The population dynamics of *Patella vulgata* and other limpets.

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Abstract

Useful generalisations can be made about limpet populations in much the same way as they can about individual animals. These generalisations can be expressed quantitatively and formed into a framework of population dynamics. In *Patella vulgata* populations a greater mean size (defined as the 50% accumulative weight size) indicates (i) a faster growth rate, (ii) a larger maximum size, (iii) an increased mortality rate, (iv) decreased mean and maximum life spans, (v) an increased settlement rate, (vi) an earlier and more rapid seasonal maturation of the gonad, (vii) a larger number of eggs produced per female and per unit weight, (viii) a lower radula ratio and a flatter shell at the mean size, than would be found in a population with a smaller mean size. The timing of sexual maturity and of sex change is independent of these correlated features of population dynamics. The correlations were established by the detailed study of four populations at Mount Batten, Plymouth; and verified by experimental alteration of the population structure and a survey of *Patella* on all types of shore.

The range of *Patella vulgata* in S.W. Britain is limited at the top of the shore principally by desiccation. The penetration of sheltered conditions is determined by interaction between the fucoids and the limpets. On exposed shores, the lower limit is determined by competition between *P. vulgata* and
P. aspera. There is no direct relationship between mean size and population density (expressed as weight per occupied area). P. vulgata is densest at the borders of the fucoid communities on sheltered shores, at the lowest levels on moderately exposed shores, and at the junction with the P. aspera populations on exposed shores. P. vulgata prevents fucoids from establishing communities on many rock surfaces, but where fucoids form dense stands, P. vulgata is not able to settle or feed. Physical factors do not directly limit the range of P. vulgata (except at the top of the shore), although they mediate the competition and interaction which decide the precise boundaries. Inside each P. vulgata population the growth rate is limited by intra-specific competition for the available food.
Acknowledgements

I would like to record my gratitude to Professor J.E. Smith and Professor J.E. Morton for advice and encouragement throughout this work.

I am also indebted to the Director, Dr. F.S. Russell, and staff of the Marine Biological Laboratory, Plymouth, for accommodation, advice and assistance during the field work.

This work was carried out during the tenure of a D.S.I.R. Research Studentship.
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SECTION I

A review of the literature on *Patella vulgata* together with an account of the aims of the present work.
1. Introduction

The main part of this first section of the thesis consists of a review of the literature on *Patella vulgata* L. Some data on the other British species of *Patella* are also included. The review concentrates on information which is relevant or useful to studies of ecology and population dynamics. Information on other topics is only briefly mentioned.

A study of population dynamics involves the integration of quantitative ecological data in order to show how the various populations maintain or change their character. The following survey of the literature shows that the necessary data can be obtained for *Patella vulgata* and that a study of the population dynamics of this species is theoretically feasible.

The literature also shows that there are many practical difficulties in obtaining the information required as well as theoretical problems in the integration of the data. These difficulties and problems are discussed in the last part of this section and some ways of tackling them are suggested.

2. Distribution and Habitat

*Patella vulgata* L., the Common Limpet, is found on most rocky shores in the British Isles. The species is also found along the Atlantic coasts of western Europe, from northern Norway to southern Portugal. Other species of the genus occur in many parts of the world, but *P. vulgata* is confined to
western Europe (Fischer-Piette and Gaillard, 1959). The detailed geographical distributions of the three British species of *Patella* will be discussed later.

In south-west Britain *Patella vulgata* is not found either below extreme low-water springs or much above extreme high-water springs. It has a wide range with respect to wave-action being found on even the most wave-beaten rocks and in extremely sheltered places (Colman 1933, Evans 1947a). It can be found on wood, cement, or even iron, where pieces of these materials are firmly fixed in the tidal zone. It is never found on mud, sand, or small mobile stones.

On shores exposed to considerable wave-action in south-west Britain, *Patella vulgata* is partly replaced by two other species - *P. aspera* Lamarck and *P. depressa* Pennant (Orton and Southward 1954). In places sheltered from wave-action, where large areas of the rock are covered with the fucoids *Ascophyllum nodosum*, *Fucus vesiculosus* and *F. serratus*, *P. vulgata* occurs only at the edges of the fucoid areas, in all clearings amongst the seaweeds and on the open rock (Fischer-Piette 1948).

Throughout south-west Britain *Patella vulgata* is abundant on the open barnacled rocks of shores exposed to moderate wave action (Crisp and Southward, 1958).
3. Anatomy and Physiology

The general anatomy of *Patella vulgata* was the subject of a monograph by Davis and Fleure (1903). Pieron (1909) reviewed almost all earlier work on the biology of *Patella* and made further studies on the ethology. Graham (1932) has given an account of the structure and functioning of the alimentary canal, and Yonge (1947) discusses *Patella* in his review of the functional morphology of the mantle cavity in Aspidobranch gastropods. The radula, and the patterns and shapes of its teeth, have been the subject of many studies (see next section).

A few specialised chemical studies have been reported. The composition of the radula teeth (Jones, McCance and Shackleton, 1935), the presence and distribution of carotenoid pigments (Goodwin, 1950; Goodwin and Taha, 1950) and the quantitative distribution of metallic elements (McCance and Shackleton, 1937) have all been studied in *Patella vulgata*.

Temperature tolerances (Evans, 1948; Southward, 1958), oxygen consumption (Gompel, 1937) and digestive enzyme activity (Stone and Morton, 1958) have received attention.

Thomas (1948) has studied the way in which the Australian limpet *Cellana tramoseica* maintains its grip on the rock and he also reviews previous work on *Patella vulgata*. Segal and his colleagues (1953, 1956) have shown interesting variations in the heart-beat rate of a Californian limpet (*Acmaea*) with tide-level.
The comparative functional morphology of the Gastropoda has been the subject of many studies in recent years (see Morton 1958 for a review of this topic and the key references). These studies have provided a fairly clear picture of the evolutionary trends and phylogenetic relationships within the class. The amount of information available for individual species, even the better known ones such as *Patella vulgata*, is however, very small. The detailed and integrated anatomical and physiological descriptions which are available for many vertebrates and insects cannot be matched in the prosobranch gastropods.

One reason for this state of affairs is the extreme variation in external form, anatomy and physiology in the gastropods. This variation makes it almost impossible to formulate general principles from information on a few species.

The adaptive radiation of the gastropods is spectacular (Morton, 1958). Gastropods have become specialised in an enormous variety of habits and adapted to occupy many ecological niches. The genus *Patella*, which retains certain primitive habits such as micro-herbivorous grazing, and which is relatively simple in form, is no exception to this trend. Detailed studies of shell-growth (Hamai, 1937) and the form of the larval shell (Dodd, 1957) show the simple shell-form of *Patella* to be derived from a coiled shell. The tent-like shell and large
muscular foot in *Patella* are specializations for life in turbulent waters. The simple shape of the radula teeth and the small number in each row form a strong, efficient and flexible grazing apparatus which can function over hard rough surfaces. The simple form and many details of the structure in *Patella* are adaptations enabling these animals to occupy, and frequently to dominate, regions where living conditions are very rigorous.

Adaptive radiation is a feature of many animal groups and the great range of anatomical variation, reproductive methods, feeding habits etc. in Gastropods is not altogether unexpected. Much more interesting and surprising is the plasticity of individual species; not only is there variation in features like shell-shape and colouration of the soft-parts, but also in more fundamental features. In *Patella vulgaris* there is enormous variation in life-span, size at sexual maturity, growth rate, and population structure (Hatton, 1938; Fischer-Pitte, 1941, 1948; Jones, 1948). Such variations occur between stable, natural populations only a short distance apart and are not easily explicable in terms of genetic differences. It seems that this type of plasticity may be common to many shore organisms (Savilov, 1953; Moore, 1935, 1937, 1938).

Two inter-related details of the form and anatomy of *Patella vulgaris* have been carefully studied by many workers:—
the relative height of the shell (height of the shell divided by the length) and the radula ratio (the length of the radula divided by the length of the shell).

Since shell-length is normally used as a measure of growth-rate, it is important to know the relationships between shell-length and volume. The literature on this subject is very confused owing to the absence of agreement on a basis for comparison. All workers are agreed that the range of variation in relative shell height in *Patella vulgata* is considerable and important. Relative shell height varies between populations in different habitats, and also between small and large individuals in the same habitat. Since some workers merely compare height/length ratios regardless of the size of the animals, it is very difficult to rely on the conclusions drawn. The most reliable results are those of Russell (1907 and 1909), which were further analysed by Hamai (1937). They concluded that the limpets on high-level open rocks and on wave-beaten shores had relatively steep shells, whilst those living at low-level (especially under fucoid seaweeds) had relatively flat shells. They also showed that there was a tendency to steepen with increasing size in each community.

Moore (1934) transferred marked specimens of *P. vulgata* from various habitats into a permanent pool. After a period of time the angle of the additional new shell growth was studied.
In the individuals brought from dry high-level habitats the new shell is much flatter than the old, forming a sharp ledge. The individuals brought from damp low-level habitats which already had relatively flat shells showed no signs of ledging. Moore interpreted these results as follows:

The individuals in dry places spend a long time with the shell pulled firmly down to reduce the dangers of desiccation. In damp habitats the shell remains slightly raised most of the time and this allows the mantle edge (which secretes the shell) to expand further out and produce a shell with a greater lateral growth component.

Radula ratios (radula length divided by shell length) were first studied as a method of distinguishing the species of Patella (see part 4), but later work was done on the nature of the variation inside each species. Individuals with the same volume and the same radula length will have different radula ratios if the relative shell height varies. Brian and Owen (1952) showed significant differences in the radula ratio between low-level and high-level populations of Patella vulgata in several parts of Britain. They attributed these differences partly to differences in shell shape, but also suggested that low-level individuals with greater opportunities for feeding might wear away the radula more rapidly. The higher radula ratios found in individuals from dry barnacled rocks is certainly due, in part, to the steeper shells. However there also seems
to be a real difference in the radula length. Fischer-Piette (1948) measured the shell-volume and radula length in 50 specimens from a dry high-level habitat, and repeated this procedure on 50 specimens from a damp low-level habitat. The ratio of the radula to the cube root of the volume was significantly greater in the high-level population.

4. Classification, Identification and Nomenclature

The genus *Patella* is classified by Thiele (1931) as follows:

Class: Gastropoda

Sub-class: Prosobranchia

Order: Archeogastropoda (= Aspidobranchia)

Super-family: Patellacea (= Docoglossa)

Family: Patellidae.

This classification is accepted by Morton (1958).

There has been considerable confusion in the past over the identification and nomenclature of *Patella* species. The species are difficult to separate because the few external characters (shell shape, colour and sculpture, and the colour of the soft parts visible without dissection) are subject to great intra-specific variation and show some interspecific overlap. An experienced worker can learn to separate the species with ordinary macroscopic examination in the field, but may find it difficult to explain precisely how he does it (Evans, 1947b). However, even an experienced worker may become confused when he first attempts to separate the same species.
in another area, since the range of variation for each species changes markedly in certain regions. Although the initial reaction to this phenomenon was the postulation of theories about hybridization, "intermediate forms" and "incompletely-separated species" (Fischer-Piette, 1935; Evans, 1953) subsequent workers continued to investigate the exact status of the limpets in these "difficult" areas (notably the Basque coast and the Isle of Wight region).

Several lines of investigation were used:
Firstly, it was shown that if several of the ordinary external characters were considered together, separation of species could frequently be achieved, although reliance on any single character led to confusion. Secondly, in an attempt to by-pass the extreme variability of the external characters, intensive studies of the radula were undertaken. Interest centred at first on the radula ratio and the shapes of the pluricuspid teeth; later the shapes of the laterals were also studied. Thirdly, surveys of additional coasts were carried out to elucidate the way in which the variability of the characters of each species altered. The original localities were studied again using the more detailed methods and the new criteria. Lastly, the reproductive cycles and spawning periods were investigated in an attempt to show reproductive isolation of the species.
By 1959, the problems of species separation and identification had been solved, at least so far as western Europe was concerned. Fischer-Piette (1935; 1948; 1953; 1959) and his co-workers (Crisp and Fischer-Piette, 1959; Fischer-Piette and Gaillard, 1959) played a key role in these investigations. Other significant contributions came from Eslick (1940), Orton (1946), Orton, Southward and Dodd (1956), Southward and Orton (in press, 1961), Southward and Crisp (1954), and Crisp and Southward (1958). Fischer-Piette and Gaillard (1959) sum up the situation as follows:

"Nous pouvons maintenant affirmer que les espèces énumérées ci-dessus sont bien séparées, ce qui met fin aux incertitudes antérieures.


Some confusion of nomenclature is met with in the literature. Some species have synonyms and one name — Patella depressa — has been used by different authors in respect of two distinct species.

Patella vulgata Linnaeus 1758 was the first species to be named. In 1819, Lamarck described P. aspera. This species was redescribed by Bean in 1844 as P. athletica and in 1865 Jeffreys listed it as P. vulgata var. depressa. Pennant in 1777,

* = P. depressa Pennant
however, had described another species as *P. depressa*, and this species was listed as *P. vulgata var. intermedia* by Jeffreys in 1865. Thus the correct names for the three species found in Britain are (with their synonyms):

1. *Patella vulgata* Linnaeus 1758
2. *Patella aspera* Lamarck 1819. = *P. athletica* Bean 1844
   = *P. vulgata var. depressa*
   Jeffreys 1865
   in many authors quoted as *P. depressa* Jeffreys
3. *Patella depressa* Pennant 1777 = *P. vulgata var. intermedia*
   Jeffreys 1865
   in many authors quoted as *P. intermedia* Jeffreys.

The only other species found on the Atlantic coasts of western Europe is *P. lusitanica* Gmelin.

For a full account of the complicated and rather unsatisfactory history of this nomenclature see the papers of Tomlin (1923), Fischer-Piette (1935), Evans (1947) and the Plymouth Marine Fauna (1931 and 1957). Two further points must be made. In the first place several authors have used the name *P. depressa* Pennant when the context clearly shows they were referring to *P. depressa* Jeffreys (true name *P. aspera*), Eslick (1940) is an example of this. Secondly some recent authors have refused to use the name *P. depressa* Pennant at all and continue to use *P. intermedia* Jeffreys for this species. Anyone who has attempted to unravel the literature will sympathize with this point of view - *depressa* is the word that has
caused most of the trouble - but *P. depressa* Pennant does have priority.

5. The life-history of *Patella vulgata*

In 1945, Orton began an extensive study of the breeding biology of *Patella*. Orton died in 1953, when the investigations were almost complete, though the analysis of the data had hardly been started (Southward and Dodd, 1956). Orton's colleagues analysed the data for *Patella vulgata* and published this together with a full account of the methods of investigation devised by Orton (Orton, Southward and Dodd, 1956).

The gonads of *P. vulgata* are, for much of the year, in a resting condition, during which time the gonad is small and the sexes indistinguishable. About the beginning of August the gonads increase rapidly in size, the male gonads become cream-coloured and the female gonads green. Orton distinguished five stages of gonad development, based on the size of the gonad relative to the whole visceral mass (see fig. 25). About the end of October a sharp decrease in the relative size of the gonad takes place and this was considered by Orton to mark the onset of spawning. A slow decrease in the size of the gonad, lasting several months, followed and this was assumed to result from a slow continuous release of gametes.

The embryology and early larval development of *P. vulgata* has been studied in detail by Smith (1935) who also reviews all
previous work. Dodd (1957) using improved techniques, reared large numbers of larvae through metamorphosis, and followed the growth of the spat for several months. Both these descriptions of the developmental processes were made entirely from laboratory-reared larvae derived from artificially fertilized eggs.

Smith (1935) states that tow-netting both in Plymouth Sound and the sea outside yielded Patella larvae from October to the beginning of March. Lebour (1937) confirms this in her description of the eggs and larvae of British prosobranchs.

Smith (1935) found numbers of spat on the rocks of Drake's Island, Plymouth in March. The smallest individual had a shell-length of about 0.2 mm., which is about the size at metamorphosis. Jones (1948) in a much more intensive study of spat settlement found that, in the Isle of Man, settlement began in January and continued until April. The smallest spat he found were 0.75 mm. shell-length, which indicated that they had been there for a considerable time. The mean shell-length in March was 2.4 mm., which should be compared with Dodd's figure of 1.0 mm. for 3 month-old laboratory-reared spat. Spat do not survive on the open face of rocks above mean low-water neaps, but they are found abundantly (up to 150 per m²) in shallow pools or under algae. By August the spat had a mean shell-length of 6.5 mm. and were beginning to move out and colonize the dry rock areas. In the following January the mean
shell-length had reached 12.5 mm. (Jones, 1948).

Orton (1920) showed a preponderance of males in the smaller size-groups of *Patella vulgaris* populations which suggested a change of sex. Later studies of very large samples (Orton, Southward and Dodd, 1956) showed that practically all specimens below 10 mm. shell-length had no visible gonad even in the breeding season. Between 16 and 25 mm. 90% of the individuals were male and thereafter the proportion of females increased to 50% at about 40 mm. shell-length and up to 70% at 60 mm. A differential growth-rate of the sexes and a differential mortality might explain these results, but a simpler and more acceptable explanation would be that about half the male limpets change sex. Similar phenomena are found in many other molluscs.

6. **Behaviour, ecology and population dynamics**

*Patella vulgaris* is a common animal of fair size living on the surface of rocks in the intertidal region and remaining motionless while the tide is out. It is thus easy to observe, count and measure accurately. Moreover its rocky shore habitat has suffered very little from human interference of any kind. For these reasons alone, *Patella* is an obvious choice for ecological studies. There are, however, other features of the biology of *Patella vulgaris* which make it especially interesting to the student of population dynamics.
It has long been realised that limpets usually remain stationary during the low-tide period, and return after each feeding excursion to the same place. This homing habit has attracted considerable attention but is far from being completely understood (see Morton, 1958, and Thorpe 1956 for reviews).

The smallest limpets do not home and the larger ones may change their home on occasion. The precision of homing and length of tenancy is greatest on rough, dry surfaces and least on smooth, wet rocks. Even in these conditions the larger limpets may retain the same home for many months. Individuals removed from their homes and replaced some distance away are often able to return to their home. The distance over which such homing can take place depends to a great extent on local conditions, but may be as much as 2-3 feet. The removal of the cephalic tentacles appears to have no effect on homing ability. These observations and experiments were made by Morgan (1885; 1895, Davis (1894), Davis and Fleure (1903), Orton (1914), Jones (1948), Dons (1948), and Lewis (1951).

Limpets feed by scraping the surface of the rocks with their radulas. The gut contents and faeces of Patella vulgata have been examined by Moore (1931), Graham (1932), Fischer-Piette (1948) and Jones (1948) in an attempt to discover the nature of the food. These studies show that P. vulgata can scrape off and ingest:

(a) diatoms (b) sporelings of all kinds (c) pieces of
Laminaria, fucoids and 'lithothamnia' (calcareous encrusting algae), (d) pieces of, or whole, green algae such as Enteromorpha, Ulva etc.

Even mites and pieces of barnacles were found in the gut, together with a variable but often large amount of rock debris. The contents of the gut and the degree to which it was filled varied with the habitat. Limpets from rocks covered with barnacles (no macroscopic algae present) have an incompletely filled gut and the proportion of debris and silt is high. Those living in a thick felt of Enteromorpha had a gut filled with fragments of the green algae. Jones (1948) agrees with Fischer-Piette (1948) that the limpet systematically grazes the area near its home, ingesting everything removable by the radula. Nothing is known of the food preferences of the relative nutritional value to the limpet of the different foods.

Limpets may move out on feeding excursions while uncovered by the tide if their environment is damp or shaded, but they rarely move when exposed to direct sunshine. The main feeding excursions in all habitats occur when the animals are covered by the tide (Orton, 1929). The distance, course and frequency of the feeding excursions are not known except in a few special cases where the feeding tracks can be seen as bare rock in a felt of small green algae (Orton, 1914; Moore, 1938; and Lewis, 1954).
The homing habit of *Patella vulgata* makes it fairly easy to follow individual animals for long periods, without disturbing the habitat. The grazing habit combined with homing means that there will be definite and relatively simple relationships between the parameters of the limpet population (density, growth rate etc.) and the available food and other conditions of the immediate area. To some extent this is true for all grazing animals, but in cases where the animals roam freely and in an completely unknown way, such relationships will be vastly more complex, more difficult to determine and will refer only to the general conditions of a wide and indeterminate region. For a student of population dynamics, limpets combine these features of sessile animals which make them easy to study with the features of free-living animals which make such study interesting and more generally significant.

