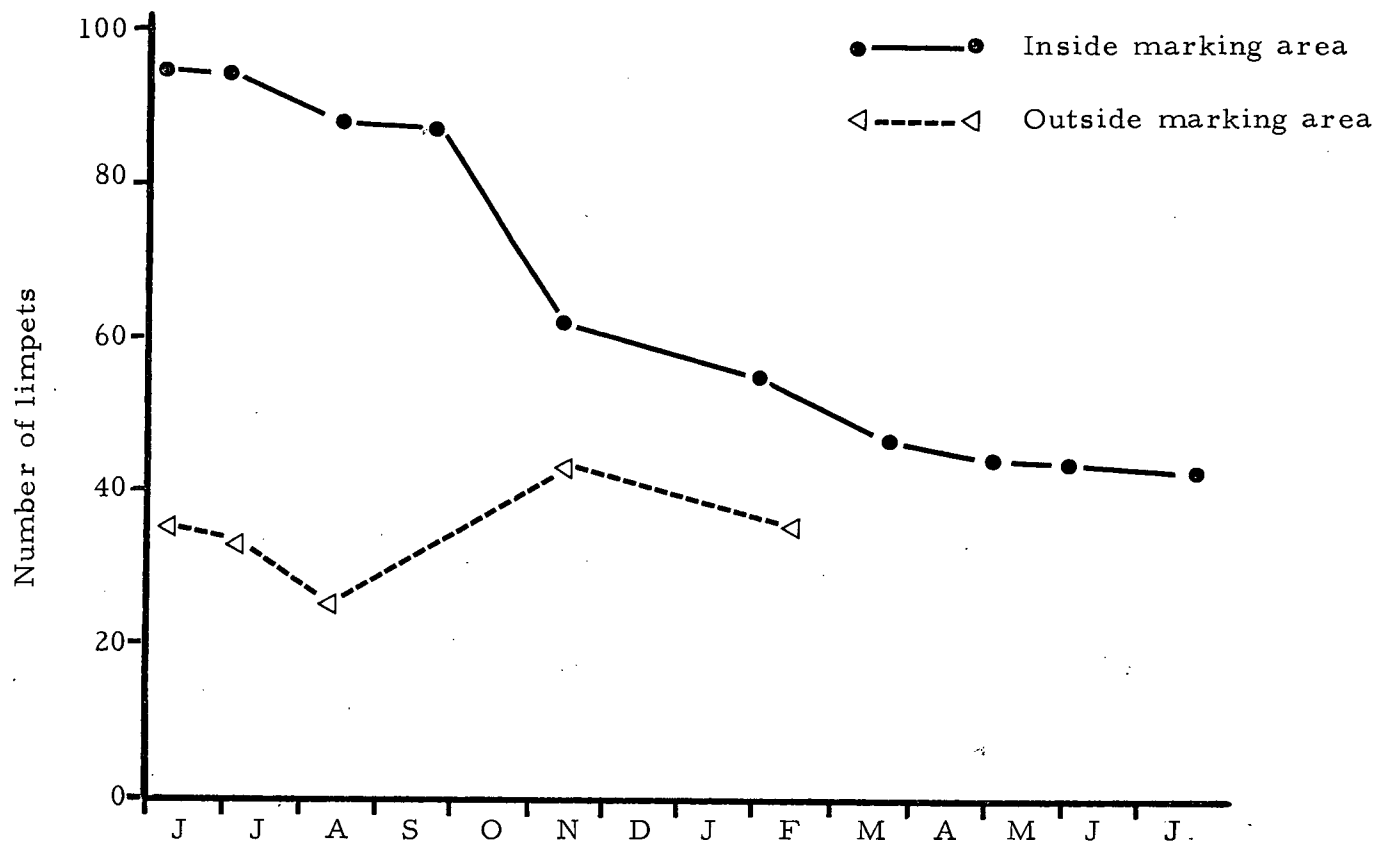


Figure 4. The numbers of limpets seen inside and outside the area where they were marked, from July, 1969, to July, 1970.

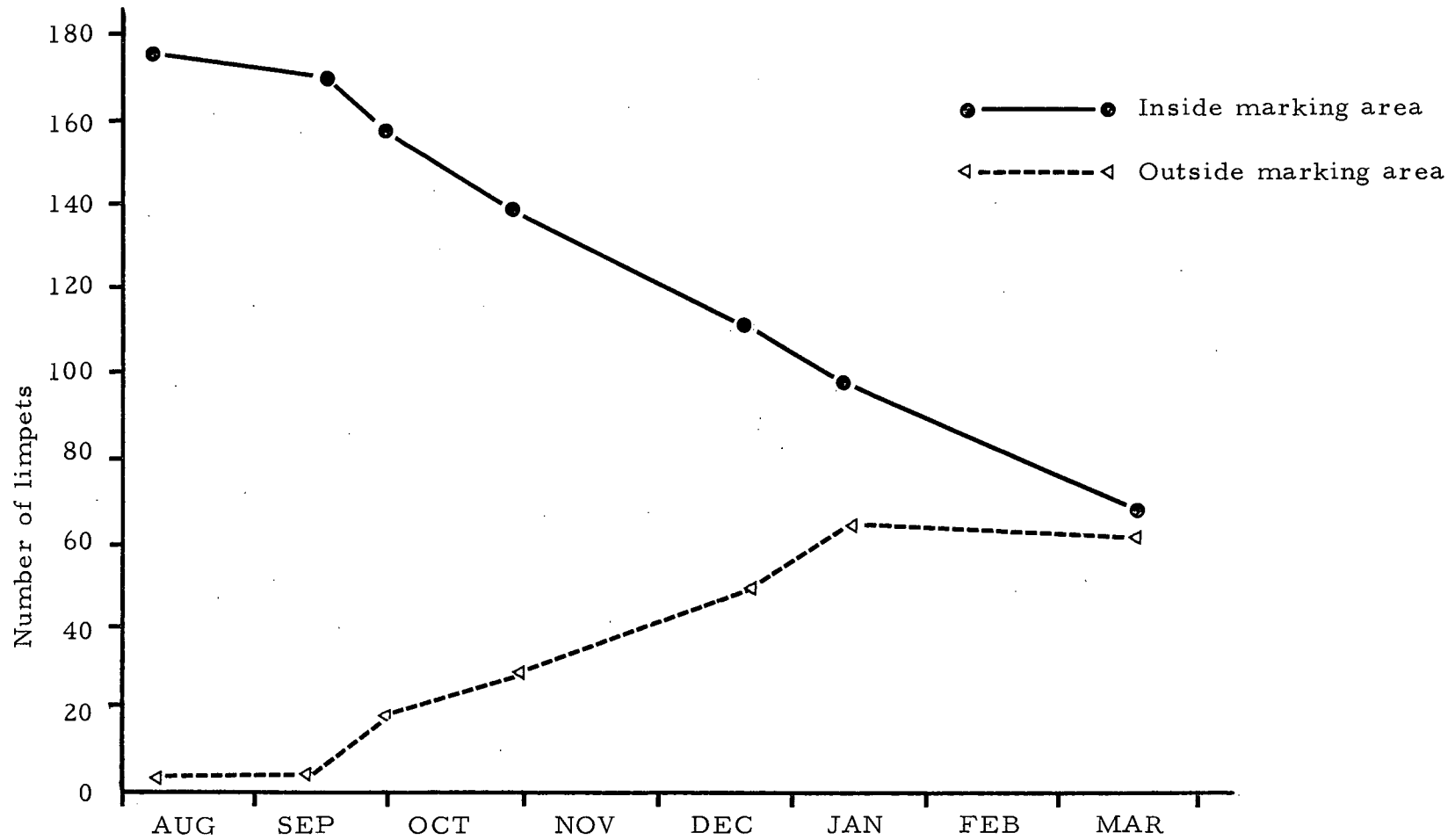


Figure 5. The number of limpets seen inside and outside the area where they were marked, from August, 1969, to March, 1970.