The growth-rate of *Patella vulgata* has been studied by Russell (1907; 1909), Orton (1928), Hatton (1936; 1938) and Fischer-Piette (1941; 1946; 1948). All these workers used shell-length as a measure of size. Many interesting points emerged from these studies:

(a) *Patella vulgata* grows relatively slowly. The fastest growth-rates reported were increases in shell-length of 15-20 mm. per year. By way of contrast, *Aplysia*, a nudibranch gastropod which feeds on the lush green algae, reaches a body-length of 120-200 mm. in a single year (Kisch, 1951).
(b) The potential life-span of *P. vulgata* is considerable. Individuals do not, apparently, become sexually mature in their first year, and, assuming sex change to take place, no females would be less than two years old.

(c) The variation in growth-rate is tremendous even on the same shore. Shell-length may increase 20 mm. in a year or the increase may be less than 1 mm. A limpet of 20 mm. may be anything between 2 and 16 years old.

(d) The variation in growth rate is clearly related to habitat. The limpets on barnacled rocks have the slowest growth rate, those at the edge of areas of *Ascophyllum* grow faster and the most rapid growth rates were found in sheltered places amongst *Fucus vesiculosus*.

(e) The growth rates of individuals in the same habitat do vary, but these variations are very small compared with the variations between the individuals of one habitat and those of another. It is thus meaningful to give the growth rate of a population, provided the habitat of the population is carefully defined.

(f) There appears to be a general inverse correlation between growth rate and maximum longevity, and a positive correlation between growth rate and maximum size.

(g) Although a number of broad relationships between habitat and growth rate were demonstrated, the factors controlling growth rates remain unknown.
(h) The growth of *Patella vulgata* seems to be continuous and indeterminate. The shell-length increases are smaller in winter and mid-summer than at other times, but some growth continues throughout life. The curve of growth becomes less steep with age, but there is no fixed size limit even in a particular habitat.

*Patella vulgata* is more abundant at certain levels of the shore than others.

Colman (1933) showed how zonation on a shore could be quantitatively described, and the Stephensons' (1949) devised a scheme whereby the zonation on different shores could be compared. Since then, numerous studies of shore zonation have been made in Britain, most of them providing information on the distribution of the *Patella* species. These studies, although useful, suffer from two severe limitations. Firstly, the habitats described differ from one another in many ways (some of which are not easily defined or measured), so that it is difficult to determine which factors are controlling the observed differences in the abundance of the *Patella* species. Secondly, the abundance of the limpets is described only as numbers of individuals per unit area. In view of the vast range of individual size which is found, such data can be very misleading.
Some authors have recorded 'average' size and maximum size in various habitats (Fischer-Piette, 1948; Jones, 1948). A few give the number of individuals in each size group as well as the total number per unit area (Das and Seshappa, 1947; Southward, 1953). Even these results are rather difficult to interpret, especially as the most detailed ones are not supported by growth rate information. A number of points, however, emerge quite clearly. On wave-beaten shores the density of first year limpets is greatest at low levels and falls off gradually upshore. On more sheltered shores successful spat settlement is greatest at the margins of the fucoid dominated areas and under scattered fucoids. Spat are very rarely found under dense Ascophyllum. These facts suggest that successful spat settlement requires a certain type of surface as well as freedom from dessication. The rock under dense fucoids is always wet, but is usually covered with a dense 'undergrowth' of encrusting animals and plants.

The numbers of post-first-year individuals of Patella vulgata on barnacled rocks lie between 80 and 200 per m² (maximum size 18-30 mm. shell-length). At the borders of the dense fucoid areas numbers are 300 - 1000 per m² (maximum size 33-40 mm.), and beneath the fucoids the maximum is 50 per m² (maximum size 43-55 mm.). These figures are from Fischer-Piette (1948); those of the other authors differ considerably but show the same trend.
The upper limit of *Patella vulgata* on the shore varies from place to place. In shaded localities or where splash is considerable, the limpets may go very high — well above high water springs. On shores open to the mid-day sun the upper limit of limpets in quantity roughly coincides with high-water neaps (Orton 1929). Orton (1933) reported spectacular mortality in limpets above neap tide level following a period of calm seas, hot, sunny weather and neap tides. Lewis (1954) has shown that the upper limit of *Patella vulgata* may fluctuate seasonally, and that downward migration or death may occur in summer while food is still available at high levels.

It has already been shown that *P. vulgata* tends to mass along the edge of the dense fucoid areas, but that numbers and settlement in side the fucoid areas are very low (Fischer-Piette, 1948). It seems that dense fucoid growth forms a barrier to colonization, though how this works in detail is obscure.

On wave-beaten shores where fucoids are absent, *Patella vulgata* appears to be in competition with the two other species, *P. depressa* occurs in the neap-tide range on well-drained, barnacled rocks and *P. aspera* is abundant at low-level and in pools (Evans, 1947a). Since the three species overlap to a great extent and feed in the same way by more or less indiscriminate grazing, the presumption that competition occurs is very strong. There is little or no direct evidence, however,
and the mechanism of competition is unknown.

So far as I am aware only one kind of experimental interference with *Patella vulgata* populations has been practised—that of clearing an area of its limpet population and observing the resulting succession. Jones (1948) and Southward (1953; 1956) have performed large scale experiments of this type. In each case a strip of shore extending from high-water to low-water was cleared of limpets and the few large algae present.

The results of these clearing experiments vary to a certain extent with the following factors: (i) the season of clearing, (ii) the exposure of the strip to wave action, (iii) the tide level on the cleared strip, (iv) the width of the cleared strip, (v) the nature of the rock topography and the mobility of the nearby limpets. Nevertheless a clear pattern does emerge from the results. Southward (1956) followed the succession of events on a strip 5 metres wide for six years. His results for the mid-tide region are reproduced in fig. 1.

In this experiment an ephemeral growth of diatoms and filamentous algae appeared almost immediately after clearance, but within a few weeks these gave place to a dense growth of *Porphyra* and *Enteromorpha*. *Fucus vesiculosus* sporelings developed in this community and one year after clearance fucoid cover had reached 100%. The barnacle numbers had by this time fallen by one third and the limpet population (produced by new settlement and fast growth) was four times the pre-clearance
Fig. 1

The changes which took place at mid-tide level on a strip 5 metres wide, cleared of limpets in 1949.
Redrawn from Southward (1956).
level (in numbers per m$^2$). During the second year the fucoid cover was maintained; the barnacle numbers were much further reduced and there was a second very heavy settlement of limpets as well as continued rapid growth by the first settlement. Five years after clearance the activities of the limpets had reduced fucoid cover to about 20%; the barnacle numbers were still very low and the limpet numbers (although no further heavy settlements had occurred) were still very high. These limpets had a greater average size than the pre-clearance population.

Southward concluded from the clearance experiments that "on wave-beaten rocky shores the populations of algae, limpets, and possibly barnacles too, are dynamically related." (Southward, 1956). Thus even the apparently unchanging communities on many shores are in fact delicately balanced in dynamic equilibrium, and cyclical fluctuations of long period are to be expected in many places. The detailed results of the experiments (see fig. 1) go some way towards explaining the mechanisms by which equilibrium is achieved and also throw some light on the observed patterns of distribution of limpet populations on different areas of the shore (see discussion of Fischer-Piette, 1948, above). Populations of limpets can prevent the development of fucoids in areas which are otherwise quite suitable for their survival. The temporary presence of
fucoids in such areas (produced by the removal of limpets) brings about an increase in the settlement and growth rate of the limpets. The increased limpet population then destroys the fucoid community but this takes some time. If the fucoid community is large and contains areas (such as very jagged rock surfaces) where limpet mobility is much reduced, conditions are favourable for limpets to crowd around the margins in the way described by Fischer-Piette (1948) and Jones (1948).

7. The aims of the present investigations

Almost all the information on the biology of *Patella vulgata* reviewed above, was already published in 1958 when my own work began. At that time three lines of investigation seemed to be required before an adequate account of the population dynamics could be given.

*Patella vulgata* occurs in a wide variety of habitats. The first requirement is a system of comparison which relates these habitats. Since relative height on the shore is one of the major factors governing the life of shore organisms, the Stephensons' scheme for vertical zonation was chosen as one coordinate of such a system. Wave-action is another major factor affecting intertidal organisms, but it is difficult to measure and the measurements cannot easily be compared. I therefore devised a biological exposure scale (Ballantine, 1961) to serve as the second coordinate in the system. This exposure
scale is based on quantitative criteria, but the measurements are of biological features not physical factors. The scale is a measure of the consequences of wave action not a direct measure of wave action itself. It is thus comparable to the Stephensons' scheme which equates biological features, not tide-levels as such. Given these two coordinates, vertical zonation and exposure scale, it is possible to draw a two dimensional diagram on which any point on any shore in a given region can be represented. Such a diagram is given in Ballantine (1961) as fig. 1. Although subject to many limitations (see enclosed paper for a discussion of these), such diagrams provide a means of relating the varied limpet populations to one another.

The second requirement is to study a few standard populations in great detail. The number of factors affecting the biology of *Patella vulgata* is very large, as is the number of ways in which individual animals or populations react to them. Many of these complicated variations and reactions are likely to be connected, and in order to establish such connections (and thus simplify the situation), it is necessary to make all the measurements on the same animals, or at least on animals under the same conditions. One example will show how important it is to have the information properly related. Orton showed that sex change takes place in *P. vulgata*. In his samples from Plymouth only about 10% of the animals with a shell length
of 30 mm. were female, although the proportion increased to 70% at 60 mm. (Orton et al., 1956). Many slow-growing populations of *P. vulgata* have a maximum size of about 30 mm. (Fischer-Piette, 1948). Do these populations have very few females, or is sex change determined by age rather than size? It is not possible to tell, since Orton did not measure growth rate and Fischer-Piette did not determine sex proportions.

Surveys of quantitative distribution and population structure form the third requirement, and their usefulness depends on the success of the first two lines of investigation. When the results of the surveys are plotted on the zonation/exposure diagrams they reveal the trends and relationships involved. Only a few simple measurements can be made if the surveys are to cover the complete range of habitats in a region. These measurements have been chosen on the basis of trial surveys and the analysis of data from the standard populations.
SECTION II

The detailed investigation of four populations of *Patella vulgata* in Batten Bay, Plymouth.
1. **Introductory: a description of the shore and the four populations.**

   The shore chosen as the site for the standard populations lies in Batten Bay at the north-east end of Plymouth Sound. It can only be reached by passing through an R.A.F. camp where security is strict, and is therefore free from the activities of holiday makers and other members of the general public.

   In the centre of Batten Bay, the low cliffs of loose drift are footed by a narrow strip of stones (2" to 4" diameter) at extreme high water springs. Below the stones the tidal region forms an extensive area of low rocks—shale and sandy shale—dipping to the south, and divided into groups by shallow, stone-filled gullies. In one place a group of tall, steepsided stacks rises from the low rocks. The base of these stacks is at mean tide level, the tops rise above mean high water neaps.

   The shore is sheltered from direct wave action of any magnitude. The maximum fetch is \( \frac{3}{2} \) miles from the W.S.W. Channel gales associated with winds between west and south produce the largest waves on the shore. Before these waves reach Batten Bay from the open sea they must be refracted round Penlee point and the breakwater, and pass over at least a mile of the shallow Sound. The extensive shore gradually dissipates...
the remaining energy of the waves. On the biological exposure scale (Ballantine, 1961) the low broken rocks, which make up most of the shore, rank as unit 7 (very sheltered). The upper parts of steep-sided stacks rank as unit 4 (semi-exposed).

The investigations at Batten Bay lasted nearly two years, from January 1959 until November 1960, and four populations of *Patella vulgata* were studied. These populations were selected to cover as wide a range of community types as could be found on a single shore.

Population 1

The lowest population on the shore consisted of isolated or semi-isolated groups of limpets in a dense surround of *Fucus serratus*. The limpets maintained clearings amongst the *Fucus* where the rock (a fine shale) was smooth and sloped at a moderate angle. The largest limpets on the shore were found in this population and each group in the population was dominated by a few very large animals which usually occupied the centre of the clearing. Many small limpets were also present most of them near the edges of the clearing. The size of the clearings varied considerably, but all of them showed a distinct radial zonation.

The surrounding region was dominated by *Fucus serratus*, *Himanthalia* was also very common. Beneath these large algae *Gigartina, Chondrus, Corallina, Rhodymenia, Laurencia, Ulva* and
Enteromorpha formed an undergrowth. These smaller algae grew further out into the limpet clearings and even formed tufts on the shells of the larger limpets. The extent of algal cover varied considerably with the season. The larger algae showed maximum cover in the late summer when the reproductive fronds of the Himanthalia were fully developed and the Fucus serratus bore numerous fruiting branches. By November the Himanthalia (an animal) had disappeared and the Fucus had shed many of its branches. The undergrowth algae were mostly seasonal annuals with a peak abundance in the late spring.

The outermost part of the clearings was covered with a pink, calcareous alga of the group called "lithothamnia"; spirorbid worms were also very common here. The lithothamnia zone corresponded roughly with the average overhang of the larger algae, and if the clearing was very small, lithothamnia might cover it entirely.

The central part of the larger clearings was bare rock which dried out at low water of spring tides.

There were no barnacles in this region and gastropods other than limpets were uncommon. Sedentary colonial animals such as sponges, tunicates, hydrozoa, and polychaetes were very common under the large algae.
Population 2

This population occurred around mid-tide level on fairly smooth, slightly sloping areas of sandy shale. Very few algae were present; only a few s all Laurencia and one or two Fucus sporelings. Most of the rock (90%+) was covered with barnacles, mainly Chthamalus stellatus with a few Elminius modestus. The limpets appeared at first sight to be all of medium size and very regularly spaced out over the area. Closer examination showed that all limpets were to be found in the cracks and depressions, and that even the larger limpets were rather more crowded in the damp hollows. Other molluscs were common; principally the top-shells onodonta lineata and Gibbula umbilicalis, but also some Nucella lapillus. This area did not change appreciably in appearance over the year, in spite of the short life of the barnacles and the heavy summer settlement of new Chthamalus. The general rock surface in this region dried out fairly quickly, but many of the cracks and depressions remained damp for some time.

Population 3

This population occurred along the edge of the Ascophyllum community, and formed a line rather than an area. In Batten Bay, Ascophyllum was confined to the more jagged and horizontal rocks (i.e. areas of poor drainage). Since the unevenness of the rock and the slope of the rock varied more
or less independently, the edge of the *Ascophyllum* community followed a tortuous and broken path. *Fucus vesiculosus* often occurred along the edge: a kind of scrub to the *Ascophyllum* forest.

In some places, an area of horizontal, uneven rock gave way to a sharp slope. In such places *Fucus vesiculosus* was rare, the *Ascophyllum* boundary was sharp, and the edge population of limpets was most clearly developed.

The *Ascophyllum* was very dense, its holdfasts were close together and each one had many long thongs rising from it. Beneath the *Ascophyllum* encrusting animals (hydroids, sponges and polyzoa) and shade-resistant algae (*lithothamnia, Gigartina*) covered the surface of the rock, which never dried out.

A little way out from the edge of the *Ascophyllum*, barnacles were found, but along the edge itself both barnacles and algae were absent. In this strip, which was partly overhung by *Ascophyllum* thongs, limpets were abundant. Many of the individuals were fairly large and they were all crowded close together. No limpets were found very far inside the *Ascophyllum* community, but most of the small limpets in this population were found around the holdfasts of the outermost plants. Well away from the *Ascophyllum*, barnacles were common and the situation was much the same as that described under Population 2.
Population 4

The highest population on the shore, was found high up on the south side of stacks. No macroscopic algae were present. The barnacles (mainly Chthamalus but some Elminius) were tall and closely packed, and covered almost 100% of the rock surface. Limpets were numerous in the lower part of the area but thinned out and finally disappeared higher up. Other molluscs were rare. The rock dried out very quickly when the tide fell and remained dry for long periods. The population lay a little below mean high water neaps.

These "populations", although differing in many ways, are more or less arbitrary selected samples of the total population of the shore.

The principal differences between the standard populations are: tide level, the general slope of the rock, and the unevenness of the surface. These last two factors seem to be connected in their effect, though not in their occurrence. Fig. 2 represents a possible picture of the shore if slope and unevenness altered together. The positions of the four standard populations on this theoretical shore show how their habitats are related.
Fig. 2

A theoretical prediction of the distribution of fucoids and barnacles (dots) on a shore like that at Mount Batten except that the unevenness of the rock surface and the general slope change together. The numbered squares show the positions of the four standard populations of limpets on such a shore.
Sub-section A: Growth

2. The methods used to measure growth

There is no way of distinguishing year groups in limpet populations (at least in the larger sizes), nor do the limpets in Britain have recognisable annual growth rings in their shells. Age must therefore be measured by following individual limpets over a period of time and noting the increase in size.

All previous workers have used shell-length as a measure of size in their studies of growth in *Patella vulgaris*. Shell-length can be measured quickly and accurately, without disturbing the limpet. In theory, since relative shell height is known to vary (see Chapter 3), weight would be a better measure of growth. There are, however, practical reasons which prevent its use.

When limpets are lifted from their homes, the foot secretes large quantities of mucus and this appears to hinder reattachment. Between 5 and 10% of the limpets from a horizontal surface failed to reattach successfully and were lost, even when great care was taken in the manner of their removal. If measurements involving periodic removal (e.g. weight) were used to measure growth, these losses would rapidly have altered the population and vitiated the experiments.

Although shell-length is the only practicable measure-
ment for the determination of growth in natural populations, it can, and should, be related to weight in each set of observations. Surprisingly enough, no one seems ever to have weighed limpets in the course of an ecological survey.

**Patella vulgata** is reported to live for as long as 16 years and growth rates may be very slow (Fischer-Piette, 1941). Accurate determinations of growth rate therefore depend on the duration of the observations as well as the accurate recognition of the individuals being measured.

The marking of large limpets is easy, but it is difficult to make marks which are visible and distinctive after several months. The shell of *P. vulgata* may be penetrated by boring worms (e.g. *Polydora*), sponges (*Cliona*), lichens (*Arthopyrenia*) and algae. Physical and chemical erosion of the shell occurs and barnacles, spirorbid worms, and algae of all kinds may grow on the shell surface. Thus, though paint marking is useful for short term studies, the number of distinctive colours is limited and the paint usually flakes off or is obscured within a few weeks. Marks cut into the shell are more distinctive and last longer. Such cuts can only be made in the larger, thicker shells, and even deep cuts loose their distinctiveness after 6 to 18 months depending on the local conditions. There is no suitable method for marking very small limpets (i.e. below about 10 mm. shell-length).
In each of the standard populations, a small but representative area (approximately 0.5 m²) was selected for determination of the natural growth rate. These areas are shown in plates 1 to 5. Distinctive grooves were cut in the shells of all the larger limpets (15 - 30 mm. shell-length and upwards depending on the habitat), using a portable drill made for this purpose. The drill specification is given in appendix A. The smallest limpets (below 7 - 15 mm) were not marked, but the intermediate sizes were marked with small blobs of dental cement. Several colours of cement were used and the blobs placed in different numbers and positions to give individual distinction. All marks were renewed after 12 months.

Measurements of shell-length were made about every two months, using spring screw dividers and sliding calipers. Measurements were made to 0.1 mm., but for various reasons the results are subject to an average error of ± 0.2 mm.

Marking was not completely reliable, but this was anticipated and two other methods were used to help distinguish groups. The limpets in these special areas will be referred to as Groups, numbered after the population they represent, e.g. Group 1 in Population 1.
the individuals. At each bi-monthly assessment the position of each limpet was marked on a map of the area with its shell-length. Standard photographs of the areas (in black and white and colour) were also taken at intervals. In this way, although some individuals lost their marks and some moved their homes occasionally, there were always three ways of identifying an individual (mark, size and position), and where one failed there were two in reserve. These precautions were found to be necessary, and the absence of such precautions throws considerable doubt on the accuracy of the results of earlier workers. Fischer-Piette (1941) in fact states that when a limpet, which was being measured periodically, was lost, measurements were continued on a nearby one of the same shell-length and 'similar' appearance.