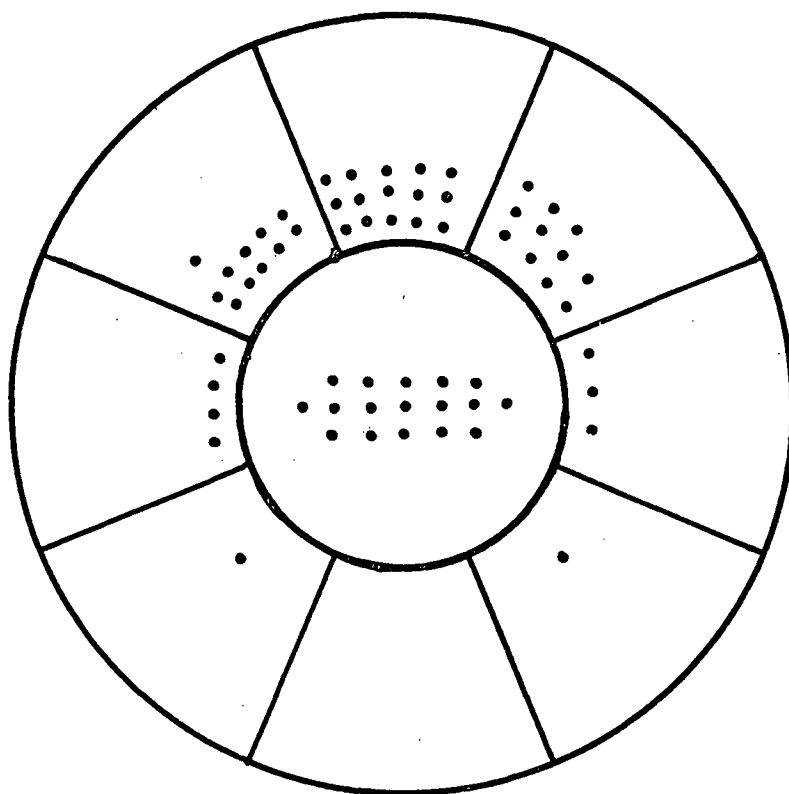


Figure 6. The number of limpets which migrated in each direction during the period from September 1, 1969, to February 16, 1970. Dots in the centre represent limpets that did not migrate; dots in the upper part of the circle represent limpets that migrated upward; and so on.

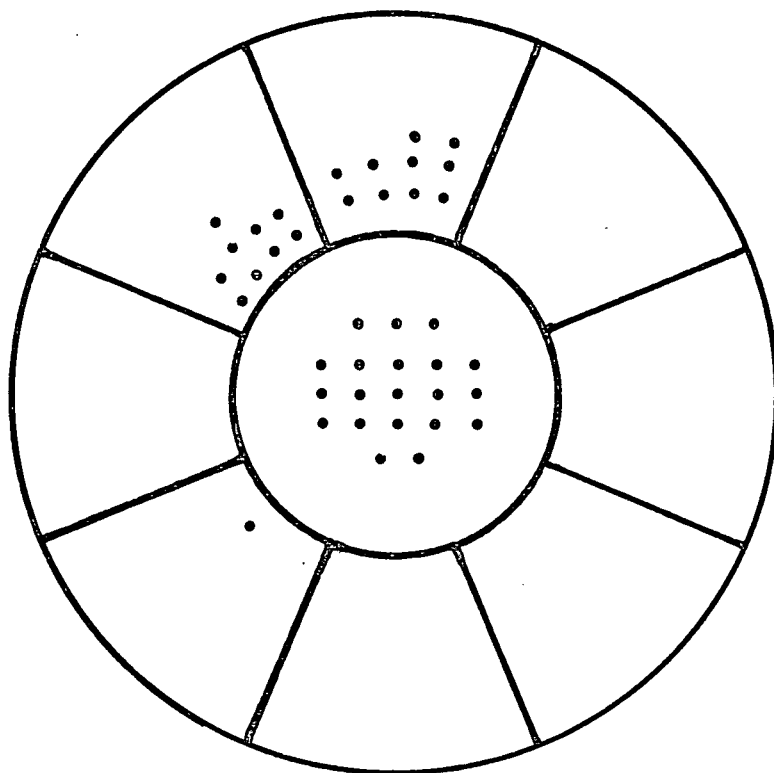


Figure 7. The number of limpets which migrated in each direction during the period September 1, 1969, to February 16, 1970.

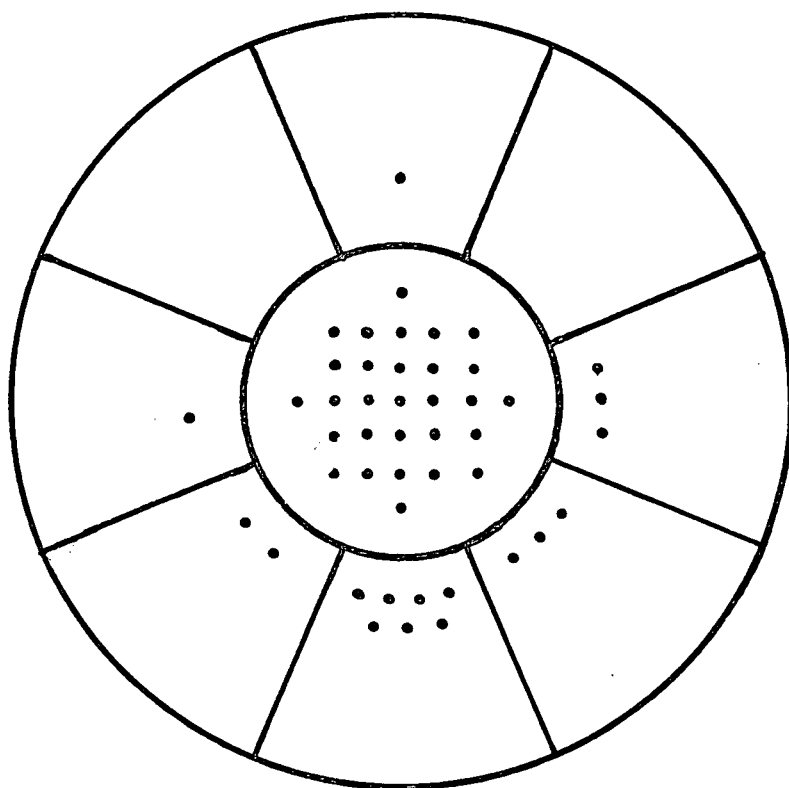


Figure 8. The number of limpets which migrated in each direction during the period February 16 to June 5, 1970.

(Table XVI). The mean length of the immigrant limpets was significantly less than that of limpets previously marked. This is what one would expect from the facts that limpets tend to be smaller as one goes down the shore (Figure 3), and that the winter migration tends to be upward in direction (Figures 6 and 7).

Relation of upward migration with density

The hypothesis states that the proportion of limpets that migrate upward increases with density. An experiment was designed to test this statement. In June, 1970, 160 limpets found on and near a low metamorphic concretion, which was 1.5m across and projected 0.5m from a flat sandstone shelf, were marked individually. Two wedge-shaped areas containing most of the limpets were then partially enclosed by means of plastic mesh fences. The fences, from the top of the concretion 1.5m onto the sandstone shelf, prevented limpets from migrating laterally. Within each area, holes 10cm apart were drilled to indicate a series of horizontal strips, which were numbered and used to describe the positions of the limpets.

Limpets in one wedge-shaped area were designated as the control group. The approximately equal number of marked limpets in the other area was used as a test group. The number of limpets in the experimental area was increased by the addition of limpets taken from elsewhere. Density was increased gradually over the summer to determine whether any immediate effect on migration could be observed. The positions of all limpets were recorded at intervals of approximately two weeks. In addition, the marked limpets were measured on July 5 and November 22, 1969.

Figure 9 shows the number of marked animals remaining in each area from June through December, 1969. There was little change until October, when the number in the experimental group began to decline sharply. The number in the control group declined by a comparatively small amount. The number of limpets remaining within each strip in the control area is shown in Figure 10, and the number in each strip in the experimental area is shown in

TABLE XVI. A comparison between the mean length of limpets that immigrated to an area during fall and winter, and the mean length of limpets which remained on the same area from the previous summer (residents). Lengths were measured on February 16, 1970.

	Residents	Immigrants
Number	50	60
Mean length (cm)	1.799	1.660
Variance of length	0.103	0.058
F ratio of variance	1.79 n.s.	
Student's 't'	2.59*	

*Significant at $\alpha = .05$; d.f. = 108.

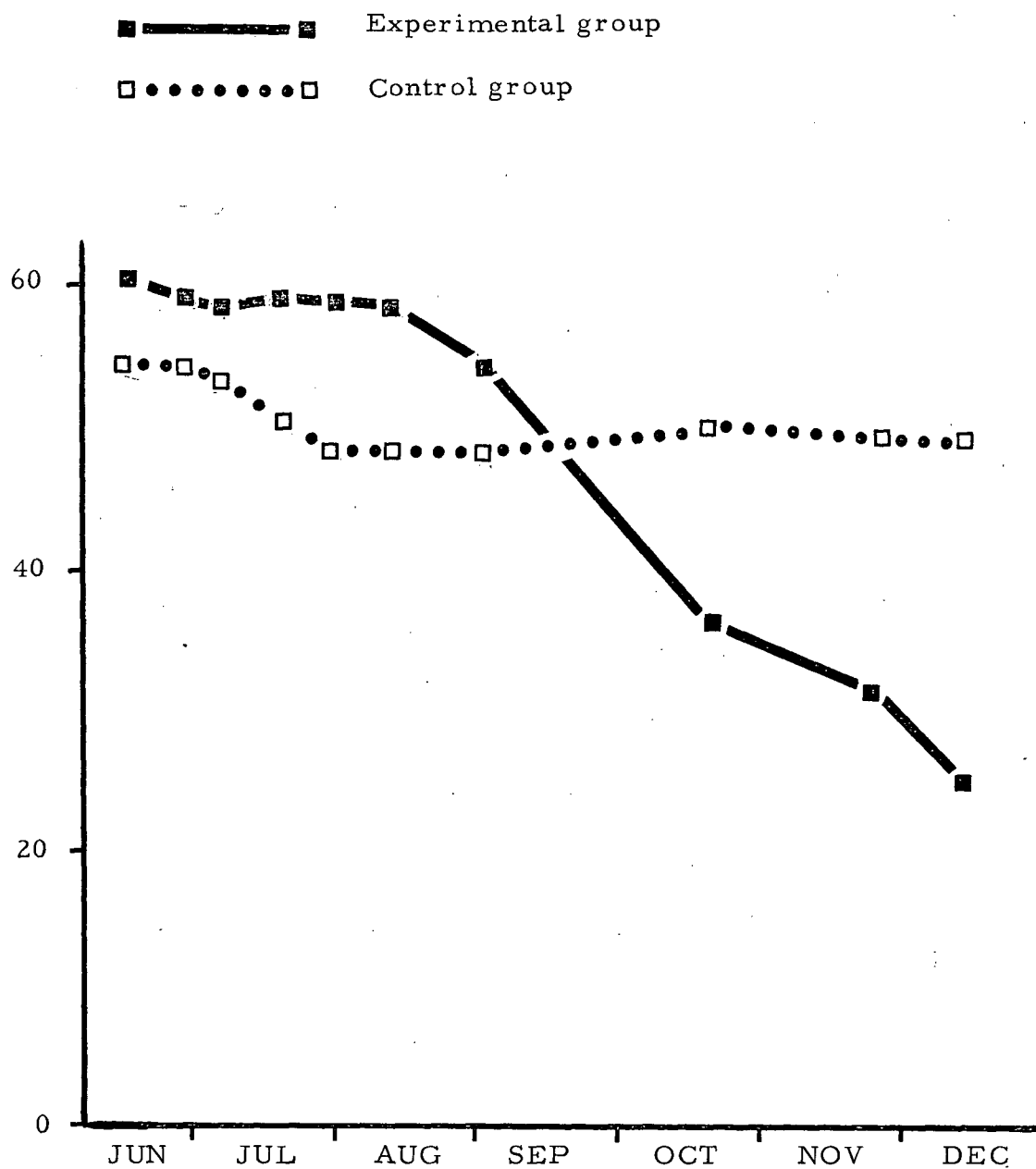


Figure 9. Numbers of limpets in the experimental and control groups remaining in the partial enclosures over time. (See text for explanation.)