The time of settlement and the growth rate during the first year were of special interest, since the literature is vague and contradictory on these points. The small size and mobility of the young limpets made it impossible to follow individual growth, so two other methods were used. All the small limpets in each Group were measured at the same times as the marked individuals. Initial results showed that it was possible to separate the first year limpets (and sometimes the second year as well) from the rest of the population by simple size group: frequency analysis. The small limpets in the
Groups were not, however, very suitable samples for such analysis. In Group I, there were so many tiny limpets it was difficult to measure all of them in the short time (at L.W.S.) available. In the other Groups, small limpets were not always sufficiently numerous for accurate analysis and those that were present often occurred in cracks where measurement in situ was impossible. For these reasons, during 1960, samples were taken at intervals from other places in the standard populations, and measured in the laboratory. Care was taken to ensure that these sample sites were equivalent to the Group areas and the results of the two methods were always compared for discrepancies.

3. The measurements of growth and the calculation of growth curves.

The data needed for the production of a growth curve was described in the last chapter. The collection of such data is a lengthy, tedious and difficult process. The growth curves will be used to give the age of individual limpets and to test other, easier, ways of determining age. It is therefore necessary to follow the processes by which the growth curve is produced in order to understand and measure the errors at each stage.

Table 1 gives the numbers and size distribution of the small limpets in the central area of Group 1 (area 0.5 m²). It
was difficult to find or to measure accurately the smallest (below 5 mm.) individuals without risking damage to the habitat or the limpets. It was impossible to find individuals below 1 mm. Moreover small limpets could, and probably did, move in and out of the area. In the second year group the numbers were often too small for accurate analysis. But in spite of these difficulties and reservations a reasonably clear picture of the growth during the first two years emerged from the data.

Harding (1944) has shown how probability graph paper can be used to analyse overlapping normal curves such as year groups in size/frequency distributions. Year groups of small limpets (e.g. 12. 1. 59., in table 1) unfortunately do not always fit a normal curve either when size is plotted linearly or when size is plotted logarithmically. The initial growth of the limpets appears to follow a power curve, but an inflection occurs during the second year (see fig. 8). Mortality appears to be greater in the fastest growing and slowest growing limpets than in those near the mean. In practice these possible sources of error do not have much effect. The means and standard deviations calculated by the two methods do not differ significantly and the more convenient logarithmic plot for size was used (see fig. 4 for an example).
Table 2 gives the numbers and size distribution of small limpets in samples from other parts of Population 1. These data are in several ways more satisfactory than those derived from the Group 1 limpets. Measurements were made under a microscope to 0.05 mm. (0.5 mm. for measurements in the field). Since the destruction of the habitat did not matter, a much larger proportion of the tiniest individuals were found. The samples were much larger and the exact number in each could be altered to suit the circumstances. Each sample however did consist of different limpets and although the sample areas were chosen for their similarity to that of Group 1, conditions could have been somewhat different in them.

In the sub-section on reproduction, evidence is produced to show that spawning took place in the first half of November in 1959 and 1960. For the graphs showing the growth rate of limpets during the first two years (figs. 5 and 6), zero age has been taken to be November 1st for each year group. This involves an error of about 14 days either way, and ignores the planktonic larval phase estimated by Dodd (1957) to last about 10 days. The agreement between the results for 1959 and 1960 in Group 1 is fairly close. In July 1959 a hundred first-year limpets were removed from the central area of Group 1 and measured in the laboratory, the result is plotted with the "in situ" measurements in fig. 5. The removal of
these individuals probably resulted in a temporary increase in the food supply to the other small limpets and may account for the discrepancy between the September results for second-year limpets. The laboratory measurements on the removed specimens confirmed suspicions that "in situ" measurements for first-year limpets were too high.

The general agreement between the sample data and the "in situ" data for 1960 (compare figs. 5 and 6) is good. By the end of the second year the results of the two methods are identical. Because of this final agreement and the evidence that "in situ" measurements are biased in the first year, the sample data are used in the growth curve for the population.

The bi-monthly survey information on the marked individuals in Group 1 was transferred to 1:4 scale plans on transparent sectional paper. Each sheet represented one survey, and the position, size and serial number of each limpet was marked on it. A simplified part of such a plan is shown in fig. 3. The positions and mortalities recorded on the sketch maps made in the field were checked against the standard photographs. When the plans were arranged in time sequence, it was easy to follow the growth of each individual (and any migrations or mortalities).

There was considerable evidence for seasonal variation in growth rate. This is most obvious in young limpets (see
fig. 6), but a similar pattern persists throughout life. In view of this seasonal variation, it was decided that annual increments of shell length would be the best basis for growth rate determinations. Only those limpets which were followed continuously for at least one year were used in the calculations. Where possible the year for which the increments were measured, began and ended in winter, a season of little growth. This reduced any possible errors arising from the variation in the timing of the seasons in different years.

The annual increments of shell-length were plotted against initial shell length (see fig. 7). The increments lie in a narrow belt, starting at about 12.5 mm. at 20 mm. initial shell length and falling to zero at about 60 mm. By adding successive increments a growth curve can be produced. Fig. 8 shows three such curves, the middle one results from using the average annual increments, the outer ones from using the extreme upper and lower increments.

There are two objections to this method of calculating the growth curves. Firstly, the growth during 1959-60 may not have been the same as (or even typical of) the preceding years. The growth rates in 1959 and 1960 were, however, very similar if not identical, although these two years had very different weather conditions. The second objection is more serious. Plotting the annual increments against initial shell length implies that all individuals with the same shell length are the
same age; yet the fact that there is variation in the annual increments at the same shell length shows this to be untrue. If variation in age at the same shell length is random with respect to growth rate, the growth rate curves as calculated will be accurate. However, two kinds of systematic variation are possible. Growth rate could be to some extent self-regulatory; periods of slow growth in each individual tending to be succeeded by compensatory periods of faster growth. If this occurred the present method of plotting annual increments would give too low an estimate of the variation in growth rate (fig. 9a). The evidence indicates that the opposite occurs; fast-growing individuals generally continue to grow faster than the others and slow-growing ones to grow slower. This is clearly seen when different populations are compared (see fig. 20), and the same trend also occurs inside each population. This type of growth means that the present method of plotting annual increments is more accurate than it appears at first sight (see fig. 9b).

It has already been mentioned that, in young limpets, mortality appears to be greatest at the extremes of growth rate. The standard deviation of shell length after the first winter is smaller than that of the previous autumn, although the mean is unaltered (fig. 6). It is not clear whether or not this tendency persists in later life. Since limpets in other populations on the same shore grow at quite different
rates (see fig. 20), and the growth rates within a population cover only a small part of this range, some mechanism must operate to produce this restriction. The evidence shows that individual self-regulation of growth does not occur, but various patterns of competition and differential mortality could produce the same results. These will be discussed more fully at a later stage. Fig. 10 illustrates two possible population structures, by showing the relationship between age at death and size at death. The actual state of affairs in natural populations appears to be somewhere between these two.

The growth curves of the other standard populations were calculated in essentially the same manner. Accuracy decreases as growth, settlement, density, and mortality decrease. It will be seen that Populations 1, 3, 2 and 4 form a series as regards these variables. The data for Populations 2, 3 and 4 is set out in tables 3 - 5 and in figs. 11 - 19.
The legends to Plates 1-5 and Fig. 3

Plate 1 Group 1 and the surrounding area, 26/2/59. The sparse winter growth of *Fucus serratus* has been pushed aside to show the clearing. See Fig. 3 for scale.

Fig. 3 An example of one of bi-monthly maps of Group 1, showing the position of the limpets, but not the measurements of shell length. The shading indicates algal attachment areas. The scale divisions at the base are 20 cm. The dotted line marks the limit of the central area used in the analysis of the growth of small limpets.

Plate 2 A close-up of the left side of Group 1, 12/5/60. The dividers are set at 5 cm. Bare rock and large limpets with algae on their shells at right. Lithothamnia and spirorbid zone with 7 and 19 month old limpets at left.

Plate 3 Part of Group 2, 7/9/60. Dividers set at 5 cm. Note the regular spacing of the larger limpets and the barnacled, algal-free rock surface.

Plate 4 Part of Group 3, 16/2/60. Scale same as Plate 5. Note the limpets crowded along the edge of the *Ascophyllum* community. About the same number are hidden beneath the algae.

Plate 5 Part of Group 4, 2/11/60. This is a vertical face, the top at the left of the photograph. Note the very dense barnacles. The circle has a diameter of 4.5 cm.
Plate 1 (for legends to this previous page)

Fig. 5 (see previous page)
Table 1. The numbers of small *Patella vulgata* in the central area of Group 1.

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Total in sample: 94  100  200  143  357  262
Table 3. The numbers of small *Patella vulgata* in samples from Population 2.

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Total in sample 65 52 126 178 172
Table 4. The numbers of small *Patella vulgata* in samples from Population 3.

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Table 5. The numbers of small limpets in samples from Population 4.

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Fig. 4 An example of the probability analysis dividing a sample of young limpets into two year groups.

Fig. 5 The growth of limpets during the first two years of life in the central area of Group 1. Solid dots 1959 results, circles 1960.
Fig. 6 The growth of limpets during the first two years of life in Population 1, 1960.

Fig. 7 The annual increments of shell length growth in Group 1. Solid dots 1959 results, circles 1960.
Fig. 8 The mean and extreme growth curves for Group i

Fig. 9 Systematic errors in converting annual increments into growth curves
Fig. 10
Two possible types of population structure

Fig. 11 The growth of limpets during the first two years of life in Population 2. 1960 results
Fig. 12 The growth of limpets during the first two years of life in Population 3. 1960 results

Fig. 13 The growth of limpets during the first two years of life in Population 4. 1960 results
Fig. 14 The annual increments of shell length growth in Group 2 solid dots 1959, circles 1960, over 30 mm average of two years

Fig. 15 The mean and extreme growth curves for Group 2
Fig. 16 The annual increments of shell length growth in Group 5. Solid dots 1959, circles 1960, over 30mm average of two years.

Fig. 17 Growth curves (mean and extremes) of Group 5.
Fig. 18 The increase in shell length of Group 4 limpets over two years.

Fig. 19 The mean and extreme growth curves for Group 4
Fig. 20
A comparison of the mean growth curves of the four Groups

Fig. 21  Fischer-Piette's growth curves for *P. vulgata* reproduced from his 1948 paper.
The patterns of growth in the four standard populations

The mean growth curves calculated for the four standard populations are compared in fig. 20. These growth curves are certainly more complete, and probably more accurate than those of earlier workers (compare figs. 20 and 21). The principal conclusions reached by earlier workers on the nature of growth in *Patella vulgata* were listed in Section I, 6. These conclusions are fully confirmed by the present studies. The greater detail of the present work allows further deductions to be made regarding the growth during the first two years, the variation in growth within a population, and the relationships between habitat and growth rate.

The mean shell length at the end of the first year is much the same in all habitats. For the standard populations, the means are between 6 and 7.5 mm. Hatton (see curve I, fig. 21) gives 7.5 mm. for a population amongst barnacles near St. Malo (Brittany). Jones (1948) found 6.5 mm. to be the August (9-10 months old) mean for two populations in the Isle of Man. Fischer-Piette (1948) did not actually measure the growth of the smallest limpets and may have misjudged the origins of his curves. (see fig. 21). Dodd (1957) reared limpets in the laboratory from artificially fertilized eggs and reported a mean shell length of 1.6 mm. six months after fertilization. All these figures agree closely with the figures obtained for the standard populations in 1959 and 1960.
Although the mean growth during the first year is remarkably similar in a wide variety of conditions, the individual variation within each population is very great. In Population 1, 3-10 mm. is a conservative estimate of the range of shell lengths found in one year old limpets, and similar figures apply to the other populations. At the end of the first year, growth slows down or stops altogether for the winter. In older limpets the rebuilding of reserves after spawning could account for the seasonal pause in growth, but first year limpets are reproductively immature and do not produce any gametes. Their cessation of growth is probably due to some combination of low temperatures, lack of suitable food, and competition.

As already mentioned the standard deviation of shell length in the first year group is reduced after the winter, probably as a result of differential mortality. Mortality is certainly high during the winter, but there is no evidence that it is much higher than during the previous months. Growth during the second year follows a similar pattern to that of the first: rapid growth in spring and early summer, increased standard deviation, and high mortality rates. At 24 months there is a clear difference between the mean shell length of the algal dominated populations (1 and 3, about 18.5 mm.) and that of the populations on barnacled rocks (2 and 4, about 14.7 mm.). The inter-population differences are still small compared with those found within a population (e.g. 12-28 mm.)
During the succeeding years (data from marked individuals) the mean growth curves of the four populations steadily diverge (fig. 20); the intra-population variation in growth rate is reduced; yet the tendency for the individuals in a population to maintain initial differences in growth rate is still found. The apparent contradiction between these last two facts would be resolved if (a) competition for food between individuals in a population produced an upper limit for growth rates in that population and (b) if failure to find sufficient food for a certain minimum rate of growth resulted in death.

Experimental evidence will be produced later showing that competition for food did occur and did limit growth. The second point of the theory (b) may seem rather obvious until it is remembered that the lowest viable growth rate in Population 1 was considerably higher than that of Population 4 (compare figs. 7 and 18). It is easy to see that starved individuals will die, but it is difficult to see why the lethal limit (as measured by growth rate) should vary between populations. The planktonic dispersion of limpet larvae makes it extremely unlikely that there was any genetic difference between the populations at settlement; and since growth rates in the older limpets could be experimentally altered (see later) there did not seem to be any post-settlement selection of different genetic growth potentials in the different populations.
Mortality from causes other than that of starvation and associated weakness did occur but formed only a small part of the total death rate; moreover it is difficult to see how much mortality could produce the observed higher death rate of slow-growing limpets. It seems that each individual must maintain a certain rate of growth, which is dependent on the local conditions, or die. These local conditions include not only the physical and biotic factors normally listed, but also possibly such factors as the metabolic rates of the individual and stresses of competition.

The inverse relationship between longevity and growth-rate noted by Fischer-Piette (1948) is fully confirmed by the present studies (see figs. 20 and 21), as is the positive correlation between growth rate and maximum size. The faster the growth, the greater the maximum size but the shorter the life - this is a summary of the pattern of growth for a population of Patella vulgata. There remains the question of how this pattern is regulated and controlled. Bourlière (1957) has reviewed the connections between metabolic rates and ageing. He shows that the mean length of life in Daphnia is inversely related to temperature; that the life span is also inversely related to the food supply; and that the metabolic rate (measured by the heart beat) increases with a rise in temperature or an increase in food supply. Thus, generally speaking, better conditions produce an increased metabolic rate and a shortening of the life span. This simple picture does not
apply to some lower animals in which ageing does not occur, and is considerably complicated in some higher animals (e.g. mammals, some insects) with determinate growth. However there is no a priori reason why it should not apply to limpets and it does fit the available facts. I was not able to investigate the physiological aspects of this problem in Patella and the only information available for prosobranchs relates to a Californian species of Acmaea, which has a similar habitat to Patella vulgata and is a member of the same super-family. Low-level populations of this animal were found to have a higher heart-beat rate at the same temperature than high-level populations. Segal (1956) regarded this as "thermal acclimation" (i.e. acclimatization) but since he did not determine growth rate, it is possible that the difference arose from the presumably greater growth rate at low level. The problem of metabolic rates is now being investigated in Patella vulgata by Mr. P. Davies (Ph.D. student at Millport, personal communication).

Although some of the foregoing argument is only conjecture, there are enough data to place some doubt on the explanations of Fischer-Piette (1948) of the causes of the differences in growth rate between limpet populations. He suggested that growth is favoured by currents and by a high organic content in the water. He did not suggest how these factors actually affect growth, and the only evidence for the
idea seemed to be the correlation of high growth rate with these factors. At Mount Batten, the range of growth rates was nearly as great as that on the shores Fischer-Piette investigated, but there was no evidence for any difference in the currents or the organic content of the water on the various parts of the shore.

Sub-section B : Reproduction

5. Sexual maturity and sex change

In order to determine the timing of sexual maturity and sex-change, very large samples (600 - 1200) from each of the standard populations were analysed during the 1959 breeding season. The proportions of immature, male and female individuals in each 5 mm. shell length size grouping were calculated and are plotted in figs. 22 and 23. In each population there is a size at which all individuals are male. This size varies from 32 mm. in Population 1 to 18 mm. in Population 4, but in each case it corresponds to the mean size of a three year old limpet for that community. The first females appear at four years of age and the change of sex appears to be strictly governed by age. Fig. 24 compares the samples representing Population 3, were taken from a rather lower area on the shore than they should have been for strict equivalence, because sufficient sup lies were not available at the right level.
the change to female in Populations 1 and 4. Even allowing
for errors in converting shell length measurements to mean age,
the similarity of the process of sex change in the two popula-
tions is very close. It seems clear from these results that
about half the males change sex between three and six years of
age. It is not clear whether this process continues at a
diminishing rate after that or whether there are two genetically
different kinds of male, one which will change and one that
does not.

The date on first sexual maturity show that in all
the populations first year limpets were immature and third
year limpets were all functioning males. In Population 1, at
least 95% of the second year limpets were immature; in Population
2 only about 10% were immature and in Population 4 about 50%
were immature. The gonad formed by the second year limpets is
always very small, often needing the use of a hand lens to
discover it, and for practical purposes gamete production can
be said to start in the third year.

6. The seasonal gonad cycle

The gonad index which Orton devised for investigating
the gonad cycle in Patella is reproduced in fig. 25 (from Orton
et al, 1956). The index is quantitatively based and therefore
a great advance on the use of descriptive terms such as ripe
or full. The index is easy to use and large samples can be
measured rapidly (an important point since only fresh material
Some criticism must be made of the way in which the index was actually used by Orton. In the first place it is mathematically improper (and biologically misleading) to treat the stages as if they were additive, which is what Orton did in calculating the 'mean state of development' of each sample. The volume of the gonad in stage V is clearly more than five times that of stage I. In the present work a conversion of the index was made which expresses each stage as a relative volume. In stage I the gonad volume is 2.75% of the volume of the total visceral mass, in stage II 8%, in stage III 20%, in stage IV 47%, and in stage V 63%. Using these figures the different stages can be added and a proper average given for the sample.

The second criticism is that Orton did not take adequate steps to investigate or allow for possible variation in relative gonad size with age, habitat, or sex. He used only specimens about 30 mm. shell length and these were collected from approximately the same tide level. These precautions meant that the samples contained approximately equal numbers of each sex and that the minimum age of the specimens was 3 years. This still leaves room for very considerable variation in size, age, sex and growth rate in the samples. In the present work the sexes were treated separately; samples were taken from a particular population; and only individuals above the size at
which one third of the population was female were used in the general gonad cycle surveys. Each sample consisted of 50-100 specimens.

The third criticism relates to Orton's opinion that developing and spawning stages could be separated by visual examination. He stated that this was a difficult and subjective distinction requiring considerable experience. No such distinction was made in the present work, and as later evidence will show, it is doubtful whether Orton's separations were as accurate as he supposed.