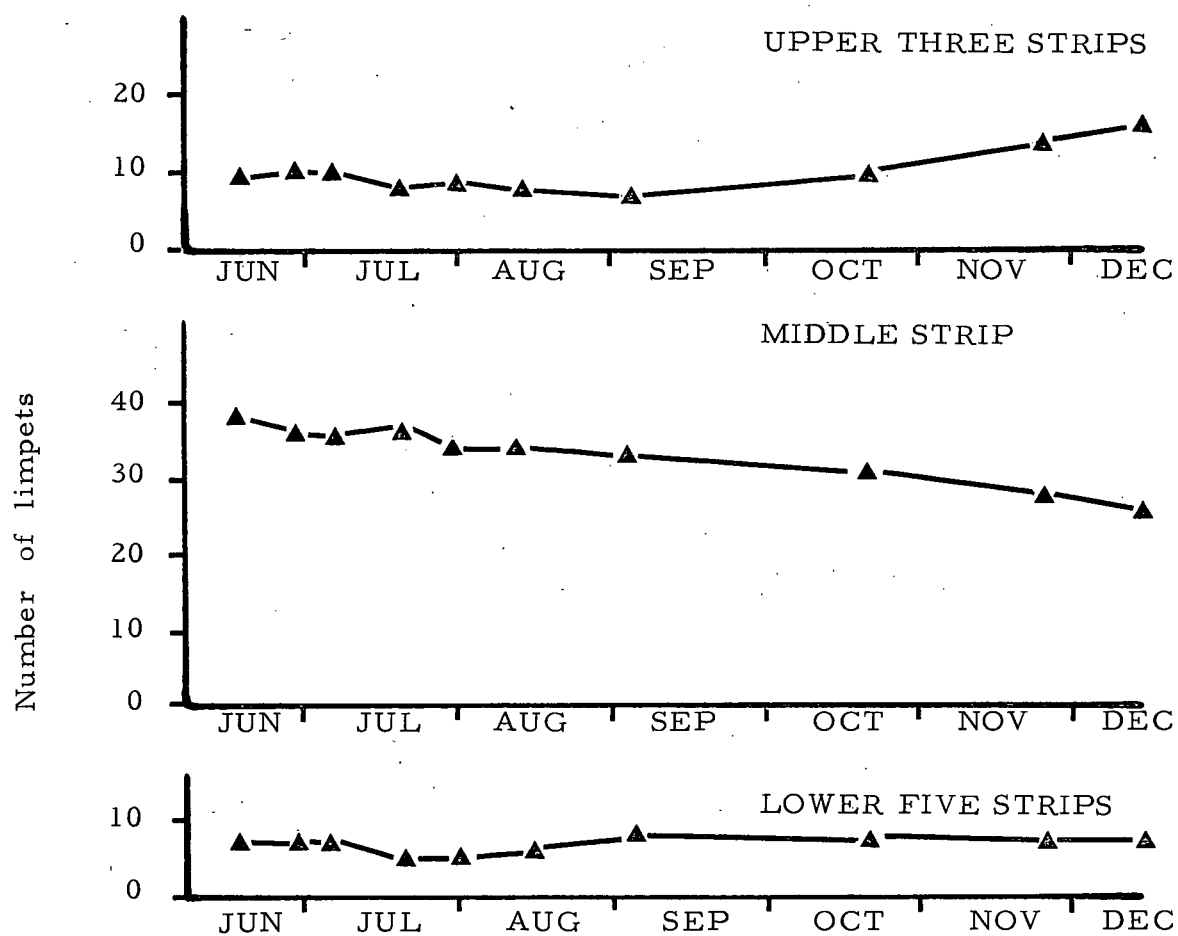


Figure 10. The number of limpets remaining in each part of the control area during the course of the experiment. (See text for explanation.)

Figure 11. The decline was greatest in those strips which had the highest number of limpets during the summer.

It was not possible to determine conclusively whether the change in the experimental area was a product of emigration, mortality or both. A search was made in December within a radius of 5m from the concretion, but only five limpets from the experimental area and one from the control were found. This indicates that there may have been a higher rate of emigration in the experimental group than in the control. The five limpets found do not by themselves account for the change in the experimental area, but observations elsewhere suggest that A. digitalis are capable of moving much more than 5m during several months. It was concluded that emigration was responsible for the decline of marked limpets in the experimental group.

Growth rates of marked limpets in the two areas were compared (Table XVII). Limpets in the control group showed significantly higher growth during the period July 5 to December 10 than those in the experimental group. Higher density in the experimental area appeared to be responsible for the difference in growth rates.

Results from the previous experiment indicated that the proportion of limpets that migrated in fall was greater in the area with higher density. Further experiments were planned in which limpets were to be marked in similar areas and densities subsequently manipulated by addition or removal of animals. It proved to be impossible to mark limpets during the fall and winter (see Experimental Methods), so these experiments could not be carried out.

Circumstantial evidence was obtained, however, from six groups of limpets that had previously been marked in widely different locations on the beach for different purposes. Densities in these areas increased naturally during the fall and winter as a result of immigration from the adjoining regions. The amount by which density increased at each location was calculated by

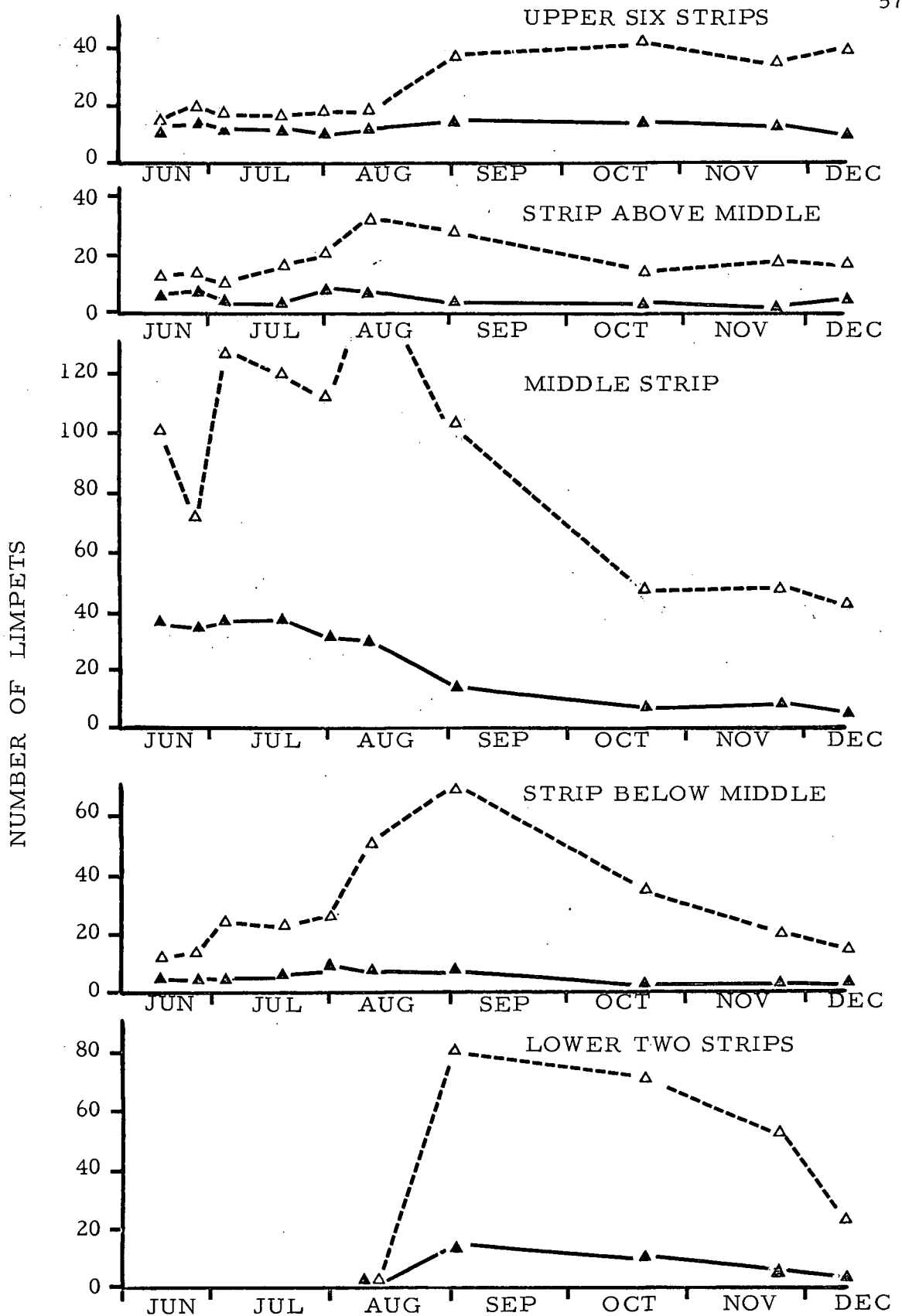


Figure 11. The number of limpets remaining in each part of the experimental area during the course of the experiment. (See text for explanation.)