Despite these criticisms and modifications of Orton's method, the general form of the gonad cycle at Mount Batten in 1959-60 was similar to that reported by Orton for the Plymouth Breakwater 1946-9. It is only when the quantitative aspects are discussed that significant differences in the conclusions are found. The new method of plotting the gonad index data automatically produces a sharper rise and fall (in the graph of gonad development and decline) than Orton's method would give. That the new method is a real improvement on the old is supported by the fact that the more nearly equivalent and more homogeneous samples of the present work also produce a sharpening of the graph of gonad development. The gonad cycle for Population 2 is shown in fig. 26 (the full results for all the standard populations are given in Table 6) and should be compared with
Orton's results reproduced in fig. 27. In Population 2 the gonad began to develop in August, and increased in size rapidly and continuously until the beginning of November. Between 5th and 14th of November in 1959, and between 1st and 2nd November 1960, there was a sharp drop in gonad volume. In 1959 this decrease in volume continued rapidly until the end of November and then slowed down. This decrease is taken to indicate spawning, which appears from this evidence to take place almost entirely (a two-thirds drop in gonad volume) during November. Orton's results of the time of the onset of spawning are thus confirmed, but his view that spawning was slow and continued for several months is questioned. The ripe gametes will probably occupy most of the volume of the gonad, but as Orton himself points out, post-spawning gonads contain considerable empty spaces (between the remaining eggs or as near-empty tubules). For this reason the two-thirds fall in gonad volume probably represents the voiding of all the ripe gametes formed up to that time. It is possible that further gametes are produced, ripened and released after this, but the process would have to be slow and continuous and the gametes would therefore stand little chance of achieving fertilization. All the populations at Mount Batten began spawning at the same time (see fig. 28) and rapid synchronous spawning is typical of shore organisms. From the evidence of the gonad cycle alone it seems most likely that spawning in Patella vulgata is sudden and synchronous and takes place about the first fortnight in November.
7. Variations in gonad development

A comparison of the males and females in Population 2 (fig. 26) shows that ovaries were consistently smaller than testes during the breeding season. In each standard population, the female gonads just prior to spawning were between three-fifths and four-fifths the size of the male gonads. The testis when ripe was whitish and, against the dark viscera, tended to look larger than a green-brown ovary of the same size. The possibility of a systematic error due to this was real, but does not account for all the observed inter-sexual difference, as is shown by the fact that the males began developing sooner than the females, and a size difference was apparent before the testes became white.

The development of the males from the four standard populations is compared in fig. 28. The gonads of Populations 1 and 3 began developing earlier, increased in size more rapidly, and reached a greater relative size before spawning than did those from Populations 2 and 4. A comparison of the females of each population shows that they followed a similar pattern (see Table 6).

In order to investigate the variation of relative gonad size with age, some very large samples (100 - 300), covering all sizes, were taken at intervals from Populations 1, 2, and 4. The results of three of these samples from Population
are given in fig. 29. In two year old individuals any gonad that may be developed is very small and for practical purposes insignificant. The testes of three year old individuals developed to about 20% of the volume of the whole visceral mass before spawning began. In limpets of four years of age and upwards the maximum development of the gonad was around 48% of the visceral mass. There may have been a small increase in the relative size of the ripe testes after 4 years but it must have been less than 2.5% per annum, and it seems more likely that a constant level of relative size was maintained after the 4th year. During development and spawning, limpets four years of age and over, all maintained the same relative gonad size. Limpets three years of age not only had relatively smaller gonads before spawning; they also failed to spawn properly (no decrease in relative volume of the gonad at the appropriate time). For these reasons it seems useful to regard only such limpets as are four or more years old as fully mature 'adults'. It will be remembered that samples for the gonad cycle survey included only those individuals above that size at which at least one third had become female. This ensured that almost all the individuals in the sample were four or more years old.

In Population 4, the same pattern of variation with age occurred as just described for Population 1, the only difference being the consistently lower size of the gonad at all ages. The three year old limpets developed to about 12%
Table 6. The average volume of gonad (sexes separated where possible), expressed as % of the total visceral mass. Four populations at Mount Batten, Plymouth 1959-60.

<table>
<thead>
<tr>
<th>Date</th>
<th>Population sampled:</th>
<th>1</th>
<th>3x</th>
<th>2</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 Apr.</td>
<td>σ♀ 7.6 σ♂ 3.3</td>
<td>σ♀ 2.1</td>
<td>σ♂ 1.4</td>
<td>σ♀ 0.3</td>
<td></td>
</tr>
<tr>
<td>27 Apr.</td>
<td>1.9</td>
<td>1.6</td>
<td>0.8</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>25 May</td>
<td>1.6</td>
<td>1.6</td>
<td>0.9</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>16 June</td>
<td>1.9</td>
<td>1.9</td>
<td>1.2</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>21 July</td>
<td>1.6</td>
<td>2.2</td>
<td>1.8</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>24 Aug.</td>
<td>6.2 σ♀ 3.3 σ♂ 3.1</td>
<td>3.9</td>
<td>3.4</td>
<td>2.5</td>
<td>1.8</td>
</tr>
<tr>
<td>3 Sept.</td>
<td>13.4 σ♀ 7.8 σ♂ 5.8</td>
<td>12.6</td>
<td>5.8</td>
<td>4.5</td>
<td>2.6</td>
</tr>
<tr>
<td>22 Sept.</td>
<td>21.6 17.5</td>
<td>20.1</td>
<td>18.8</td>
<td>12.1</td>
<td>7.4</td>
</tr>
<tr>
<td>7 Oct.</td>
<td>34.1 28.5</td>
<td>32.3</td>
<td>23.6</td>
<td>13.0</td>
<td>8.9</td>
</tr>
<tr>
<td>24 Oct.</td>
<td>-</td>
<td>33.3</td>
<td>33.6</td>
<td>17.5</td>
<td>14.8</td>
</tr>
<tr>
<td>5 Nov.</td>
<td>46.6 40.4</td>
<td>-</td>
<td>-</td>
<td>32.2</td>
<td>19.2</td>
</tr>
<tr>
<td>14 Nov.</td>
<td>32.0 15.6</td>
<td>-</td>
<td>-</td>
<td>18.3</td>
<td>12.2</td>
</tr>
<tr>
<td>17 Nov.</td>
<td>30.3 16.9</td>
<td>-</td>
<td>-</td>
<td>16.1</td>
<td>9.9</td>
</tr>
<tr>
<td>28 Nov.</td>
<td>23.0 13.6</td>
<td>15.9</td>
<td>9.1</td>
<td>10.4</td>
<td>5.5</td>
</tr>
<tr>
<td>17 Dec.</td>
<td>11.9 7.8</td>
<td>10.2</td>
<td>7.0</td>
<td>7.6</td>
<td>4.3</td>
</tr>
<tr>
<td>16 Jan.</td>
<td>8.1 4.6</td>
<td>8.8</td>
<td>6.5</td>
<td>7.0</td>
<td>5.2</td>
</tr>
</tbody>
</table>
Thus the relative size of the ripe male gonad in *Patella vulgata* was governed by the age of the individual and its habitat. It is important to note that there was no direct relationship between the size of an individual and the relative size of its ripe gonad. An individual from Population 4 with a shell length of 25 mm. had a ripe testis forming about 20% of the visceral mass and an individual from Population 1 of the same shell length had a ripe testis forming only about 5% of the visceral mass. Furthermore, the individual from Population 4 was fully mature and representative of the adult condition in its population, but the individual from Population 1 was definitely immature and quite unrepresentative.

8. **Spawning**

The gonad index indicated the timing and pattern of the gonad cycle, and showed which factors affected the relative size of the gonad. Certain inherent disadvantages in the gonad index, however, prevented it from giving a completely quantitative picture of absolute fecundity or the rate of spawning. Gonad index assessment was entirely subjective and there were only five stages to describe what must have been a continuous process. The index measured only relative volumes of the gonads not the absolute ones, and it was quite possible for the volume of the visceral mass to alter. Such alteration would
affect the interpretation of the results but would not be detectable or measurable. Finally the density of the gonad could vary without detection, and thus there was no direct connection between the numbers of gametes produced and the gonad index, or between the drop in gonad index and the rate of spawning. For these reasons another method was sought.

It was found that the eggs in a ripe ovary could easily be separated from the gonad tissue. Although the eggs were heavier than water and sank fairly rapidly, it was possible to stir them into a uniform suspension for sufficient time to take representative samples. The total number of eggs in an individual limpet was estimated by counting all the eggs in three samples (0.58 cc. each - the dilution arranged so that each of these contained 200-300 eggs), averaging the results, and multiplying by the appropriate dilution factor. Counting was done on squared slides at a magnification of x 50. Only ripe eggs were counted, these were distinguished by the swelling and eventual disappearance of the chorion, and the rounding of the egg after removal from the ovary. Dodd (1957) has shown that only eggs with these characteristics are capable of being fertilized and developing normally. No significant variation in the size of ripe eggs was found either between individuals of different age or habitat, or inside a single ovary.

Egg counts were made of samples from Populations 1, 2, and 4 on November 5th, 1959, when gonad development reached
its peak. The results (egg numbers on a log. scale against shell length) are shown in fig. 31. The variation within a population is not easy to systematize, but all the results taken together lie near the upper line shown in the figure. The approximate average results for the Populations are:

Population 1  500,000 eggs per individual, mean shell length of females 52 mm.
Population 2  90,000 eggs per individual, mean shell length of females 39 mm.
Population 4  27,000 eggs per individual, mean shell length of females 28 mm.

In these samples almost all (95% +) the eggs appeared to be ripe, whole and normal. The individual eggs counts are subject to an error of + 10%.

Further counts were made on the 14th and 17th of November when the gonad index had dropped sharply. There was no significant difference between the results obtained on these two days and the results are plotted together in fig. 32. The variation of egg number at the same shell length was even greater than on the 5th, but most results lie near the lower line shown in the figure. This line is parallel to and ten times lower than the line representing the results of the 5th. The simplest and most likely explanation of these results is that most of the individuals spawned about 90% of their eggs between the 5th and the 14th of November, but that a few did
not spawn at all. In the samples of the 14th and 17th, many of the eggs (up to 30%) that remained were visibly deformed, broken or unripe, suggesting that all ripe eggs had been spawned and that the remainder were either unripe or failures of some kind.

Further counts were made on 28th November, 17th December, and 16th January. The number of eggs decreased slowly, but the most striking change was a very rapid increase in the proportion of broken and deformed eggs, their appearance strongly suggesting that resorption was taking place. By January 16th the great majority of even those eggs with full sized membranes had lost some of their contents.

In 1959 spawning took place during the nine days 5th - 14th November, but no samples were taken between those dates. In 1960, it was possible to show that spawning took place within 24 hours after the morning of November 1st (see fig. 33). The evidence from the egg counts shows that spawning is sudden, complete and synchronous. However, it is easy to see how earlier workers came to believe that spawning went on for a considerable time. An individual from Population 1 in the middle of December 1959 had an ovary containing 50,000 eggs and occupying 20% of the visceral mass. Unless it was known that it previously held more than 500,000 eggs and that the remaining eggs were being resorbed it is unlikely that one would risk calling it fully spent.
Orton et al. (1956) suggested that heavy onshore winds and waves were the trigger for the start of spawning. On the 13th November, 1959 there occurred one of the biggest Channel storms for many years, and during the day and night of the 1st November, 1960 there was a gale and heavy wave action in the Plymouth area. Lubet (1955) showed that in *Mytilus edulis* spawning was not possible before the release of neurosecretory granules from the visceral and cerebral ganglia, but that when this had occurred, a sharp change in temperature, or mechanical stimulation, could trigger off spawning. In many marine organisms with external fertilization, gametes (or gamete extracts) can stimulate spawning. A severe gale is likely to be accompanied by sharp changes in air (and possibly inshore sea) temperatures. The generated waves will produce increased mechanical stimulation of all kinds. The gametes of some limpets will probably be forcibly released if the gonad is sufficiently developed. Thus three possible spawning stimuli will be present at the same time, and although *Patella vulgata* undoubted spawns at the time of such gales, it is difficult to say which stimuli are actually effective. Most probably they reinforce one another and insure the rapid, synchronous spawning observed. A few individuals did not spawn at all and these were mostly isolated individuals. Medem (1942) suggested that propinquity was a requirement for successful reproduction in *Patella vulgata*. It seems likely that a high level of chemical stimulation from the gametes of
nearby individuals is an important factor for the spawning of at least some individuals.

Samples throughout the gonad cycle were preserved in Bouin's fixative for investigation into neurosecretory mechanisms by Dr. D.B. Carlisle.

Several reports have been received of spawning in *Patella vulgata* being visible on the shore. The best documented of these is by Dr. Jefferson of Cardiff University. He reports (personal communication) that on 26th September, 1957 at Castlebeach, Dale, Pembrokeshire, most of the limpets were seen to be spawning. Mr. J.H. Barrett, Warden of Dale Fort Field Centre, has noticed the phenomenon on at least two occasions in the years 1948–58, and describes it as puddles of light coloured fluid around each limpet (personal communication). These observations seem to fit the theory of rapid, synchronous spawning. Because of the time of year at which it occurs and the association with it of bad weather it is not very surprising that the process has rarely been noticed. There is an even chance that the phenomenon will occur during the night, as seems to have happened at Mount Batten on 1st November, 1960, and there is also the possibility that the whole process may sometimes take place during the time when the limpets are covered by the tide.
9. **The measurement and variation of fecundity**

The number of eggs produced seems an accurate measure of fecundity and reproductive potential both for an individual and for a population. No variation in egg size is known, nor does the proportion of eggs spawned vary, so total egg production is a comparative quantity.

Although there was a general correlation between the size of female limpets at Mount Batten and the number of eggs they produced, the variation of egg production with size within a particular population was probably of a different order (compare figs. 31 and 34). Within each population there seemed to be a slight increase in egg numbers with increasing size, weight and age, but this was largely obscured by the large individual variation and the small range of female size (see fig. 33). The individual variation is partly due to the counting error (+10%), but also to some unexplained differences in "prosperity" between limpets of equal size in the same population. This individual variation is greatest in the slow-growing Populations and least in the fast-growing ones – Population 4 (+60%); Population 2 (+40%); Population 1 (+20%) are the approximate values. This suggests that egg production is a delicate and sensitive measure of individual "prosperity", a view also supported by the analysis of inter-population variation.

Population 1 females not only produce a larger total
number of eggs than those from Population 2, (as is only to be expected since they are larger), they also produce more eggs per unit weight. Population 1 females produce an average of 31,000 eggs per gram total wet weight (i.e. whole animal including shell). The corresponding figure for Population 2 is 9,900 per gram and for Population 4 is 5,700. Taking these figures as measures of efficiency in egg production, Population 1 females are three times as efficient as those from Population 2 and five and a half times as efficient as those from Population 4.

10. Larval life, settlement and the establishment of homes

Although artificial fertilizations have frequently been made and the whole process of embryology and larval development studied from embryos produced in the laboratory by this process, scarcely anything is known about the same processes in natural conditions. Between spawning and the settlement of the metamorphosed larvae, the only information available is that larvae may be recovered from the sea in small numbers (Smith, 1935; Lebour, 1937). Even the actual process and timing of settlement is unknown since the tiny spat cannot be seen until they reach a shell length of about 1 mm.

In an attempt to discover some facts about larval life, two-nettings were made inside Plymouth Sound at weekly intervals from September to January 1959-60. Not a single limpet larva or even egg was found at any time. There seemed nothing wrong
with the type of net or method of hauling, since plenty of Rissoa
and other mollusc larvae of the same size as Patella larvae
were caught. Further tow-nettings were made both inside and
outside the Sound in 1960 at a time when the larvae must have
been somewhere in the vicinity (i.e. 5, 10, and 15 days after
spawning); but again without success. No satisfactory explana-
tion can be offered for this failure; it may be that the limpet
larvae remain on the bottom most of the time, or that their
numbers are very small compared with the other plankton.

Limpet spat were found on the damp rocks and in
crevices from February onwards. Very careful search of small
areas with the aid of a hand lens and a fine needle revealed
limpets down to 1 mm. shell length. From February to July the
numbers of first year limpets in a given area increased, but
this was apparently due to their rapid growth making them
easier to detect. From July onwards, heavy and continuous
mortality was detectable in these first year limpets and it seems
certain that this also occurred back to the time of settlement -
presumably at the end of November. Thus definitive counts of
the latest settlement could not be given until July, when the
numbers were of eight month old survivors. The approximate
numbers per square metre were 200 in Population 1, 100 in Popula-

Spat less than six months old, or less than 2 mm. shell
length, did not survive if the surface to which they were attached
dried out for more than a few minutes (certainly less than 30 minutes). Survival for one year only occurred where there was freedom from such desiccation. Whether such sites are actively selected at settlement is not known, but limpets a few months old (which do not home) did tend to retreat into crevices and beneath algae as the tide went down. All limpets are very slow-moving - 25 cm. out and back again was a typical feeding excursion for an adult limpet and might take two or three hours. The equivalent distance for a six-month old limpet (relative to shell length) would be only about $2\frac{3}{2}$ cm.

A limpet of 1 mm. shell length has a radula 0.9 mm. long and only 0.025 mm. wide. These tiny spat were observed to graze in exactly the same way as the adults, rasping the surface with short forward strokes of the radula. Survival of spat only occurred on relatively clean surfaces i.e. those not coated with mud or silt; not covered with encrusting sponges, polyzoa, tunicates and hydroids; and not having a dense growth of algae (not even small Enteromorpha sporelings). The delicate feeding mechanism of the young limpets is probably unable to work efficiently except on surfaces which are smooth relative to the width of the radula, i.e. microscopically smooth.

On the upper and barnacled parts of the shore, spat survived only in cracks and crevices, and on the edges of pools. Those in pools were easy to find, but only very careful splitting of the rock with a sharp chisel revealed the much more numerous
spat in tiny crevices. In the fucoid dominated areas, limpet spat were found mainly at the edges of the algal areas where the rock was kept clean by adult grazing but was nevertheless shaded and kept damp by the adjacent fucoids.

The following list of places on the Mount Batten shore, where limpet spat successfully survived, shows roughly the suitability order down the shore, although considerable overlap occurs.

1. Large shaded cracks, 2. Small crevices, 3. The edges of large pools, 4. Small pools, 5. Limpet-cleared rocks shaded by fucoids, 6. Limpet-cleared rocks shaded by seasonal green and red algae (including those growing on adult limpet shell). 2 and 5 were by far the most important habitats in numbers of spat which they supported, but the others are interesting from the theoretical viewpoint. Each of these habitats had a survival range for limpet spat - the upper limit being controlled by desiccation and the lower limit by the occupation of the habitat by other organisms (either algae or encrusting animals). Silt was also a limiting factor in some places, but its action was governed by local topography rather than shore level, though it was more common at the lower levels generally.

Suitably damp habitats for successful limpet survival and growth were only clear of other organisms either because they were small, shaded, and fairly high on the shore; or because they were continually grazed by adult limpets. On the lower parts of the shore there is thus a strong tendency for successful settlement to occur only in the immediate vicinity of adult limpets,
a quite different form of gregariousness from that which occurs in barnacles.

The number of limpet spat surviving on barnacled rocks was much smaller than in the algal dominated regions, yet it seemed to be quite adequate as a replacement for the populations there. The factors which decrease the available sites for successful settlement correlate with a reduction in the growth rate and mortality rate of the adults. There is no need to postulate any large scale movements of young limpets to the upper parts of the shore, and no such migrations were observed. This contrasts with the upward migration of young Littorina littorea (Smith and Newell, 1955) and of young Nucella lapillus (Moore, 1938).

The weight increase of the limpet spat during the first year of life is enormous, probably about a thousandfold. The simplest physical requirements — living space, the size of suitable food etc. — will alter very rapidly during the first twelve months. These first year limpets did not home at all, but moved about inside their micro habitats at first and then later from one damp area to another. During the second year, resistance to desiccation was nearly as good as that of the adults, and the establishment of homes began to take place. This process was most easily followed in Population 2. The limpets first came out of the crevices at about 5 mm. shell length and moved from one damp crack to another at irregular intervals. When about 10 mm. in length they occupied small damp hollows
(which dried out occasionally) and would remain in these for several weeks at a time. By the end of the second year some limpets had established permanent homes, the most common method being the occupation of the scar (i.e. home, free from barnacles) of an adult limpet which had died or moved. Others would establish a permanent home in a place where the barnacle cover was not complete, gradually squeezing out the surrounding barnacles to form a complete shell contact with the rock. This was a dangerous time for the limpet, for if the barnacles died suddenly before the shell had undercut them there was a temporary gap between the shell and the rock, through which evaporation could take place. When barnacles were picked away with a needle, exposing such gaps, about half the limpets disappeared (presumed dead - since they were marked), some grew a piece of shell rapidly to fill the gap, and others migrated back to the damp cracks and hollows.

In Population 4 the process of establishing permanent homes is very similar to that in Population 2, although the switch from crevices to permanent homes is more rapid and decisive, often taking place by one move. In Population 1 where much of the area is permanently damp the process is slow and, even in the adults, never proceeds so far without as those in Population 2. Some second and third year limpets have temporary homes, others continue to wander freely. The oldest limpets keep to roughly constant positions in the centre of the clearings.
Fig. 22 The proportions of the sexes in each 5 mm shell length size group of Population 1 (solid dots) and Population 5 (circles). Males above the line, neuter to the left, females at right. The mean age in years for Population 1 is given at the base.

Fig. 25 The proportions of the sexes in each 5 mm size group of Population 2 (circles) and Population 4 (solid dots). The mean age in years of Population 4 is given at the base.
Fig. 24  Sex change with age in Populations 1 (circles) and 4 (solid dots).

Fig. 25  Orton's gonad index. Neuter also represents the resting stage and counts 0. Reproduced from Orton et al (1956).
Fig. 26 The gonad cycle in Population 2. The size of the gonad is expressed as a % of the total visceral mass. The solid line represents the male gonads and the dashed line the females.

Fig. 27 Orton's results for the gonad cycle of *P. vulgata* from the south side of the breakwater, Plymouth. Males and females combined. Gonad size expressed as an average gonad index stage. Redrawn from Orton et al (1956).
Fig. 28 The development of male gonads in the four populations at Mount Batten in 1959. Gonad size is expressed as a % of the volume of the total visceral mass. Solid line Population 1, dashed line Population 5*, dotted line Population 2, dash-dot line Population 4.
Fig. 29 Gonad development plotted against shell length for Population 1 (mean age in years at top). Circles 5/11/59, solid dots 14 and 17/11/59 (immediately post-spawning), circles with lines 22/9/59 (early development).

Fig. 50 Pre-spawning gonad size (5/11/59) against shell length in Population 1 (circles), Population 2 (circles and lines), and Population 4 (solid dots).
Fig. 51 (above) Egg numbers against shell length for Population 1 (circles at right), Population 2 (solid dots centre) and Population 4 (circles at left) on 5/11/59.

Fig. 52 (below) The same on 14 and 17/11/59.

The dashed lines are in the same position on both figures and represent a fall in egg numbers of 90%.
Fig. 53
Egg numbers against shell length in Population 2.
Circles 1/11/60
Solid dots 2/11/60

Fig. 54
Egg numbers against shell length in Population 1.
Circles 5/11/59
Dots 14 and 17/11/59
The lower dashed line is the best fit for all but the upper four dots, the dotted line is one of those shown in Fig. 52.
Sub-section C: Population analysis

11. Methods and aims.

Detailed measurements were made of two samples from each of the standard populations. The first sample was collected in February 1959. The second sample comprised the four Groups whose growth rate had been followed for 21 months (removed November 1960). Both samples consisted of the entire population of a small area (about 0.5 m²). The following measurements were made on each of the larger individuals:

1. Total wet weight and shell weight.
2. Shell length, breadth, and height.
3. Sex and gonad index.
4. Radula length and the number of rows of teeth.

Below 20 mm. shell length, if the number of specimens was very large, only a sub-sample was measured.

The principal difficulty in analysing differences of any kind between individuals or populations of *Patella vulgata* is the lack of suitable constants or standards which could form a basis for comparison. In the past, most authors have used shell length as a standard for comparison. Two other possibilities are age (or growth rate), and weight. The advantages and disadvantages of these three standards are set out below:

**Ages:** By far the best standard, since time is independent of any limpet activity.

Very difficult to determine (see Section II sub-section A)
Weights: Reasonably easy to determine; genuinely additive quantities; more meaningful biologically and with more equivalence than shell length.

The inert shell forms 60 - 70% of the total weight, so that small changes in shell thickness or shape tend to obscure more significant differences in body weight. Even if body weight is used, there is the problem of seasonal variation (up to 20% of body weight is lost at spawning) as well as inaccuracies due to variability in gut content and the degree of hydration. Weights cannot be measured without removal of the animals.

Shell lengths: The simplest and most rapidly made measurements; can be determined without disturbing the animals.

Even inside a particular population, the equivalence of individuals of equal shell length is only approximate, and the degree of approximation is difficult to determine. Between different populations there is no equivalence whatever (equal shell length does not mean equal age, weight, volume or anything else of real interest).

No simple solution was found to these difficulties. The first step was the selection by eye of the four standard populations (see section II, 1). Each of these populations has already been shown to be more or less homogenous as regards growth rate, sex proportions, rate of gonad development and fecundity (see section II parts 4, 5, 7, and 9 respectively). The second step was to characterise the structure of the four standard populations
in quantitative terms and to show that these structures were more or less stable. The third step was to determine the variation with age of such functions as relative shell height and radula ratio. To do this, the functions were first plotted against shell length (a rough measure of age) in each of the standard populations. Then the fast-growing and the slow-growing populations were compared, the large differences of age at a particular shell length making it easier to see the trend of the variation with age.

The general aim was to find functions which were easy to determine and reasonably accurate measures of age or growth rate.

12. Numbers, sizes and weights.

The total number of *Patella vulgata* individuals per metre$^2$ in each of the four standard populations in November 1960 were:

- Population 1, 156
- Population 2, 218
- Population 3, 198
- Population 4, 116

It has already been shown that the numbers of small limpets fluctuate considerably with season, and in any case it makes for clearer comparisons if the smallest individuals are ignored when discussing population density. The numbers of limpets of 20 mm. shell length and above (November 1960) were:

- Population 1, 42 per m$^2$
- Population 2, 95 per m$^2$
- Population 3, 123 per m$^2$
- Population 4, 83 per m$^2$

These figures show the same trend of population density recorded
by Fischer-Piette (1948). He found a high density in barnacled areas, a very high density at the edge of the fucoid regions, and a low density amongst the fucoids. An even better method of measuring population density would be to exclude from the total numbers individuals less than 3 years old (i.e. the totally immature, see II, 7). The figures for the standard populations were: (comparison with the previous figures shown)

<table>
<thead>
<tr>
<th>Population</th>
<th>Individuals</th>
<th>Individuals</th>
<th>Total Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>19</td>
<td>42</td>
<td>156</td>
</tr>
<tr>
<td>2</td>
<td>91</td>
<td>95</td>
<td>218</td>
</tr>
<tr>
<td>3</td>
<td>106</td>
<td>123</td>
<td>198</td>
</tr>
<tr>
<td>4</td>
<td>91</td>
<td>83</td>
<td>116</td>
</tr>
</tbody>
</table>

These figures show that numbers per unit area are not good comparative quantities unless some aspect of the population structure, such as the distribution of numbers with size or age, is also considered at the same time. Figs. 35 to 38 show the numbers of limpets in each mm. size group (shell length) per square metre of rock surface, in each of the standard populations. These diagrams are comparative and adequately demonstrate the differences between the populations in such points as maximum size, numbers of small limpets, etc. These comparisons are, however, restricted to particular aspects of the populations; it is not possible to sum up these differences in a single comparable quantity, mainly because shell lengths are not additive terms.

A more serious objection to all comparisons which include an area measurement is that there is a great difference between available area and occupied area in some populations. In Popula—
tion 1, the clearings actually occupied by limpets formed less than 30% of the total surface area in that zone. In Population 4, the population thinned out slowly at the top of the shore, so that population density depended on the exact position of the area chosen for the sample. Population 3 was a border population, the density varying sharply on both sides of the Ascophyllum border, so that density varied with the width of the sample area across this line. Only in Population 2 was there little variation of density with the size or position of the sample area.

Occupied area has been used in all the calculations of the present work and the sample areas have been chosen from typical parts of each population. This gives reasonably satisfactory results, but a method of comparison not dependent on area would be a great improvement.

Figs. 39 to 42 show the variation of weight with shell length in the four standard populations. The weight is total wet weight of specimens fixed and preserved in formalin. The limpets were collected in November 1960, after spawning had occurred. When the weights are plotted logarithmically the relationship with shell length is described by a slightly curved line. The deviation from a straight line is partly caused by the fact that the larger individuals release as gametes a larger percentage of their weight than smaller ones, and partly by the fact that the largest specimens had slightly lower relative shell heights (see later). Populations 2, 3 and 4 had approximately the same mean values of weight at all shell lengths, but Population 1 had
consistently lower values:

<table>
<thead>
<tr>
<th>Shell Length</th>
<th>Population 1</th>
<th>Populations 2, 3 and 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 mm.</td>
<td>0.09 grams</td>
<td>0.12 grams</td>
</tr>
<tr>
<td>20 mm.</td>
<td>0.45 &quot;</td>
<td>0.74 &quot;</td>
</tr>
<tr>
<td>30 mm.</td>
<td>1.9 &quot;</td>
<td>3.8 &quot;</td>
</tr>
<tr>
<td>40 mm.</td>
<td>4.5 &quot;</td>
<td>11.2 &quot; (populations 2 and 3)</td>
</tr>
<tr>
<td>50 mm.</td>
<td>12.8 &quot;</td>
<td>-</td>
</tr>
<tr>
<td>57 mm.</td>
<td>22.0 &quot;</td>
<td>-</td>
</tr>
</tbody>
</table>

Individual variation of weight at constant shell length in a particular population was less than ± 25%. The difference between Population 1 and the other populations was about 100% for most shell lengths.

The total weight per square metre rock surface for the four populations was (November 1960):

- Population 1: 273 grams per m²
- Population 2: 450 grams per m²
- Population 3: 685 grams per m²
- Population 4: 45254 grams per m²

These figures are better estimates of population density than the number of individuals per area, but they also suffer from the lack of a description of population structure and from being related to area.

In order to provide a picture of the weight structure of the populations, accumulative percentage weights were calculated and plotted against shell length (see figs. 43 to 46). The calculations were made as follows: all individuals in each mm.

size group (shell length) were weighed together, and these weights listed. The weights were then transformed into accumulative
weights starting from the smallest size group. The accumulative weights were then expressed as percentages of total weight. The calculation for Population 3 is given as an example in Table 7.

All the graphs of accumulative percentage weight against shell length have the same form - a sigmoid curve. The curves rise very slowly at first, since even large numbers of small limpets form only a small part of the total weight. Between 20% and 80% the curves rise very steeply, showing that the majority of the weight of each population lay within a very narrow size range. The curves slope off slightly before reaching 100% due to the occasional very large individual.

The size at which the steepest rise in the curve took place seemed to be a good quantity for characterising the populations. The 50% accumulative weight size (termed mean size of the population) was used as the precise figure. The mean size in the four populations:

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean Size (mm)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>51.5</td>
<td>(this size is reached in 6 years at the mean rate of growth)</td>
</tr>
<tr>
<td>2</td>
<td>38.5</td>
<td>(see later for discussion)</td>
</tr>
<tr>
<td>3</td>
<td>37.2</td>
<td>(reached in $8\frac{1}{2}$ years)</td>
</tr>
<tr>
<td>4</td>
<td>30.7</td>
<td>(reached in 11 years)</td>
</tr>
</tbody>
</table>

* Figs. 43-46
Table 7. The accumulative percentage weight analysis of
Population 3.

<table>
<thead>
<tr>
<th>mm. size group shell length</th>
<th>Number of individuals</th>
<th>Weight grams.</th>
<th>Accumulative weight grams.</th>
<th>Accumulative % weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 mm.</td>
<td>2</td>
<td>0.042</td>
<td>0.042</td>
<td>Negligible</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>0.062</td>
<td>0.104</td>
<td>&quot;</td>
</tr>
<tr>
<td>7</td>
<td>5</td>
<td>0.187</td>
<td>0.291</td>
<td>&quot;</td>
</tr>
<tr>
<td>8</td>
<td>2</td>
<td>0.104</td>
<td>0.395</td>
<td>&quot;</td>
</tr>
<tr>
<td>9</td>
<td>3</td>
<td>0.227</td>
<td>0.622</td>
<td>&quot;</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>0.192</td>
<td>0.814</td>
<td>&quot;</td>
</tr>
<tr>
<td>11</td>
<td>2</td>
<td>0.275</td>
<td>1.089</td>
<td>&quot;</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>0.133</td>
<td>1.222</td>
<td>0.3</td>
</tr>
<tr>
<td>13</td>
<td>0</td>
<td>0.000</td>
<td>1.222</td>
<td>0.3</td>
</tr>
<tr>
<td>14</td>
<td>2</td>
<td>0.519</td>
<td>1.741</td>
<td>0.5</td>
</tr>
<tr>
<td>15</td>
<td>3</td>
<td>0.981</td>
<td>2.726</td>
<td>0.7</td>
</tr>
<tr>
<td>16</td>
<td>3</td>
<td>1.560</td>
<td>4.280</td>
<td>1.2</td>
</tr>
<tr>
<td>17</td>
<td>0</td>
<td>0.000</td>
<td>4.280</td>
<td>1.2</td>
</tr>
<tr>
<td>18</td>
<td>3</td>
<td>1.730</td>
<td>6.010</td>
<td>1.7</td>
</tr>
<tr>
<td>19</td>
<td>2</td>
<td>2.07</td>
<td>8.08</td>
<td>2.2</td>
</tr>
<tr>
<td>20</td>
<td>3</td>
<td>2.72</td>
<td>10.80</td>
<td>3.0</td>
</tr>
<tr>
<td>21</td>
<td>2</td>
<td>1.74</td>
<td>12.54</td>
<td>3.5</td>
</tr>
<tr>
<td>22</td>
<td>1</td>
<td>1.13</td>
<td>13.67</td>
<td>3.8</td>
</tr>
<tr>
<td>23</td>
<td>3</td>
<td>3.52</td>
<td>17.19</td>
<td>4.8</td>
</tr>
<tr>
<td>24</td>
<td>0</td>
<td>0.00</td>
<td>17.19</td>
<td>4.8</td>
</tr>
<tr>
<td>25</td>
<td>1</td>
<td>1.72</td>
<td>18.91</td>
<td>5.0</td>
</tr>
<tr>
<td>26</td>
<td>0</td>
<td>0.00</td>
<td>18.91</td>
<td>5.0</td>
</tr>
<tr>
<td>27</td>
<td>4</td>
<td>11.1</td>
<td>29.0</td>
<td>8.0</td>
</tr>
<tr>
<td>28</td>
<td>3</td>
<td>9.9</td>
<td>38.9</td>
<td>10.5</td>
</tr>
<tr>
<td>29</td>
<td>3</td>
<td>11.4</td>
<td>50.3</td>
<td>14.0</td>
</tr>
<tr>
<td>30</td>
<td>3</td>
<td>13.4</td>
<td>63.7</td>
<td>17.5</td>
</tr>
</tbody>
</table>

(Continued overleaf)
Table 7. (Continued)

<table>
<thead>
<tr>
<th>mm. size group</th>
<th>Number of shell individuals</th>
<th>Weight of grams.</th>
<th>Accumulative weight grams.</th>
<th>Accumulative % weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>31</td>
<td>1</td>
<td>3.5</td>
<td>67.2</td>
<td>18.5</td>
</tr>
<tr>
<td>32</td>
<td>4</td>
<td>17.5</td>
<td>84.7</td>
<td>32.23</td>
</tr>
<tr>
<td>33</td>
<td>3</td>
<td>16.5</td>
<td>101.2</td>
<td>28</td>
</tr>
<tr>
<td>34</td>
<td>3</td>
<td>17.7</td>
<td>118.9</td>
<td>33</td>
</tr>
<tr>
<td>35</td>
<td>2</td>
<td>15.6</td>
<td>134.5</td>
<td>37</td>
</tr>
<tr>
<td>36</td>
<td>3</td>
<td>21.4</td>
<td>155.9</td>
<td>43</td>
</tr>
<tr>
<td>37</td>
<td>5</td>
<td>41.4</td>
<td>197.3</td>
<td>54.5</td>
</tr>
<tr>
<td>38</td>
<td>3</td>
<td>25.6</td>
<td>222.9</td>
<td>61.5</td>
</tr>
<tr>
<td>39</td>
<td>5</td>
<td>54.3</td>
<td>277.2</td>
<td>77</td>
</tr>
<tr>
<td>40</td>
<td>2</td>
<td>24.0</td>
<td>301.2</td>
<td>83</td>
</tr>
<tr>
<td>41-42</td>
<td>-</td>
<td>-</td>
<td>301.2</td>
<td>83</td>
</tr>
<tr>
<td>43</td>
<td>1</td>
<td>13.0</td>
<td>314.2</td>
<td>87</td>
</tr>
<tr>
<td>44</td>
<td>2</td>
<td>28.2</td>
<td>342.4</td>
<td>95</td>
</tr>
<tr>
<td>43-47</td>
<td>-</td>
<td>-</td>
<td>342.4</td>
<td>95</td>
</tr>
<tr>
<td>48</td>
<td>1</td>
<td>19.3</td>
<td>361.7</td>
<td>100%</td>
</tr>
</tbody>
</table>

N.B. (I) These accumulative percentage weights are plotted in fig. 45.

(II) The very sharp rise in acc. % weight between 33 and 39 mm.

(III) The absence of the single very large individual (48 mm.) would only alter the mean size by about 0.4 mm. in spite of the fact that it weighs as much as all the 42 limpets less than 26 mm. put together.
Mean size is an excellent descriptive characteristic of *Patella* populations. It combines the advantages of all three methods of comparisons, since it uses both weights and shell lengths, and is clearly related to growth rate. It does not depend on any measurement of area, although, of course, the sample must be collected entirely within the particular population being studied. The average weight of the mean size is also a useful quantity:

<table>
<thead>
<tr>
<th>Population 1</th>
<th>14.5 grams</th>
<th>Population 3</th>
<th>8.5 grams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population 2</td>
<td>8.9 &quot;</td>
<td>Population 4</td>
<td>4.0 &quot;</td>
</tr>
</tbody>
</table>

13. **Shell variation**

The shell in *Patella vulgata* varies in shape, size, thickness, sculpture and colouring (both internal pigment patterns and surface stainings and iridescent colours). The main subject for discussion here is the variation of shape and its causes.

In the pre-metamorphic veliger the larval shell has a deep cup-shape - forming about half a coil. At metamorphosis a peristome develops from the rim of the cup, and gradually forms a roughly conical shell. Settlement occurs at this stage. See fig. 47 redrawn from Dodd (1957). The larval shell remains as a small cap just behind and slightly to the left of the peak of the main shell. The larval shell and the first part of the conical shell are thin, smooth apart from very fine growth lines, translucent and horny. There are no ribs, and apparently little calcification. Animals collected on the Mount Batten shore in
February 1959 had shells of this type (see fig. 48). Apart from the larval shell, the right and left sides were symmetrical, but there were important differences between the anterior and posterior ends. The peak was nearer the anterior end and the anterior slope was steeper than the posterior. As growth continued both slopes became more concave, and the shell relatively flatter (see fig. 48). At about the end of the first year there was an inflexion in the curve of the shell, which thereafter became progressively taller (see fig. 49). At about the same time as the alteration in the angle of shell growth, ribs developed at the growing edge of the shell and the thickening of the shell from the inside commenced (see fig. 49). The ribs were more resistant to the action of the drill (used to mark shells) and presumably served to strengthen the shell.

Figs. 50 - 53 show the variation of relative height (shell height as a percentage of shell length) against shell length for the four standard populations (samples collected November 1960). The twelve month old limpets had nearly reached the point of inflexion, and after the second year the relative height increased steadily in each of the standard populations. Compared with shell length, the rate of increase in relative height (and the final value reached) was greater in the slower growing populations. There was considerable individual variation in relative shell height at the same shell length. Plotted against age relative height shows a much greater correspondence between populations, but there are still differences:
Moore (1934) showed that limpets transferred from a dry habitat (e.g. high level rocks in sunny place) into permanent pools, grew the new shell at a different and lower angle, producing relatively flatter shells (see fig. 55). He thought this resulted from the fact that in damp places the shell was raised more often, allowing greater expansion of the mantle. In dry places, the shell must be kept firmly pressed to the rocks for long periods, whilst in pools the shell may be slightly raised at all times without the risk of desiccation. Moore suggested that it was the constriction of the mantle which produced the tall shells found in dry places. There is a quite different explanation which fits the facts equally well: that shell angle is connected directly to growth rate (possibly combined with an inherited pattern of shape linked to age). Fast growing limpets would always tend to 'outgrow' their shells (i.e. to have the mantle nearer the shell edge than slow growing ones). This would mean a flatter shell in the same way as a more frequently extended mantle would. On the information
presented up till now, there is no way of distinguishing between the two theories, since any increase in the dampness of the habitat probably also increases the food supply and the growth rate.