TABLE XVII. A comparison between the growth of limpets in the experimental and control groups of an experiment designed to test the migration responses of limpets to high density. The density of the experimental group was made high by adding limpets. In this comparison the regressions of attained length on initial length for each group are compared. Initial length was determined on July 5 and attained length on November 22, 1969.

	Group	
	Experimental	Control
Sample size	31	42
Regression equation	$Y = 0.28 + 0.85X$	$Y = 0.42 + 0.80X$
F from comparison of slopes	0.40 n.s.	
F from comparison of adjacent means ($X = 1.74$)	7.45*	

* Significant at $\alpha = .01$.

dividing the total number of animals in February, 1970, by the total number of animals in August, 1969. The percentage of marked limpets that did not migrate from each location during winter was compared with the degree of density increase (Table XVIII, Figure 12). The percentage that did not migrate was used rather than the percentage that did migrate because searches were much less effective at finding the latter. It was assumed that mortality in migratory and non-migratory groups was equal, so that each group was the complement of the other.

The correlation between degree of density increase and the percentage of limpets that did not migrate was $r = -.573$. The inverse correlation indicates that a small proportion of limpets in areas of low density increase migrated during the fall. The correlation coefficient was not significant, but it should be noted that a limited range of density increases was observed in this study, and that the six areas observed varied widely in such factors as tidal height, exposure, original density, and mean limpet length.

It was concluded that upward migration in fall and winter is density dependent. A smaller proportion of limpets migrated from areas of low density than from areas of high density.

Mortality

According to the hypothesis which was being tested, mortality during the summer is highest at the upper levels of the shore. The effect of summer mortality is dependent upon the proportion of limpets that migrate to the upper parts of the shore during the preceding fall and winter. If a high proportion of limpets migrate, then the proportion of limpets that die during the summer is higher than if only a small proportion of limpets migrate.

This component of the hypothesis was tested by measuring survival of limpets at different heights on one part of the shore during the summer of 1970. Three groups of limpets, each containing 75 individuals of varying size,

TABLE XVIII. Comparison between density change and the percentage of limpets that did not migrate during the period August 11, 1969 through February 16, 1970. Change in density was calculated by dividing the total number of limpets present in February by the total number in August. Six different locations on the beach are compared. A correlation coefficient between percent remaining and density change is calculated.

Area	August, 1969		February, 1970		Density change	Percentage remaining
	number marked limpets	total number limpets	number marked limpets	total number limpets		
1	90	90	52	152	1.69	57.78
2	199	199	100	218	1.10	50.25
3	44	56	20	420	7.50	45.45
4	42	82	26	105	1.28	61.91
5	24	26	20	37	1.42	83.33
6	34	41	26	38	0.93	76.49

For the correlation between density change and percentage remaining, the value of $r = -.573$.

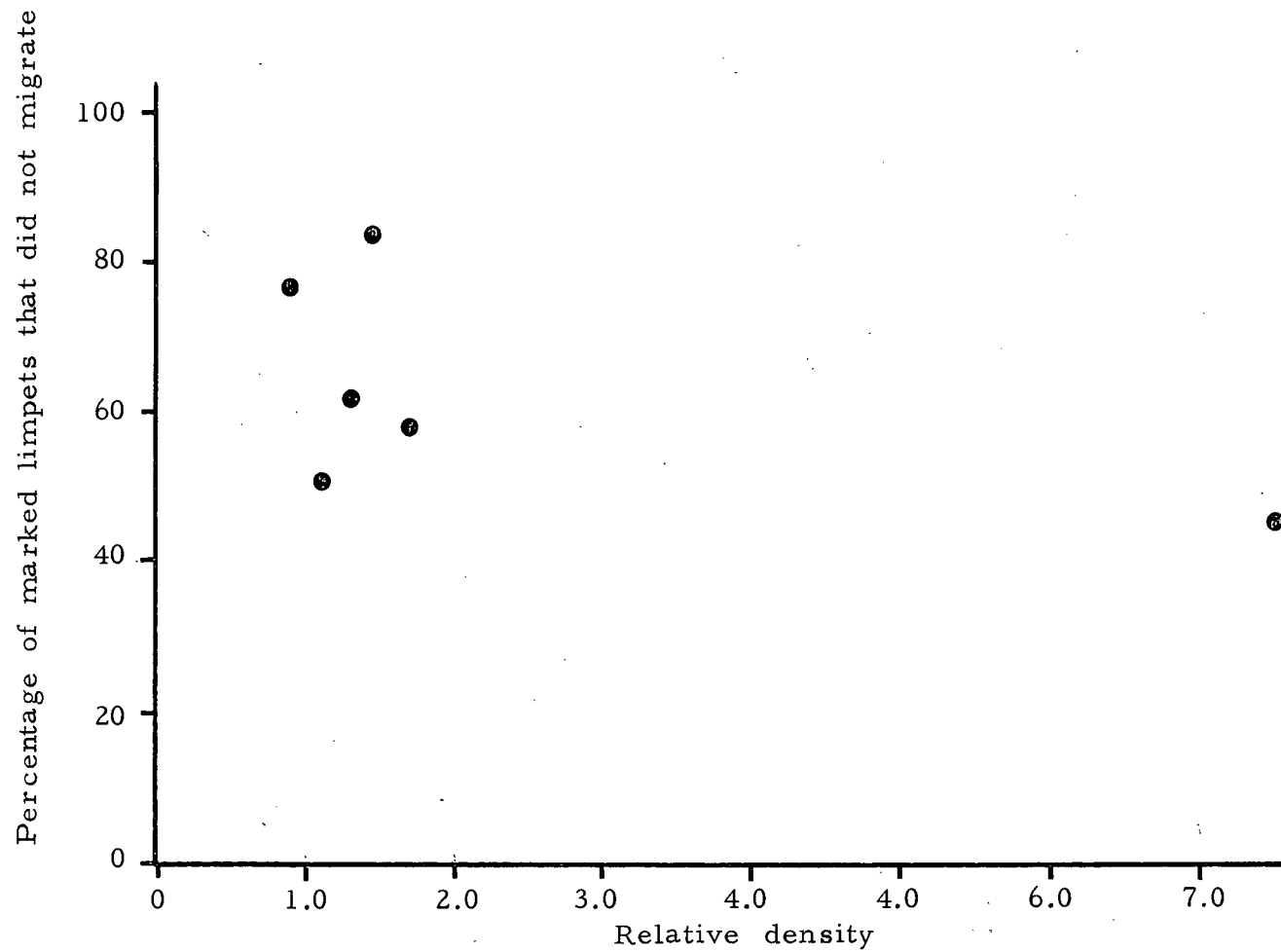


Figure 12. The relation between relative density and the percentage of marked limpets that did not migrate from the area during fall and winter. (See text for explanation.)

were marked individually and measured on February 1, 1970. The groups were then released at three different tidal heights. It was hoped that survival of each group could be followed through the summer, and that the relative mortality of the different size classes of individuals within each group could be determined. Mortality in the three groups during the night following release varied from 21 per cent to 53 per cent. By March 31, only 36 of the original 225 animals could be found. These were so widely dispersed from the points of release that the experiment was abandoned. The high mortality immediately after release was probably caused by limpets being washed away by the heavy surf present, but the cause of the later mortality is not known.

A second attempt was made to measure mortality at different tidal levels in May, 1970. Six permanent squares were marked on one part of the shore at different tidal heights. The number of limpets within each square was recorded several times during the summer. Because the density was higher at the lower part of the shore, the uppermost square (square 1) was made largest, and the squares decreased progressively in size toward the lowest square (square 6). The measured tidal height, original number of limpets and area of each square are shown in Table XIX.