The actual margin of the shell is very thin. The first layer is laid down by the extreme edge of the mantle, contains all the internal colour patterns, and forms the outer sculpturing. There is a close relationship between sculpture, pigment patterns and structure of the mantle edge. The ribs always occur opposite one of the larger pallial tentacles, and the centre of each rib is always light in colour, flanked by dark pigment bands. The shell is being constantly thickened from the inside by successive layers of translucent material. If the growth of the shell is rapid, the edge will be finely pointed in section; but in slow growing individuals the thickening comes close to the edge and produces an almost 'square' edge (see fig. 54). Erosion of the shell may be rapid, especially when the shell is not protected by a cover of barnacles or encrusting algae. Several Group 3 shells had only a few barnacles on them. When these barnacles were scraped off it was seen that they stood on a small pedestal of shell standing 2-3 mm. clear of the rest of the shell. Thus shell erosion could amount to about 2 mm. per year.

The power of shell regeneration and repair is limited. When holes were cut in shells they were never filled in, although sometimes a repair was effected by laying a new layer of shell
right across below the hole (see fig. 55).

14. The radula and its variation

As the individual limpet grows, the length and width of the radula increase; the teeth become larger; the number of rows of teeth and the spacing of the rows become greater; and, in the early stages of development, the pattern of the teeth alters. The more fundamental processes - the rate of radula production by the radula sac and the rate of wear and removal at the functioning end - cannot be directly measured.

The extraction of the radulae from freshly killed animals is fairly simple. The complete radula has a transparent horny flange at the functioning end and a soft bulbous radula sac at the other (see fig. 62) so it is easy to be sure that the whole radula has been obtained. In formalin-preserved specimens the radulae were brittle and did not separate easily from the tissues. It was necessary to boil them in caustic potash to make them clean and flexible. This process destroyed the radula sac and shortened the radulae by about 2 - 5%. All the samples removed in November 1960 had to be preserved in formalin and were treated with KOH solution before examination.

The pattern of the teeth in the radula of the pre-metamorphic veliger and of newly settled s at have been described by Smith (1935), see fig. 56. Limpets collected in February 1959, at Mount Batten (i.e. 3-4 months old) had very short, wide radulae, with a well developed median tooth in each row. The pattern of
the teeth follows on from those described by Smith (see fig. 56). The radulae of the limpets raised by Dodd (1957) from artificial fertilizations, seem to have been abnormally slow in developing. The description Dodd gives of the radula of a seven month old limpet fits that of the pre-metamorphic veliger given by Smith.

By the end of the first year the median tooth was only present as a thin sliver between the two first lateral teeth (see fig. 57). This thin median tooth (without a cutting point), is characteristic of the genus Patella sensu strictu; but is not normally visible in untreated limpet radulae. It is not shown in any of Fischer-Piette's drawings of the adult radulae of the five European species of Patella. When the radula has been boiled in KOH solution, the median tooth is much easier to distinguish (see fig. 57).

The radula ratios of the four standard populations (November 1960) are plotted against shell length in figs. 58-61. Radula ratio = R/L = radula length divided by shell length. The radula becomes relatively longer and thinner as it grows. The radula ratio of a three month old limpet was only about 0.7 (see fig. 62); but by the end of the year this had increased to 1.0 or more, in spite of the great increase in shell length. After this early increase in radula ratio there were further small increases - fairly continuous in the slow growing populations but the trend seems to reverse in Population 1.
The following table gives the radula length and the radula ratios of the four populations against age:

| Age Years | Population 1 | | Population 2 | | Population 3 | | Population 4 |
|-----------|--------------|--------------|--------------|--------------|--------------|--------------|
|           | R/L Length   | R/L Length   | R/L Length   | R/L Length   | R/L Length   | R/L Length   |
|           | mm.          | mm.          | mm.          | mm.          | mm.          | mm.          |
| 1         | 1.1 7.4      | 1.3 8.5      | 1.2 7.2      | 1.1 7.4      |
| 2         | 1.4 26       | 1.65 25      | 1.4 25       | 1.3 19       |
| 3         | 1.45 46      | 1.7 34       | 1.5 36.5     | 1.45 27.5    |
| 4         | 1.4 58       | 1.75 41      | 1.55 44      | 1.6 37       |
| 5         | 1.3 68       | 1.75 48      | 1.6 54       | 1.75 47      |
| 6         | 1.3 73       | 1.8 56       | 1.55 57      | 1.75 51      |
| 7         | 1.3 73       | 1.8 60       | 1.55 60      | 1.80 54      |

It can be seen that the radula was longer in the fast growing populations relative to age, but shorter relative to shell length.

Figs. 63-66 show the spacing of the rows of teeth in the radulae of the four standard populations. The number of rows of teeth was counted from the functioning end backwards, stopping where the teeth became transparent. In a fresh radula there were 20-25 rows of completely transparent teeth after this point. The majority of the rows had black teeth with yellowish brown bases. The rows are much easier to count in KOH treated radulae; in fresh material the teeth are covered with tissue which apparently impregnates the teeth with iron (Jones et al, 1935).

Twelve month old limpets had between 75 and 95 rows of teeth (+ the 20 or so transparent rows), this number increased steadily with age, but did not keep pace with the increasing length.
of the radula so the spacing of the rows increased. There were about 11 rows per mm. of radula in the twelve month old limpet, but only about 2.6 in the oldest limpets. The size of the teeth increased with the increased spacing so that the appearance of the radula did not alter (apart from the scale). There was no change in the shape of the teeth after the first year. The spacing of the rows along each radula was constant (within the limits of measurement error) in November 1960; so it seems that, either the change in spacing takes place suddenly (perhaps each winter), or else is very gradual and obscured by a rapid production and wearing away (turnover) of the radula.

Careful dissection of the anterior part of the radula showed that only a small part was in use at any time. The teeth of the first six rows are worn at the tips, but from the eighth row back they were finely pointed and undamaged. The teeth in the first four rows are worn down to stubs (see fig. 62).

The spacing of the rows of teeth in the radula is constant in relation to mean size of the four populations (2.6 rows per mm. at the mean size in each population).

The number of rows in a radula is given by the formula:

\[ \text{length of radula in mm.} \times 1.65 + 70 (\pm 20-25 \text{ rows of transparent teeth}) \]

These rather complicated points may be summed up as follows:
(i) Fast growing limpets have a shorter radula in relation to their size and weight than slow growing lipets, although in terms of age the radula is actually longer.

(ii) The number of rows of teeth in the radula is related to the length of the radula. An increase in radula length means an increase in the number of rows of teeth and their size and spacing.

(iii) The spacing of the rows and the annual excess of radula production over annual wastage (i.e. annual increase in radula length) are both related to growth rate and life span.

The spacing at the mean size of each population is 2.6 rows per mm. radula length; and the annual increase in radula length in each population has fallen to about 1 mm. by the mean size.

15. Population structure

From the data already presented, it may be seen that Populations 1, 3, and 4 form a series which includes the following features: growth rate (-ve, i.e. decreasing down the series), mean size (-ve), maximum size (-ve), longevity (+ve), mortality rate (-ve), settlement density (-ve), pre-spawning gonad size (-ve), number of eggs produced (-ve), radula ratios (+ve); as well as several other minor features.

Population 2 fits into this series between in some respects but is clearly aberrant in others. Close examination and comparison of the various results lead to the conclusion that Population 2 contained no limpets of 5 or 6 years of age.
(November 1960) and that the limpets above 30 mm. shell length had earlier been growing at a much greater rate than they were in 1959-60. These conclusions are best demonstrated by two points. Populations 1 and 4 had 40% females at 48 and 25.5 mm. shell length respectively. The mean age of these lengths was 5 years in both cases. Population 2 individuals would reach 26 mm. shell in 5 years according to 1959-60 growth rates, but there were no females at that size in the 1959 breeding season. Secondly the mean size for Population 2 was 38.5 mm. but this size would never be reached by the mean growth rate of 1959-60.

The mean sizes of Populations 1, 3, and 4 were reached in 6, 8½ and 11 years respectively at their mean growth rates for 1959-60.

It was not realised that Population 2 was in any way unusual when this work commenced, but it was anticipated that even 4 populations would be inadequate for the purpose of deducing principles of population dynamics (which would be valid for Patella vulgata over a wide area). Three other lines of evidence were sought. These support the conclusions already reached and suggest their wider applicability.

Where Fischer-Piette (1948) and other workers provide equivalent data the present conclusions do apply. In particular the correlations between growth rate and maximum size, and between growth rate and longevity apply to 10 populations reported by Fischer-Piette (see fig. 21). The correlation between mean size and growth rate, a new and important correla-
tion suggested by the present work, is a necessary corollary of the first two provided the rates of recruitment, growth and mortality remain constant.

Whilst correlations are the easiest evidence to obtain and have provided most of the ideas; direct experimental evidence, if it can be obtained, is more convincing. The main difficulty was that such experiments take as long as the normal growth rate measurements (nearly two years), so that there was no possibility of repeating them. They had to be designed at the beginning of the investigations when it was not yet clear which propositions required proof. Experiments were set up to produce increased growth rates (see next sub-section) in each of the standard populations, so that whatever criteria for increased growth rate were suggested by correlation of the results from the standard populations, they could be tested by reference to these forced-growth impets.

The third line of supporting evidence for the correlations worked out for the four standard populations was that of cross-checking the correlations. Growth rates cannot be worked out for a large number of populations, but mean sizes, sex proportions, radula ratios and shell heights can be measured much more easily, and if these things correlate with one another in the manner predicted by the general theory, it is good evidence that the correlation with growth rate also holds (see Section III).
Before these lines of evidence are given, it may be useful to list the correlations which it is hoped to establish:

<table>
<thead>
<tr>
<th></th>
<th>Populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1. Mean size (mm. shell length)</td>
<td>51.5</td>
</tr>
<tr>
<td>2. Weight at mean size (grams)</td>
<td>14.5</td>
</tr>
<tr>
<td>Average age at mean size (years)</td>
<td>6</td>
</tr>
<tr>
<td>3. Size at which 100% are male</td>
<td>32</td>
</tr>
<tr>
<td>Age of this size</td>
<td>3</td>
</tr>
<tr>
<td>4. Size at which 40% are female</td>
<td>48</td>
</tr>
<tr>
<td>Mean age of this size</td>
<td>5</td>
</tr>
<tr>
<td>5. Radula ratio at mean size</td>
<td>1.3</td>
</tr>
<tr>
<td>No. of rows of teeth at mean size</td>
<td>2.6</td>
</tr>
</tbody>
</table>

The proposition is that each of these five features necessarily correlate with the growth rate in stable *Patella vulgata* populations, and that most populations are stable. Other features also correlate with growth rate but are either less important or more difficult to measure.
Fig. 55 The number of limpets per metre$^2$ in each mm shell length size group of Population 1, November 1960.

Fig. 56 The number of limpets per metre$^2$ in each mm shell length size group of Population 2, November 1960.
Fig. 57 The number of limpets per metre$^2$ in each mm size group (shell length) of Group 3, November 1960.

Fig. 58 The number of limpets per metre$^3$ in each mm size group (shell length) of Group 4, November 1960.
Fig. 59
Total wet weight in grams against shell length
Group 1, Nov. 1960

Fig. 40
Total wet weight in grams against shell length
Group 2, Nov. 1960
Fig. 41
Total wet weight in grams against shell length.
Group 5, Nov. 1960

Fig. 42
Total wet weight in grams against shell length.
Group 4, Nov. 1960

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<th>SHELL LENGTH MM</th>
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<th>20</th>
<th>30</th>
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</tr>
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</table>

Fig. 41
Total wet weight in grams against shell length.
Group 5, Nov. 1960
Fig. 43 The accumulative % weight against shell length in Group 1, November 1960.

Fig. 44 The accumulative % weight against shell length in Group 2, November 1960.
Fig. 45 The accumulative % weight against shell length in Group 5, November 1960.

Fig. 46 The accumulative % weight against shell length in Group 4, November 1960.
Legends to Figs 47-49.

**Fig. 47** Redrawn from Dodd (1957).
1. Pre-metamorphic larval shell  
2. Larval shell with peristome, 2 weeks after fertilization  
3. Larval shell with peristome, 4 weeks after fertilization  
4. Young spat, 6 weeks after fertilization  
5. Spat, 11 weeks after fertilization.

**Fig. 48** Young limpets collected at Mount Batten 1959.
1a and b Two views of a 4 month old limpet showing the larval shell still in place.  
2. A 5 month old limpet with fine growth lines  
3. A 6-7 month old limpet, the larval shell now lost

**Fig. 49** (above) A 12 month old limpet with the ribs beginning to develop and the curve of shell growth starting to turn downwards.  
(below) An adult limpet shell showing the curve of shell growth which causes the increase of relative height with age. The points of inflexion are marked with arrows.
Fig. 47
see previous page for legends

Fig. 48

Fig. 49
Fig. 50  Relative shell height (height as % of length) against shell length (horizontal axis) in Group 1. The large dots are average values.

Fig. 51  Relative shell height against shell length in Group 2
Fig. 52 Relative shell height against shell length in Group 5.

Fig. 53 Relative shell height against shell length in Group 4.
Fig. 54 (above) The shell edge in section of fast (A), medium (B), and slow growing (C) limpets.
(below) The relationship between the mantle tentacles (pallial tentacles), the shell ribs and the pigment patterns of the shell. (diagrammatic)

Fig. 55 (above) The shape of the shell of a limpet transferred the previous year from dry rock to a pool.
(from Moore, 1954)
(below) The repair (shown in section) of a hole made in the shell a year before.
Fig. 56

1. The radula pattern in a pre-metamorphic larva
2. The radula pattern at settlement (1 and 2 redrawn from Smith, 1955)
3. The radula pattern of a 4-5 month old limpet from Mount Batten, February 1959.

Each of these drawings show one row of teeth from the anterior part of the radula.

Fig. 57

(above) Two rows of teeth from the radula of an adult limpet. Note the minute median tooth. Natural colours - tips black, bases yellow brown, marginals colourless.

(below) The same radula viewed from the side.
Fig. 58 The radula ratios (radula length divided by shell length) against shell length for Group 1, November 1960.

Fig. 59 The radula ratios against shell length for Group 2.
Fig. 60 Radula ratios against shell length for Group 3, Nov, 1960.

Fig. 61 Radula ratios against shell length, Group 4
Fig 62

1. The radula from a four month old limpet
   shell length 1.3 mm
   radula length 0.92 mm
   number of rows of teeth 64

2. The radula from an adult limpet
   shell length 57 mm
   radula length 76 mm
   number of rows of teeth 190

5. The side view of the lateral teeth of the 1st, 3rd, etc. rows of the radula shown in 2.
Fig. 63 The spacing of the rows of teeth in the radula (No. of rows per mm) against shell length for Group 1, Nov. 1960.

Fig. 64 The spacing of the rows of teeth in the radula (No. of rows per mm) against shell length for Group 2, Nov. 1960.
Sub-Section D: The experimental alteration of population structure and habitat.

16. Alterations of the habitat

In Populations 2 and 4, small areas (approximately 0.4 m$^2$) were carefully cleared of all barnacles leaving the limpet population unaltered (February 1959). The limpets in these two areas were marked, positioned, measured and photographed until November 1960, in the same way as Groups 1-4 (see sub-section A). The barnacle clearance was repeated every six months. The results of these experiments were very similar and can be considered together.

The cleared areas dried out much more quickly when the tide fell than the neighbouring barnacled rocks, and they dried out more uniformly, few damp hollows remaining. Immediately after the barnacle clearance, there was noticeable inefficiency in the homing of many of the limpets, and there were some migrations and some deaths. These were commonest in 2nd and 3rd year limpets; the reduction of population density (in terms of weight per area) was less than 10%. After about two months the populations settled down and resumed "normal" activities. There was no significant difference in growth rate (over the whole period of the experiments) between the altered areas and that found on the equivalent barnacled rocks (i.e. Groups 2 and 4).

It seems that the presence of barnacles has little effect on the population structure or growth rate of limpet populations.
on rocks devoid of large algae and open to the sun. Barnacles form a rough awkward surface which makes free-grazing by limpets more difficult. A barnacled surface has a greater water-holding capacity than bare rock; and this benefits small limpets, protecting them from desiccation, as well as aiding the settlement and growth of algae. Barnacles compete for space with limpets, especially with the young limpets leaving the crevices and trying to establish permanent homes on the open rock. Barnacles probably filter off some of the diatoms and spores which would otherwise settle and provide food for limpets.

In Populations 2 and 4, the changes in the limpet habitat caused by the removal of the barnacles appeared to cancel one another's effects. If the rock surface was not subject to long dry periods, the presence of barnacles would be decidedly detrimental to limpet growth (see the circumstances of Population 3, which is at the same level on the shore as Population 2, but has a higher growth rate). On the Mount Batten shore, however, any great reduction in the severity of desiccation was always accompanied by the presence of fucoids which would smother any barnacles (for method see later). On wave-beaten shores, where fucoids cannot develop, barnacles may be abundant on surfaces which rarely dry out. In such places the barnacles may limit the growth rate of Patella vulgata. On the Mount Batten shore, barnacles only develop on surfaces where the growth of Patella vulgata would in any case be slow; and their presence, whilst affecting the detailed pattern of grazing and homing, has little
effect on the general growth rate or the stable population structure.

In Population 4, the barnacles within 1 cm. of all the limpets in a small area were removed. The limpets were untouched, and the vast majority of the barnacles remained as they were. The only alteration was the artificial increase of each limpet's scar - i.e. the barnacle-free area of the home - which under normal conditions was usually the exact shape of the shell. It was found that this alteration adversely affected the homing efficiency of many of the limpets and caused the death or migration of many of the smaller ones. The visible effects were, in fact, much the same as those following the removal of all the barnacles. These observations will be discussed more fully in the next sub-section in relation to the method of homing.

Several experiments were performed in an attempt to understand the effect of fucoids and other algae on limpet populations. In Population 1, several areas were cleared of algae. In all cases the repopulation by algae was extremely rapid, and rather complex because of the number of species involved. When *Fucus serratus* and other algae were removed cleared areas became completely covered by green algae (mainly *Enteromorpha* and *Ulva*) within a month (clearing February 1959). This cover was very dense and thick, but was invaded quickly by red algae (*Porphyra* first, then *Gigartina*, *Chondrus*, and *Rhodymenia*, this last being the most abundant) and *Fucus serratus* sporelings. During the
winter (1959-60) the cover of the red and green algae was greatly reduced, but the *Fucus serratus* continued to develop and achieved 100% cover about a year after the clearance. After that the continued growth of the *Fucus*, and the development of epiphytes and undergrowth, quickly restored the original community. If the area from which algae were removed adjoined a limpet clearing and formed an artificial extension of this, the sequence of events was altered hardly at all. Some of the limpets entered the newly cleared area and grazed away part of the developing green algal cover, but they could not keep pace with this, still less prevent the establishment and growth of the *Fucus* sporelings. The final result was only a slight increase (about 10%) in the size of the original limpet clearing, no matter how large the artificial extension. It seems that in Population 1, the limiting factor for the extension of the limpet clearings was the inability of the limpets to keep pace with the very rapid algal growth. The actual existence of limpet clearings at this level was very precarious as will be shown later.