The number of limpets found in each of the marked squares during the summer are seen in Figures 13 and 14. Declines occurred in squares 1, 2 and 3 (the upper three squares), and square 6 (the lowermost square); while squares 4 and 5 showed increases in numbers during the summer. In square 6 only, limpets smaller than 0.5cm were found; these were counted separately and are presented separately in Figure 14. The decline that occurred in the lowermost square appeared confined to the smaller limpets.

To check whether migration from the squares occurred, some limpets were marked in situ on May 1. All the limpets in square 1 were marked, and 50 were marked in each of squares 2, 3, and 4. Limpets in squares 5 and 6 could not be marked because their shells did not dry. By July 26, no marked

TABLE XIX. The original number of limpets, tidal height and area of six marked squares, in which censuses were carried out during the summer of 1970 to determine mortality rates at different tidal heights.

Square number	Tidal height (feet)	Area (m ²)	Original number of limpets
1	14.73	2.21	35
2	14.58	0.83	279
3	12.04	0.85	410
4	10.93	0.62	327
5	10.40	0.45	252
6	9.35	0.21	450

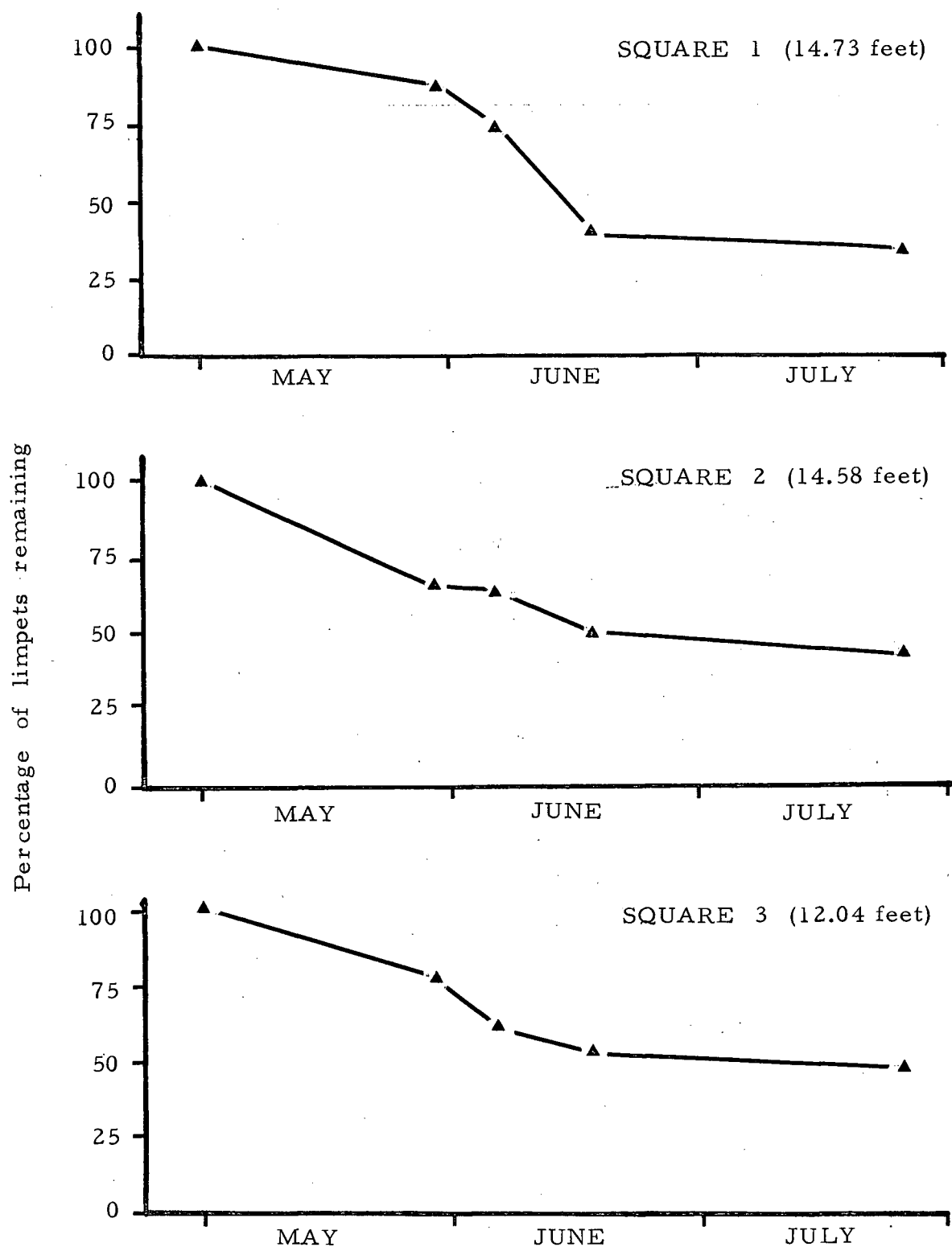


Figure 13. The percentage of limpets found in the upper three census squares over the summer. Tidal heights are given in parentheses for each square.