A little above mean tide level and just inside the dense *Ascophyllum* community, an area of about 1 m² was completely cleared of large algae (principally *Ascophyllum*, some *Fucus vesiculosus* and undergrowth). Although *Ascophyllum* cover was 100% before clearance, the individual holdfasts were not very close together and about 40% of the rock surface was free of encrusting animals and algae (apart from lithothamnia). There were a number of limpets in these areas, which their grazing
apparently kept clear. In size, distribution and appearance these limpets were the equivalent of those limpets of Group 3 which lay inside the Ascophyllum edge. The limpets were marked, measured, mapped and photographed in the usual way. Clearance took place in February 1959, and within a month all the encrusting animals and lithothamnion had died from desiccation (the lithothamnion bleached white and flaked off). Many of the smaller limpets, which were now living on open rock, died and two empty marked shells were actually recovered. These showed no marks of any injury, and it seems that they also died from drying up, or from starvation caused by the drying of their food. A few of the larger limpets apparently died, but many were found to have migrated from the open rock to the edge of the cleared area, and to have taken up new homes under the Ascophyllum cover there. No green algae appeared in the cleared area, but a complete cover of Porphyra developed within a few months and sporelings of Fucus vesiculosus settled and grew beneath this. The limpets that remained in the cleared area began to grow very fast and were reinforced by small limpets which appeared from cracks once there was some algal cover. These limpets kept the flatter parts of the area (about 40%) clear of Fucus sporelings; but these parts were scattered, and the continuous growth of the Fucus on the rest of the area was rapid. Total cover by Fucus was achieved by the summer of 1960. By November 1960, the area had returned to its original condition, apart from the replacement of Ascophyllum by Fucus vesiculosus. Thus although the dense Ascophyllum community was originally
preventing the expansion of the limpet population, its total removal only destroyed the limpet population structure. Before the limpets could reform in an open rock pattern like that of Population 2 (which occurs at the same tide level), the algae had already re-established their predominance. From the detailed pattern of events (recorded in a series of photographs), it was clear that detailed topography had a decisive influence on the establishment of the Fucus. Where the rock was fairly smooth even a few limpets could keep it clear of sporelings, but in places where there was jagged or soft crumbling rock, or where the rock was deeply creviced, the sporelings developed in corners where grazing by limpets was infrequent or impossible. Because such places were common and closely spaced the adult plants dominated the whole area, shading and keeping it damp.

Below mean tide level, a large area (about 7 m²), consisting largely of a low, flat, badly drained platform of rock, was completely cleared of the thick Ascophyllum which covered it (February 1959). There were no limpets in the main part of the area; but, at its edge, there were some pieces of rock rising about 50 cm. above the general level. These were free from Ascophyllum and crowded with limpets. These limpet "clumps" were equivalent to small isolated sections of the Ascophyllum edge population described as Population 3; though they were rather lower on the shore than Group 3, had a larger mean size and probably had a somewhat faster growth rate. These limpets were not marked or measured individually, but their
movements were followed in a series of standard photographs over the next 18 months. The encrusting animals and lithothamnia on the low platform died fairly quickly, except where there was standing water. The "clumps" of limpets at the edge gradually dispersed; some limpets moving down into the low-level area, others moving back to the Ascophyllum edge. Mortality was not measured but did not seem to be high. Very few green algae or Porphyra developed in the area, but Fucus sporelings developed strongly in the crevices and damper parts. By November 1960, Fucus cover had reached 50% and the limpets seemed to be losing ground steadily.

17. Alterations of the limpet populations

In the first part of this sub-section, experiments were described showing that barnacles had little effect on the limpet populations of the Mount Batten shore, but that fucoids had profound effects - controlling the expansion of the limpet populations in many places, yet conferring on the limpets in their vicinity certain benefits such as protection from desiccation and possibly an increased food supply. The experiments now to be described are concerned with the reciprocal influence - that of the limpets on the barnacles and the fucoids. They also show the effect of competition between limpets. The general design was very simple. In each standard population an area of about 1 m² was thinned to about 10% of its original limpet population. The remaining limpets were marked, and events followed by periodic measurements, maps and photographs.
In Population 1, an area of 0.8 m\(^2\), containing a limpet clearing similar to that of Group 1, was completely cleared of algae and the limpet population was thinned (February 1959). After the first few weeks it was obvious that the remaining limpets were unable to keep down the rapid growth of green algae or to stop the continued succession towards fucoid domination. Since this succession was being followed in other experiments (described above), the algae in this area were re-cleared every two months to discover the effect of artificially-maintained super-normal feeding areas on the rate of limpet growth. After 8 months algal clearance was stopped, but no green algae developed during the winter and by the following spring (1960), the area was shaded by the Fucus serratus which had settled and grown around the edges and in the deeper cracks of the area. The limpet population was further thinned in February 1960 to counter-balance growth in the previous year. The growth rate of the limpets (termed Group 1a) in this area was greater than that of Group 1. This shows that limpets are capable of utilizing a greater area for grazing than they can protect from invasion by large algae. Rough, rapid grazing of small lush green algae provides more food than the detailed systematic grazing required to prevent the development of fucoids. Thus fucoids not only limited the expansion of the limpet clearings they also limited the individual growth rate of the limpets in this population. The annual increments and growth curve of Group 1a are shown in figs. 67 and 70. The growth curve is slightly artificial since the later part is based on the annual increments of limpets
already several years old when the experiment began. If the experiment could have lasted 6–7 years the growth curve would probably be slightly higher.

In another clearing of Population 1, the large limpets were removed but the first year group was left in place (February 1959). The clearing quickly shrank to less than one third its former size and the algal-free rock was completely shaded by overhanging seaweed. This did not appear to have any immediate detrimental effect on the young limpets, which continued to grow at a somewhat increased rate and with a lower mortality than those of Group 1. By November 1960, however, it was obvious that the limpets were not able to extend the clearing (except perhaps very slowly), but were already finding it too small for the continued rapid growth. Thus it seems that the presence of large limpets in the clearings of Population 1 was necessary, both for the provision of a suitable surface for settlement, and for holding open a large clearing to which some of the young limpets would eventually succeed. Nevertheless the large limpets were in direct competition for food with these young limpets and were the limiting factor for their growth and continued existance.

In Population 2, an area of 1.4 m² was thinned to less than 10% of the original population. The remaining limpets were marked and events were followed in the usual way (April 1959 – November 1960). It was found that the limpets from nearby areas of normal population density frequently migrated into the thinned area. To protect the experiment, a guard area was set up round
it from which all limpets were removed at frequent intervals. Even so, it was impossible to prevent small limpets settling in, or migrating into, the experimental area and frequent clearings of unmarked limpets were required. A short Enteromorpha turf had developed on parts of the area by June 1959, but did not last long. Fucus vesiculosus sporelings settled during the late summer and by the following year had developed 100% cover over the area (see plates 6, 7, 8). Beneath these fucoids the surface remained continually damp and encrusting polychaetes, tunicates and hydroids developed over the barnacles (see plates 9 and 10). Even before the barnacles were overgrown in this way, many had died, either smothered by the silt which settled under the fucoids, or from starvation due to the fucoids' interference with the water currents. Many barnacles were eaten by Nucella lapillus which gathered in great numbers once the fucoids provided cover. The limpets in the experimental area (termed Group 2a) grew very much faster than those of Group 2 (see figs. 68 and 70). The settlement in the area in the winter of 1959-60 was very much greater than that which took place in Population 2 generally.

It seems clear that the limpets in Population 2 were in competition with one another for food and that this normally limited their growth rate. The experiment also shows that the area of Population 2 is quite suitable for the development of fucoids, and that this is only prevented by the action of the limpets. The barnacles of the area only existed because the
limpets prevented the growth of fucoids. A dense cover of fucoids indirectly brought about the death of all the barnacles.

The site chosen for the experiment in Population 3 was not very suitable. It contained only a few Ascophyllum plants, the rock was soft and crumbly and subject to considerable mechanical erosion. The limpets were thinned in March 1959. Fucoids developed as in the Population 2 experiment and the growth rate of the remaining limpets increased. The crumbling of the rock interfered with the grazing of the limpets and the growth of the fucoids caused large lumps of rock to be dragged out by the waves. For these reasons the results were not analysed in detail, but it should be noted that no events in this experiment showed any reason to doubt the conclusions drawn from the others.

In Population 4, there was no site exactly equivalent to Group 4, so a lower piece of the vertical face of the same stack had to be used. The limpets were thinned in April 1959 and the experiment proceeded similarly to that of Population 2. The growth rate of the limpets is shown in figs. 69 and 70, and was much greater than that of Group 4. The fucoids in this experiment did not develop so rapidly or abundantly as in Group 2a, and their effect on the barnacles was less severe (see plates 11-15). As in Group 2a, the thinning of the limpets was followed by migrations of limpets into the experimental area from the unaltered population nearby. This migration was again
controlled by means of a guard area. The settlement density in the experimental area in the spring of 1960, was very much greater than that of the rest of Population 4. About 140 limpets of the first year group were found per m$^2$ of the experimental area in May 1960 (cp. 25 per m$^2$ in normal Population 4).

It was clear that, even on vertical rock faces high on the shore, *Fucus vesiculosus* could develop 100% cover if the grazing of the limpets was sufficiently reduced. The growth rate of *Fucus vesiculosus* was lower in this region than in the Population 2 area (see Appendix B), and it seems that both the growth rate of the *Fucus* and the growth rate of the limpets are factors in deciding whether limpets or fucoids will dominate an area.

None of the experiments showed the establishment or re-establishment of *Ascophyllum*; *Fucus vesiculosus* was the only fucoid which grew during the experiments even in the areas originally occupied by *Ascophyllum*. Since *Ascophyllum* was much commoner and more important than *Fucus vesiculosus* on the Mount Batten shore, this discrepancy requires comment. *Ascophyllum* lives much longer than *Fucus vesiculosus*. *Ascophyllum* thongs 5-6 years old were common at Mount Batten (one air-bladder is added terminally to each thong per year), but the normal age of *Fucus vesiculosus* plants was only about 2 years. *Ascophyllum* occurred in dense stands, large numbers of thongs arising from each massive holdfast. These stands normally regenerate by producing new thongs from the holdfasts. It was rare to find a
young plant, i.e. a single isolated young thong not developing from an older holdfast. If the holdfasts of *Ascophyllum* are removed from an area, the stand is not re-established for many years. Dr. M. Parke reports that in one of her experiments no recolonization by *Ascophyllum* had occurred 13 years after clearance (personal communication). Sporelings did settle and begin to develop, but quickly died or were eaten by molluscs. *Fucus vesiculosus* occurs in many places and under various conditions, but it rarely, if ever, forms dense permanent stands. Its relationship to *Ascophyllum* is analogous with that of Hawthorn or Birch scrub to Oak or Beech woods. *Fucus vesiculosus* settles densely on a wide variety of rocks and grows quickly, it is thus less likely to be reduced by limpet attack than *Ascophyllum*. *F. vesiculosus* can survive in conditions of greater wave action, more severe sand scour, on smaller stones, and on steeper slopes than *Ascophyllum*. On vertical rock faces in extremely sheltered conditions (see Ballantine 1961) *Ascophyllum* occurs abundantly and covers the whole zone of the middle shore; but, in more exposed conditions, it is progressively restricted to horizontal areas of jagged rocks. On every shore, *Ascophyllum* stands tend to be bordered by *Fucus vesiculosus*. It seems reasonable to conclude that the two plants are influenced in the same way by the same factors and that *Fucus vesiculosus* requires less protection than *Ascophyllum* but is not able to compete with *Ascophyllum* under the most favourable conditions. Thus the growth of *Fucus vesiculosus* in an experimental area is not proof that *Ascophyllum* would eventually develop there, but it is proof that
conditions were tending towards that result. The nature of the conditions favouring Ascophyllum development are known - freedom from wave-action, freedom from limpet grazing, damp, badly drained surfaces. What is not known is how long these conditions must be maintained before Ascophyllum actually develops.

Another point that requires discussion is the distribution and possible influence of molluscs other than Patella vulgata. There were four species of free-roaming herbivorous molluscs common on the Mount Batten shore; two species of top-shells - Monodonta lineata and Gibbula umbilicalis and two species of winkles Littorina littorea and L. littoralis. These molluscs move freely about and it was not possible to exclude them from the experiments without building barriers which might themselves influence the results. Counts of the molluscs present in each experimental area and on the same area of unaltered population were made at intervals (see Appendix C for full results). Although the results were interesting in themselves, they gave no reason to suspect any of the conclusions drawn from any of the experiments.

18. Analysis of the limpets from the experimental areas

The limpets from Groups 1a, 2a, and 4a were removed in November 1960 and analysed in the same way as those from Groups 1-4 (see sub-section C). In addition to the increased growth rates and increased settlement densities already reported, significant differences were found in the weight/shell length
relationships, the radula ratios and the relative shell heights. The numbers of limpets in the experimental areas were much too small to attempt to measure sex proportions against size. The differences between the experimental area limpets and their equivalent standard population were greatest in Groups 2a and 4a, where there was a very large change in growth rate. The differences were small and not significant in Group 1a where the increase in growth rate was smaller and more difficult to produce.

The artificial reduction of population density in the Group 2a and 4a areas led to an increased growth rate, an increased settlement rate and an increased maximum size. If the thinning of these populations had been continuously maintained for some years (at that level which would just allow the remaining limpets to hold the fucoids in check) it seems that the resulting population structure would have become very similar to that of Population 1. The thinning was equivalent to an increased mortality rate and resulted in lessened competition for food and an increased growth rate, which in turn tended to produce increased mean and maximum sizes. Without further thinning the increased settlement rate and the migration of limpets from the unaltered population nearby would restore the original population structure within a few years.

Changes in the relationship between weight and shell length make some adjustments necessary when evaluating the increased growth rates (see figs. 71-73). In Group 2a a 30 mm.
limpet weighed only 2.7 grams compared with 3.5 grams for the same size in Group 2. However there is no doubt that there was an increase in growth rate - a limpet weighing 5 grams in Group 2 would be about $8\frac{1}{2}$ years old, whereas this weight would be reached in $3\frac{1}{2}$ years at the Group 2a growth rate.

The radula ratio was much lower in the Group 2a and 4a limpets than in the standard populations (see figs. 74-76). The relative shell height was lower (compared to shell length) in the altered groups (see figs. 77-79). Fig. 80 shows what happened to an average 30 mm. shell length limpet over two years in the standard and altered populations. It can be seen that the actual increase in radula length of the fast growing limpets is as great, or greater, than that of the standard population limpets. The increase in shell height of the fast growing limpets is greater than that of the slow growing standard population ones. The alteration in the ratios (radula ratio and relative shell height) must have been brought about by an alteration in the angle of shell growth (possibly with an increase in the rate of radula production).

The growth of fucoids in the Group 2a and 4a areas resulted in damper surfaces and the change in shell angle would by Moore's theory be due to this (see discussion, sub-section C, 13). However the fucoids only achieved dominance late in the experiments, and the alternative theory - that the change in shell angle was due to the increased growth rate - seems more likely. In northern Norway many specimens of *Patella vulgata*
show annual rings in the shell (see fig. 81). Specimens collected in August 1959 all showed a curved section at the shell edge. This is interpreted as a fast spring growth with a low angle, then a gradually decreasing growth rate and an increasingly high angle of shell extension. Thus the annual rings are lines of abrupt change in shell angle, and mark the winter season. *Mytilus edulis* shows the same type of annual rings in this region. Savilov (1953) showed that *Mytilus edulis* in the White Sea region had annual rings of this type and also that slow growing specimens had relatively flatter shells than the fast growing ones. This point was also verified in Norway (see fig. 81). The general shell shape in *Mytilus edulis* could be interpreted by Moore's theory, but in the case of the annual rings only the theory that connects growth rate and shell angle fits the facts.

From the evidence of the limpets from Groups 2a and 4a it seems that a low radula ratio is indicative of a fast growth rate, and that the shell angle is also related to growth rate. Relative shell height is not necessarily correlated with growth rate (Group 3 limpets had a greater relative shell height than those from Group 4) because it is a summation of all the shell angles up to the time of measurement but not of the length of time for which they operated. Spurts of rapid growth upset the correlation of relative shell height with growth rate (see fig. 82).
Fig. 67  The annual increment of shell length against initial shell length for Group 1a

Fig. 68  The annual increment of shell length against initial shell length for Group 2a
Fig. 69 (above)
The annual increments of shell length against initial shell length in Group 4a

Fig. 70
A comparison of the mean growth curves of all the Groups.
Legends to Plates 6-15

Plate 6 The area of Group 2a, 26/2/59. The thinning of the limpets had commenced, but the original population is present at the right.

Plate 7 The area of Group 2a, 8/9/60, from a slightly different angle. Note the 100% cover of the rock, by large Fucus vesiculosus. The dividers were set at 5 cm.

Plate 8 A close-up of the Fucus vesiculosus in the Group 2a area, 8/9/60. Note the numerous, often paired bladders. Dividers set at 5 cm.

Plate 9 A close-up of the rock surface beneath the Fucus in the Group 2a area, 8/9/60. Note the dead and overgrown barnacles, the encrusting animals (centre), the silt (left centre) and the young Nucella feeding (top right). The divider points (top) are 5 cm. apart.

Plate 10 An area of Group 2, 8/9/60, equivalent to that shown in Plate 9. Note the dense cover of healthy Chthamalus and Elminius.

Plate 11 The area of Group 4a, 26/2/59. The thinning of the limpets had commenced, but the original population is present at the right. The penny (top centre) has a diameter of 3 cm.

Plate 12 The upper left part of the Group 4a area, 15/7/59. Note the short, dense Enteromorpha turf and the few tiny Fucus plants. Some of the limpets have made small clearings in the Enteromorpha.

Plate 13 The lower left part of the Group 4a area, 16/2/60. The Enteromorpha had disappeared by this time, and numerous short Fucus vesiculosus were developing. The limpet at the extreme right was 57 mm long.

Plate 14 The area of Group 4a, 12/7/60. Note the dominance of the Fucus over a large part of the area. The dividers (centre base) were set at 5 cm.

Plate 15 A close-up of the rock surface of the Group 4a area, 8/11/60. Compare with plates 5, 9, and 10. The barnacles here were sparse and were nearly all Elminius, but there were no encrusting animals.
Plate 6 (for the legends to this and the following plates see the previous page)

Plate 7
Plate 14

Plate 15
Plate 15
**Fig. 71**
Total wet weight against shell length in Group 1a, Nov. 1960.

**Fig. 72**
Total wet weight against shell length in Group 2a, Nov. 1960.
Fig. 73
Total wet weight against shell length in Group 4a, Nov. 1960.

Fig. 74 The radula ratios against shell length in Group 1a, November 1960.
Fig. 75 Radula ratios against shell length for Group 2a, Nov. 1960. The dotted line gives the mean values for Group 2.

Fig. 76 Radula ratios against shell length for Group 4a, Nov. 1960. The dotted line gives the mean values for Group 4.
Fig. 77 The relative shell height (height as % of length) against shell length in Group 1a, November 1960.

Fig. 78 Relative shell height against shell length in Group 2a, Nov. 1960. Large dots are average values. The dotted line gives the mean values for Group 2.
Fig. 79 Relative shell height against shell length in Group 4a, Nov. 1960. The dotted line gives the mean values for Group 4.

Fig. 80 The changes in shell dimensions and radula length over two years in a 50 mm shell length limpet. Upper left and right The shell and radula from Groups 2 and 4 respectively in January 1959. Below The changes by Nov. 1960; the larger shells and longer radulas are from Groups 2a and 4a.
Fig. 81
(above) A limpet from North Norway with annual rings in the shell.

(below) A large, fast growing mussel and a small slow growing mussel from North Norway both with annual rings.

Fig. 82 Variations in shell shape and size
1 and 3 have the same shape, but different shell lengths.
2 and 4 have the same shell length as 5, but have different shapes. 2 could be the result of a high initial growth rate rapidly decreasing, and 4 could be the result of a low initial growth rate slowly decreasing.
SECTION III

The reproduction, distribution and population structure of the three Patella species in south-west Britain.
1. **The gonad cycle and spawning times of the three Patella species at Renney Rocks.**

Samples of limpets for the determination of the gonad index were collected at Renney Rocks from the end of March 1959 to the beginning of December 1959. All three species of Patella - P. vulgata, P. aspera, and P. depressa - were investigated. Samples were taken from two different shores (see fig. 83). The exposed shore was on the outer face of Renney Rocks themselves and rated unit 2 on the exposure scale (see Ballantine, 1961). The other shore was Renney Point, in the lee of Renney Rocks, and therefore much more sheltered. It rated between units 3 and 4 on the exposure scale. Collections of Patella vulgata were made at two levels on each shore - from the lowest and the highest populations. P. depressa collections were also made from high and low level populations on both shores. P. aspera samples were taken from two levels on the exposed shore, and from the lowest level and from high level lithothamia-lined pools on the sheltered shore. Altogether over 8,000 limpets were measured, sexed and had the gonad index determined during this investigation.