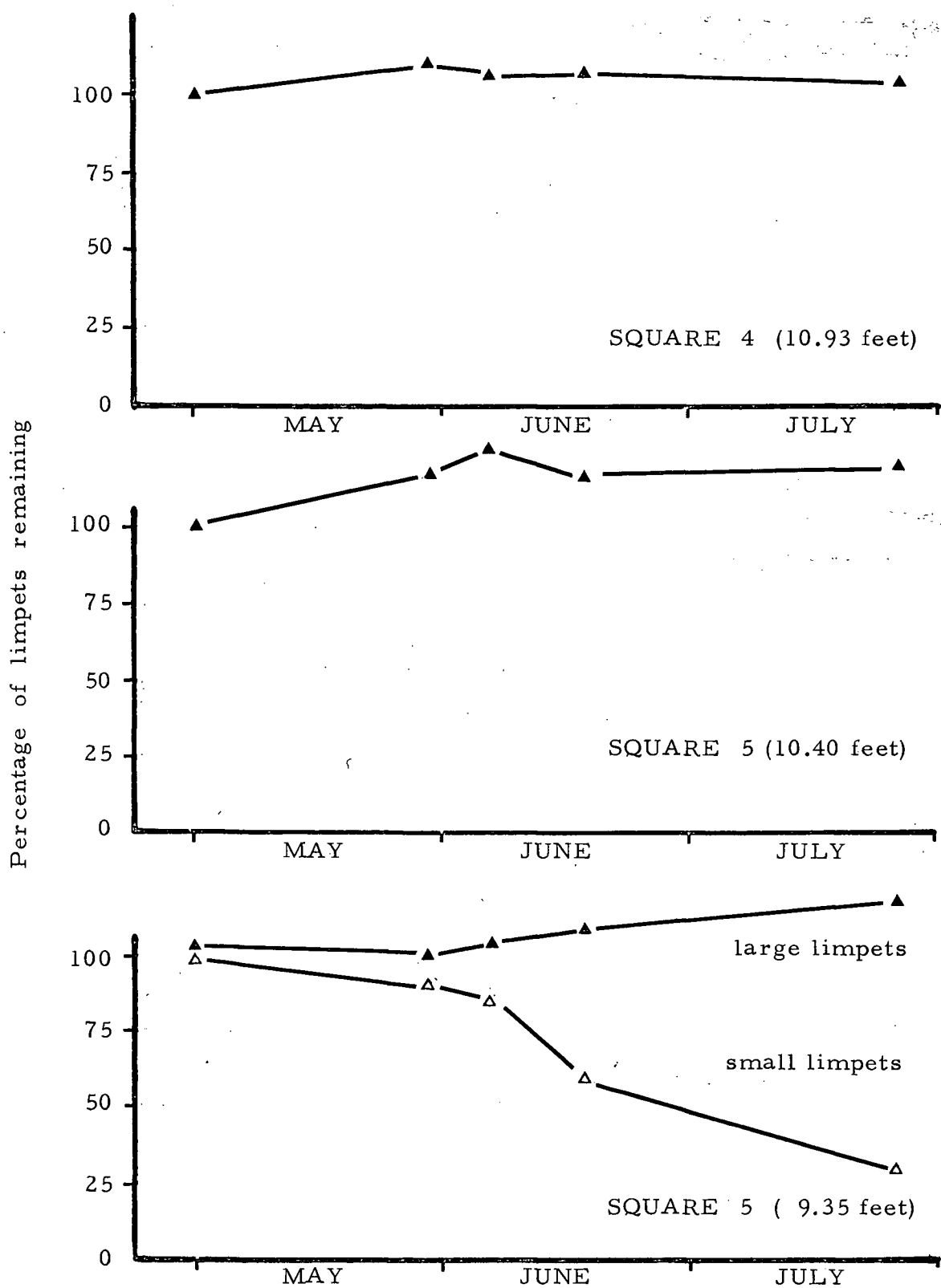


Figure 14. The percentage of limpets remaining in the three lower census squares during the summer. Tidal heights are given in parentheses for each square.

limpets had been found outside squares 1 and 2; two were found outside square 3; and nine were found outside square 4. Thus, declines in number in the upper three squares did not seem to be the result of migration from the squares. It was concluded that mortality was responsible.

Conditions observed during the summers of 1969 and 1970 suggested that desiccation may be a factor contributing to summer mortality. In July, 1969, after a week of hot, dry weather and neap tides, limpets at the upper regions of the shore were examined to determine whether any effects of this long dry period could be observed. The limpets were given a sharp knock on the side of the shell, which does not usually dislodge limpets. Those limpets which were dislodged were placed in cold sea water and observed after 15 minutes. Of 75 limpets thus tested 54 were not dislodged from the rock, 18 came away easily from the rock but revived in sea water, and the remaining three were dead. All 21 limpets that were dislodged appeared shrunken and dry, indicating the effect of desiccation.

In summer of 1970, the same test was carried out several times during periods of hot weather or neap tides. No limpets were easily dislodged from the rock. Some were removed with a knife, and these appeared normally moist. When the beach was under observation in 1970, potentially long periods of desiccation were interrupted by surf or rainfall. It is possible that periods of desiccation occurred between visits to the beach.

Groups of shells, containing bits of limpet meat, were sometimes found below the high tide mark. This indicated that they could have been eaten by terrestrial or aerial predators since the previous high tide. Although several possible predators, including mink, mice, oyster-catchers and other birds, were seen on the intertidal it was not possible to observe the prey of these animals. Crows and surf birds were watched carefully; these were not seen taking limpets.

It was concluded that mortality was most severe on the upper part of

the shore during the summer and decreased progressively at lower regions, except that limpets smaller than 0.5cm did not survive as well at the lower-most level as larger limpets. The observation of high mortality at the upper levels of the shore agrees with those reported by Frank (1965) and Lewis (1954). This component of the hypothesis was concluded to be valid.

Although it was not necessary in testing the hypothesis to demonstrate the cause of summer mortality, it appears that desiccation is partly responsible. Predation may also be partly responsible. It is not possible to state, however, the major cause of summer mortality. Experiments in which limpets are protected from predators by cages could be performed to measure predation.

Conclusion

An hypothesis that describes regulation of local population density by means of vertical migration and subsequent mortality was examined. The hypothesis states that the proportion of limpets that migrate upward in fall and winter is dependent on density. It further states that mortality during summer, which is highest on the uppermost levels of the shore and less severe at lower levels, is thus density dependent.

An upward migration was observed in fall and winter, and a lesser downward migration occurred in spring. The proportion of limpets that migrated upward was higher in areas of higher density. Mortality during summer was shown to be highest at the upper part of the shore, decreasing at lower levels of the shore. The major cause of summer mortality was not demonstrated.

The hypothesis which was examined has thus not been shown to be valid. It appears that seasonal migration interacts with density and mortality in such a way that local population density might be regulated.

RELATION OF UPWARD MIGRATION WITH GROWTH

In the previous section it was demonstrated that upward migration occurs in fall and winter, followed by a lesser downward migration in spring. There is thus a net upward movement of limpets between successive summers. Mortality during the summer, however, was shown to be highest on the higher regions of the shore, and less severe at lower levels. It was suggested that upward migration of limpets may tend to regulate the number of limpets in a local population.

Because a limpet that migrates upward is exposed to greater mortality in summer than one that does not migrate, one might expect the behaviour to be selected against, and to disappear from the species. It therefore becomes necessary to explain why the behaviour is retained. Wynne-Edwards (1962) suggests that some types of behaviour, which are disadvantageous to the individual but beneficial to the species, may be selected for; and he termed such selection "group selection". It might be argued that group selection has caused the retention of upward migration behaviour. Because such behaviour prevents resources of limpets from being over-exploited, it is therefore beneficial to the species. Such an argument, however, would create a new problem: that of explaining the mechanism by which such selection might operate.

A better approach was thought to be that of explaining migration behaviour in terms of individual selection. Fritchman (1961) reports that A. digitalis breed in April and May, which is between the times of upward migration and summer mortality. It might be possible for a limpet that migrates upward and later dies to leave more offspring than a limpet that does not migrate and does not die. This could occur if upward migration allowed limpets access to better conditions for growth and fecundity.

The hypothesis that growth, and hence fecundity, is higher in those limpets that migrate was tested by comparing growth rates of migratory and non-migratory limpets. Two groups were marked and measured in July, 1969.

Each limpet was measured again in February, 1970, and position with respect to its original position was noted. In each group the growth rate between migratory and non-migratory individuals was compared.

There was no significant difference between the mean initial lengths of migratory and non-migratory limpets in each group (Table XX). In each group the migratory limpets showed a higher mean increment of growth than the non-migratory ones (Table XXI). Thus the growth rate was higher in limpets that migrated during fall and winter from the point where they were marked.

This finding could be explained in one of two ways. First, although the biomass per unit area was not measured at different tidal heights, it has been shown that density decreases with increasing tidal height (Figure 2). Higher growth rates in migratory limpets might simply result from the lower density encountered by the migratory limpets.

Second, it has also been shown that limpets are progressively larger on higher levels of the shore (Figure 3). Stimson (1970) found that the large limpet Lottia gigantea defends territories against smaller species, such as Acmaea. Within Lottia territories a mat of algae could be distinguished, while algae on the rock outside the territories was very thin. Stimson suggested that Lottia require high algal concentrations in order to feed, and maintain territories to prevent smaller limpets from grazing the algae close down to the rock. If small A. digitalis graze very close to the rock, while larger ones require a thicker algal mat, then higher growth of migratory limpets might be due to decreased competition with smaller limpets at higher shore levels. It has been demonstrated (Table XVI) that those limpets that immigrate to an area during fall and winter are smaller than limpets already present. Upward migration of the larger limpets from that area may reduce their competition with the smaller limpets, hence allowing better growth.

These two explanations of higher growth in migratory limpets were

TABLE XX. A comparison between the mean initial lengths of migratory and non-migratory limpets. Lengths were determined on July 1, 1969. The comparison is made in two separate groups of marked limpets.

GROUP 1		
	Non-migratory	Migratory
Number	42	10
Mean length (cm)	1.768	1.808
Variance	0.0460	0.0329
F ratio of variance	1.399 n.s.	
Value of student's 't'	0.51 n.s.	
GROUP 2		
	Non-migratory	Migratory
Number	17	13
Mean length (cm)	1.422	1.498
Variance	0.171	0.0308
F ratio of variance	1.80 n.s.	
Value of student's 't'	1.36 n.s.	

TABLE XXI. A comparison between the mean growth increment of migratory and non-migratory limpets. The initial lengths were determined July 1, 1969; subsequent lengths on February 16, 1970. The comparison is made in the same two groups of marked limpets as Table XX.

GROUP 1		
	Non-migratory	Migratory
Mean growth increment (cm)	0.0635	0.1185
Variance of increment	0.00365	-.00221
F ratio of variances	1.65 n.s.	
Value of student's 't'	2.71*	

* Significant at $\alpha = 0.05$; d.f. = 28.

GROUP 2		
	Non-migratory	Migratory
Mean growth increment (cm)	0.0895	0.0250
Variance	0.00562	0.00465
F ratio of variance	1.65 n.s.	
Value of student's 't'	4.96*	

* Significant at $\alpha = 0.05$; d.f. = 50.

examined in an experiment in February, 1970. In this experiment, growth was measured in three groups of limpets contained within similar enclosures. A control group contained a given biomass of limpets. A second group was composed of limpets similar in size to the control, but contained double the control biomass. The third group contained double the control biomass, but was composed partly of limpets the same size as the control, and partly smaller limpets. The effect of density on growth rate could be examined by comparing the growth rates of the first and second groups. The effect on growth rate of competition with smaller limpets could be examined by comparing the second and third groups.

In February, 1970, three adjoining plots, each 65cm square, were constructed with plastic mesh fence. The natural biomass of limpets within the plots was determined by removing and measuring all the limpets found in the plots. The length of each limpet was converted to body dry weight by means of a regression developed for the purpose from 107 individuals. The relation between length and dry body weight was found to be

$$\ln \text{ dry weight (g)} = -6.638 + 2.05 \text{ length (cm)}.$$

The natural biomass was found to be 6.87 grams per plot.

Limpets from elsewhere, 2.00 to 2.50cm in length, were marked and measured with Vernier calipers. These were larger than the limpets found in the plots originally, and were added to the plots to form three treatments. The control treatment consisted of enough marked limpets to equal the natural plot biomass. The second, called a high density treatment, consisted of enough marked limpets to equal twice the natural plot biomass. The third, called a mixed high density treatment, consisted of enough marked limpets to equal the natural plot biomass plus an equal biomass of unmarked smaller limpets (1.25 to 1.75cm in length).

The original density was maintained in each experiment for five months,

from February 19 through July 24, 1970, despite some emigration of marked animals. Limpets that emigrated were replaced by limpets of similar size. The marked limpets were removed on July 24 and measured with Vernier calipers. The mean growth increments of limpets in the three treatments were compared (Table XXII). The mean growth increment of limpets in the high density plot was significantly lower than the control, indicating that high density resulted in significantly reduced growth. The mean increments of the high density plot and the mixed high density plot were not significantly different, indicating that competition for food with smaller limpets had little effect on the growth rate.

It appears that better growth in migratory limpets results from lower densities encountered on higher levels of the shore, not from reduced competition with smaller individuals.

Upward migration has been shown to be beneficial to individual limpets in terms of growth, and possibly fecundity. This may offset the disadvantage that upward migration results in increased exposure to mortality during the summer; because breeding occurs in spring, after the upward migration has occurred and before the summer mortality begins.

TABLE XXII. Comparisons among the mean growth increment of three groups of limpets. (See text for explanation.) The control group is compared with the high density group, and the high density group with the mixed high density group.

Treatment	Control	High density	Mixed high density
Number	25	30	26
Mean growth increment (cm)	.0048	-.0417	-.0677
Variance of increment	.00443	.00208	.00259
F ratio of variances	2.13 n.s.	1.24 n.s.	
Student's 't'	3.062*	1.997	

* Significant at $\alpha = .01$ (one-tailed); d.f. = 53.

DISCUSSION

Local populations of A. digitalis may be regulated by a mechanism involving seasonal migration behaviour. Because young limpets settle at the lower end of the vertical distribution of the species, density decreases with increasing tidal height, and a differential distribution of size classes is observed. Upward migration occurs in fall and winter, and this migration appears to be density dependent. If density were to increase at the lower part of the shore, as it might following a heavy settlement of young, migration from this area during fall and winter would tend to decrease density. Density on the next highest level would increase as a result of the migration from below, limpets already present in that area would migrate, and so on. Density at all levels might be adjusted to levels suitable for the habitat by means of density dependent migration.

Limpets at the upper end of the shore are exposed to high mortality in summer. The factor that limits the upper distribution of this species appears to be desiccation (Frank, 1965). Davies, (1969) has suggested that desiccation determines the upper limit of the similar limpet, Patella vulgata. Conditions which produce desiccation are most severe during summer; in winter some limpets migrate to the uppermost regions, in which they are exposed to high mortality during the following summer. Mortality is highest in summer on the highest regions of the shore, and decreases with decreasing tidal height. Because the rate at which limpets migrate to the upper regions is density dependent, mortality during summer is density dependent. This may help to regulate local populations.

Several factors may explain why upward migration occurs. It was found in this study that limpets settle below lower high water (LHW). Although it was not shown that LHW is a critical tide level (Doty, 1946) for small limpets, Davies (1969) has shown that smaller P. vulgata are less capable of withstanding desiccation than larger ones. Upward migration may

allow limpets, as they grow, to exploit habitats that were previously unsuitable.

Second, it has been shown that migratory limpets grow at a faster rate than non-migratory limpets. It is suggested that this results from lower densities encountered by migratory limpets on higher levels of the shore. Higher fecundity may accompany higher growth rate, which would mean that migration, although it results in higher mortality during the following summer, is selectively advantageous rather than disadvantageous. Breeding occurs in late spring, between the time of migration and growth and the time at which summer mortality occurs.

Seasonal migration thus appears to be an adaptation which results in the exploitation of more favourable habitat. It occurs during a time when conditions are most favourable for growth, and when little danger from desiccation is present. Although it has been demonstrated that seasonal migration behaviour may be capable of regulating local populations, further work must be carried out to determine whether such regulation actually occurs.

An hypothesis which described regulation by means of changes in homing behaviour was also examined in this study. Homing was observed in marked individuals, and both homing and non-homing behavioural types were found. It was predicted that the proportion of non-homing limpets would increase when density was increased within an enclosed area, but this did not occur. Limpets did, however, migrate away from home clumps when food availability was reduced directly. The evidence thus appears contradictory. Other evidence indicates that limpets are conservative in movement during summer, when desiccation is a potentially dangerous factor. This may explain why the proportion of homing limpets did not decrease. Further work is required to test this hypothesis and to determine why two types of behaviour are demonstrated.

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