Professor J.H. Orton studied the breeding cycle of Patella depressa at Trevone on the North Cornish coast in the years 1946-9, and that of P. aspera at Port St. Mary in the Isle

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of Man. His results were only partly analysed when he died in 1953, and at the beginning of this work there was no immediate prospect of their publication. Dr. A.J. Southward very kindly showed me all Orton's notes and results. Although these could be criticised in the same way as his data for *P. vulgata* (see Section II B), it was clear that Orton had discovered the main pattern of the breeding cycle in *P. depressa* and *P. aspera*. The results were not so detailed as those for *P. vulgata* (Orton et al., 1956), and there were no results referring to all three species in the same locality in the same year. The present investigations were undertaken principally to cover this last point. It was also hoped to find out more about ecological variation in gonad development and spawning. The gonad index results of this work agree closely with those of Orton, but the conclusions reached differ, as they did for *Patella vulgata* and for the same reasons (see Section II B). Dr. Southward has recently prepared Orton's results on *P. depressa* for publication (Orton and Southward, in press), but it seems unlikely that those for *P. aspera* will be published.

The development of the gonad of *P. depressa* had already begun by the beginning of April at Renney. By the middle of May most gonads were at stage IV (see fig. 25), and between then and 22nd July there was little change. Between 22nd July and 19th August the index dropped from IV to II in most species, i.e. the gonad was reduced to about a quarter of its previous size between these two samples.
The gonads of *P. aspera* began to develop during June and continued to increase in size until October. Between 1st and 23rd October the gonad index fell from stage IV to stage I or II in most specimens.

The gonads of *P. vulgata* began to develop at the beginning of September and increased in size until November. A sharp drop in the gonad index occurred between 1st and the 16th November (cp. spawning took place at Mount Batten between the 5th and 14th November).

No egg counts were made on the Renney samples, but merely on the evidence of the changes in gonad index it seems that spawning was fairly sudden and synchronous in each species. *P. vulgata* apparently spawned at the same time at Renney as it did at Mount Batten. The spawning times of the three species were:

- *P. depressa* between 22 July and 19 August
- *P. aspera* between 1 and 23 October
- *P. vulgata* between 1 and 16 November

The dates of the start of gonad development in the three species fall in the same order - March, June and September respectively. The time between the spawning dates of the three species would seem to rule out any possibility of hybridisation.

Although all the individuals of each species apparently spawned at the same time, the rate of development and the final
pre-spawning size of the gonad varied between populations. At Mount Batten, the gonads of *P. vulgaris* from populations with a large mean size developed more rapidly than those from the slower growing populations with a small mean size. This correlation was also found in each species at Renney.

The populations of *P. depressa* in the upper midlittoral zone had mean sizes between 20 and 23 mm., while those on the lower parts of the shore had a mean size between 17 and 19 mm. This difference was accentuated by the fact that the high level individuals had very 'tall' shells. In May the gonads of the high level populations were about one gonad index stage ahead of the low level ones. In *P. aspera* the populations at the base of the midlittoral had a larger mean size (38-43 mm.) than those found higher up the shore (26-35 mm.). In August the low level populations were one gonad index stage ahead of the higher level populations.

On the sheltered shore *P. vulgaris* populations at low levels had a mean size of about 40 mm. and those in the upper midlittoral had mean sizes between 19 and 25 mm. At the end of September, the low level populations were one gonad index stage ahead of the higher level populations. On the exposed shore *P. vulgaris* was relatively rare at low levels (replaced by *P. aspera*) and it was difficult to obtain adequate samples or to measure the mean size. At higher levels *P. vulgaris* was much commoner, and although the mean size was small, the rate of gonad development appeared to be rapid.
The 'populations' sampled at Renney were not analysed or defined precisely, they merely consisted of the individuals at certain levels. For this reason the gonad index results have not been analysed in the same quantitative detail as those from Mount Batten. The differences between the timing of the breeding cycle in the three species and the trends in rate of gonad development were the only points investigated.

2. The quantitative distribution and population structure of the three species of Patella in the Dale area, Pembrokeshire

In April 1960, a survey was carried out in the Dale area (Pembrokeshire), to determine the quantitative distribution of the three species, their relative abundance, and their population structure. The Dale area was chosen because it was there that the exposure scale had been worked out and so all the necessary background information was already available. The following shores were investigated in the survey:

<table>
<thead>
<tr>
<th>Station No.</th>
<th>Name</th>
<th>Exposure scale unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.</td>
<td>Skomer Island (near the Wick)</td>
<td>1</td>
</tr>
<tr>
<td>5.</td>
<td>St. Ann's Head</td>
<td>2</td>
</tr>
<tr>
<td>10.</td>
<td>Dale Point</td>
<td>3</td>
</tr>
<tr>
<td>14.</td>
<td>Castlebeach Bay (North side)</td>
<td>4</td>
</tr>
<tr>
<td>19.</td>
<td>Musselwick Point</td>
<td>5</td>
</tr>
<tr>
<td>24.</td>
<td>Point Wood beach</td>
<td>6</td>
</tr>
</tbody>
</table>

This shore was investigated in June 1959, and the samples were not as accurate nor analysed as fully as the others.
The station numbers shown are those given in Ballantine (1961) which should be consulted for the positions of the shores and other general information.

At a number of levels (between 5 and 7) on each shore, all the limpets in a small area (about 0.5 m²) were collected and brought back to the laboratory for analysis. Photographs of the sample areas were taken at a standard distance (4'), and later used both for the detailed study and comparison of the habitats, and also as a check on the results of the sampling. Each sample was separated into species and the shell length of each individual was recorded. There were usually at least 100 limpets in each sample. The species were weighed in 5 mm. shell length size groupings, and from these figures the mean size was calculated. Using 5 mm. size groups, the weightings could be made quickly and a less sensitive balance was needed than if 1 mm. size groups had been weighed. Wherever a reasonable number of the species was present this method gave the mean size to within 5%. Naturally where a species was very rare the mean size could only be calculated from a very large sample. Table 8 shows how the data from one typical sample was analysed.

Fig. 84 shows the relative positions of the sample sites. The grid of this figure consists of the Stephensonian zonation scheme vertically and the exposure scale horizontally. It corresponds to fig. 1 in Ballantine (1961) with which it should be compared. Each sample site was on a shore of solid
Table 8. The analysis of the *Patella* from Collection 2, Castlebeach Bay, North shore, 23/4/60.

Collection area 0.69 m²

<table>
<thead>
<tr>
<th>Size Group mm. shell length</th>
<th>No. of limpets</th>
<th>Total weight grams</th>
<th>Accumulative weight</th>
<th>Acc.% weight</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. aspera</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50 - 55</td>
<td>2</td>
<td>32.1</td>
<td>127.0</td>
<td>100</td>
</tr>
<tr>
<td>45 - 50</td>
<td>0</td>
<td>0</td>
<td>94.9</td>
<td>75</td>
</tr>
<tr>
<td>40 - 45</td>
<td>5</td>
<td>40.9</td>
<td>94.9</td>
<td>75</td>
</tr>
<tr>
<td>35 - 40</td>
<td>5</td>
<td>23.2</td>
<td>54.0</td>
<td>43.5</td>
</tr>
<tr>
<td>30 - 35</td>
<td>5</td>
<td>15.0</td>
<td>30.8</td>
<td>24</td>
</tr>
<tr>
<td>25 - 30</td>
<td>5</td>
<td>8.1</td>
<td>15.8</td>
<td>12</td>
</tr>
<tr>
<td>20 - 25</td>
<td>6</td>
<td>6.3</td>
<td>7.7</td>
<td>6</td>
</tr>
<tr>
<td>15 - 20</td>
<td>1</td>
<td>0.4</td>
<td>1.4</td>
<td>1</td>
</tr>
<tr>
<td>10 - 15</td>
<td>7</td>
<td>1.0</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>5 - 10</td>
<td>26</td>
<td>negligible</td>
<td>negligible</td>
<td></td>
</tr>
</tbody>
</table>

| *P. vulgata*                |                |                    |                     |             |
| 45 - 50                     | 3              | 43.7               | 158.3               | 100         |
| 40 - 45                     | 5              | 46.8               | 114.6               | 72          |
| 35 - 40                     | 3              | 19.3               | 67.8                | 42          |
| 30 - 35                     | 7              | 23.7               | 48.5                | 31          |
| 25 - 30                     | 4              | 5.9                | 24.8                | 16          |
| 20 - 25                     | 12             | 8.0                | 18.9                | 12          |
| 15 - 20                     | 23             | 7.8                | 10.9                | 7           |
| 10 - 15                     | 22             | 3.1                | 3.1                 | 2           |
| 5 - 10                      | 6              | negligible         | negligible          |             |

Total weight of *Patella* per m² = 413 grams

- " P. aspera " = 184 " = 44.5% of total weight
- " P. vulgata " = 229 " = 55.5% " "
bedrock sloping more or less uniformly down to low water and open to the sun at all levels. Gullies, pools, shaded corners, loose stones and boulders, and low rocks out of sand were not included in the main survey although populations of Patella in such places were examined. Figs. 85-94 are all equivalent, i.e. on the same grid. They illustrate the changes of Patella populations with relation to level on the shore and exposure to the effects of wave action. It was considered that these two factors were the dominant local physical factors influencing the Patella populations. Certainly every type of Patella population found in the Dale area is represented by one or other of the samples, which suggests that the other physical factors have only a modifying influence. For example the P. aspera populations found in lithothamnia-lined pools high up on sheltered shores were more or less identical with those found on open rock at low level on unit 2 shores.

Fig. 85 shows the distribution of Patella in terms of total weight per $\frac{m^2}{\mu}$. The estimation of area was subject to the same difficulties that were discussed in Section II, 12. Occupied area was measured in each sample and a typical piece of the particular level was chosen. For example, on sheltered shores at low level a limpet clearing of average size was chosen as the sample site and the area on which calculations were based was the area of the clearing, not the total available rock surface. Even when this stipulation about occupied area has been made, weight per area measurements are subject to large
errors due to the relatively small samples and the often irregular nature of the rock surface. Each weight per area measurement is probably subject to an error of about ± 25%. Since differences of several hundred percent were commonly found between samples this is regarded as a permissible error.

The weight per area is a measure of the 'standing crop' of *Patella* and takes no account of growth rate or turnover of biomass. It is clear from fig. 85 that the greatest standing crop is found on sheltered shores along the edges of the fucoid communities. A narrow band of very high density ran from the middle of the midlittoral zone on shores of units 6 and 5, down to the base of the midlittoral on shores on units 4 and 3. The fucoids concerned were *Ascophyllum* (unit 6), *Fucus vesiculosus* (unit 5) and *F. serratus* (units 4 and 3). On the real shore (as opposed to the theoretical shore of the diagram), this narrow band of high density meandered irregularly around the areas of jagged rock which supported the dense fucoid stands.

On shores of units 5 and 6, the limpets were all *P. vulgata* see fig. 86, but on more exposed shores *P. aspera* formed an increasing proportion of the total *Patella* population. Figs. 86-88 show the % by weight of the total *Patella* population formed by each of the three species. Figs. 89-91 show the actual weight per m² in each species. *P. depressa* was the least common of the species, it never formed more than half the total weight of *Patella* or more than 150 grams per m². It existed over a
wide range of shores (exposure units 1-5) in the central part of the midlittoral, but only in unit 3 did it form a significant part of the total population.

*P. aspera* was much commoner and dominated the limpet populations at low level on exposed shores. It was resent only at the lowest levels of unit 4, but with increasing exposure reached almost to the top of the midlittoral in unit 1. The changeover from *P. aspera* domination to *P. vulgata* occurred over a small range of shore level on units 4 and 3, but on units 2 and 1 there was more mixing. The level at which the changeover took place was higher in exposure. The intermingling and the change in boundary seem to indicate that competition is involved in the replacement of *P. vulgata* by *P. aspera*.

The mean sizes of the three species are plotted in figs. 92-94. Those for *P. depressa* are not sufficiently accurate to indicate any variation, since the number of individuals in most samples was small. In the other two species the pattern of variation in mean size was very simple - the largest mean size in each species occurred in the most sheltered population and decreased steadily with increasing exposure. From the Mount Batten investigations it was suggested that mean size was directly related to growth rate. If it is assumed that this correlation applies to all *Patella* populations, the patterns of competition become much clearer. The growth rate of *P. vulgata* is greatest at low levels in sheltered conditions, it decreases
upshore and in exposure. The decrease is sharp across the fucoid boundary. *P. aspera* also grows fastest at low level in relatively sheltered conditions, but seems unable to compete with *P. vulgata* in very sheltered places. It is unlikely to be physical conditions such as desiccation which keep *P. aspera* from occupying the lowest levels on very sheltered shores, since under fucoids the rocks are permanently damp. The greatest mean size of any *P. aspera* population was found at the sheltered edge of its range. The only two *P. aspera* individuals found in two years sampling at Mount Batten both measured more than 55 mm. in length. This suggests that *P. aspera* grows fastest at the edge of its range, and would do even better in shelter but for the competition with *P. vulgata*.

A similar population survey of *Patella* species carried out in the Biarritz area in June 1960, confirmed the view that competition is the factor that limits specific ranges locally. In the Biarritz area *P. depressa* was the dominant limpet on all shores, *P. aspera* was much commoner than in S.W. Britain, but *P. vulgata* was relatively rare, except in extreme shelter. All three species (as well as *P. lusitanica* which occurred high up in very exposed shores) showed the same pattern of variation in mean size as that at Dale. The greatest mean size was found at the most sheltered end of the range of each species. The mean size of *P. depressa* was over 40 mm. in very sheltered conditions (cp a maximum of 20 mm. at Dale).
In December 1960 a survey of sex proportions and the size of sex change was carried out at Dale. Nine populations of P. vulgata were studied. In each case the size group (shell length) at which 40% of the population had become female was slightly lower than the mean size. In the low level populations on very sheltered shores the 40% female size was about 45 mm. (cp a mean size of 47.5 mm.). On an exposed shore at high level the 40% female size was about 14 mm. (cp a mean size of 15.5 - 16.5 mm.). These results agree closely with the hypothesis that mean size is positively correlated with growth rate and that about 40% of the limpets become female by the 5th year of life.
Fig. 85 Sketch map of the eastern side of Plymouth Sound, showing the positions of the Mount Batten shore, and the exposed (right) and sheltered (left) shores at Renney.
Fig. 84 The positions of the sample sites in the Dale Patella survey. The fucoid dominated areas are shaded.
Compare with fig. 1 in Ballantine (1961).

Fig. 85 The total weight of Patella in grams per metre$^2$ of occupied rock surface, in the Dale Patella survey.
Contours at 100, 200, 400 and 800 g. per m$^2$. 
Legend to Figs. 66 - 94 (on the folded sheet following)

The top row of figures show how the total Patella population at each sample site is divided into species:

Fig. 86 (top left) The percentage by weight of *Patella vulgata* in the total *Patella* population at each sample site. Contours are shown at 50% and 90%.

Fig. 87 (top centre) The same for *P. aspera*.

Fig. 88 (top right) The same for *P. depressa*.

The middle row of figures show the density of the three species at each sample site.

Fig. 89 (middle left) The weight (in grams) of *Patella vulgata* per metre$^2$ of occupied rock surface. Contour lines are shown at 100, 200, 400, and 800 g. per m$^2$.

Fig. 90 (middle centre) The same for *P. aspera*.

Fig. 91 (middle right) The same for *P. depressa*.

The bottom row of figures show the mean size (50% accumulative weight size) for the three species at each sample site.

Fig. 92 (bottom left) The mean size in mm. shell length for *Patella vulgata*. Contour lines are shown at 20, 30 and 40 mm.

Fig. 93 (bottom centre) The same for *P. aspera*.

Fig. 94 (bottom right) The same for *P. depressa*. 
Conclusions

*Patella vulgata* is found in a wide variety of habitats on rocky shores in S.W. Britain (see figs. 86 and 89). Several factors limit the extension of this range. At the top of the shore, desiccation, lack of food, and restricted feeding time operate singly or in combination to produce the upper limit (see Section I, 6). Population 4 at Mount Batten was a typical example of all three factors operating together to produce a sharp upper limit on vertical south-facing rocks. On wave-splashed, shaded, or ill-drained rocks the upper limit is higher and less well defined.

Settlement of limpets only takes place successfully on permanently damp clean surfaces. On sheltered shores where fucoids cover most of the rocks, clean surfaces only exist where adult limpets are continually grazing. Adult limpets 'compete' with fucoids in much the same way as rabbits 'compete' with trees. If the limpets can eat all the fucoids that settle before they develop, the area remains free for further grazing; but once the fucoids grow large enough they are more or less immune from limpet attack and produce conditions which limit free grazing. Rabbits frequently prevent trees from developing in an area by nibbling the young seedlings. If full scale woodland does develop, however, the number of rabbits which the same area can support is markedly reduced. In a dense stand of fucoids there is much more plant material and more plant production than on the open rock. This material is not available to limpets.
any more than the high leaves of trees are available to rabbits. The undergrowth of algae and encrusting animals which develop beneath dense fucoids prevent the settlement of young limpets and the grazing of adult limpets. Limpets cannot climb the fucoids to graze on them although they may eat pieces from the holdfasts and thongs near the rock surface.

Limpet grazing efficiency is governed by the nature of the rock surface. Smooth slopes are the best surface for free grazing and make it easier for limpets to restrict fucoid development. In the absence of limpets, fucoid settlement and growth is controlled by a combination of wave action, topography and desiccation which is roughly measured by the exposure scale (Ballantine, 1961). Heavy wave action, steep slopes, and well-drained sunny conditions all tend to restrict the development of fucoid stands. Ascophyllum requires more shelter than the other species but forms the densest and largest stands. Some exposed shores might not support any fucoids, even in the absence of limpets. Some very sheltered shores might have only a few limpets even if fucoids did not exist. In natural conditions, however, the actual boundaries between the two communities are determined by the interaction of the activities of the organisms. Competition is probably not the correct word to describe the situation, and interaction is also used in another specialised sense (see the Symposium of the Society for Experimental Biology, 1960), but the processes involved are clear enough.
On exposed shores, *P. vulgata* is found in the upper parts of the midlittoral zone. Its lower limit is apparently governed by competition with *P. aspera* (see Section III, 2). The way this competition operates is not properly understood, but it is possible that *P. aspera* can graze and utilize the plant material which exists at these levels more efficiently than *P. vulgata*. In the upper midlittoral zone on exposed shores *P. vulgata* is apparently in competition with *P. depressa*, especially on well-drained sunny rocks. *P. vulgata* however is always the dominant species.

Visits made to Norway, the north coast of Spain and the Biarritz area showed that the range of *P. vulgata* populations in S.W. Britain covered all the types found in its geographical range. In Norway, fucoids were much commoner than in England and the *P. vulgata* populations were almost all of the sheltered shore type. In the Southern Bay of Biscay, the shores were almost completely devoid of fucoids and the *P. vulgata* populations were mostly of the exposed shore type. All the species show a shift in their exposure range from north to south, occupying more sheltered habitats at the southern end of their range (see Ballantine, 1961). The only quantitative work performed outside Britain was a *Patella* population survey in the Biarritz area, which confirmed the southern part of the trend. Much more work would be needed to follow this latitudinal trend in detail, the only point made here is that the conclusions reached at Mount Batten are apparently valid over the whole geographical range of *P. vulgata*. 
The *P. vulgata* populations in S.W. Britain show very considerable variation in structure. The principle aim of this thesis has been to show that this variation has a pattern which can be described and related to the distribution. It has been shown that the growth rate of a population is positively related to the maximum size, the mortality rate and the recruitment rate. Growth rate is inversely related to longevity. In stable populations the mean size (defined as the 50% accumulative weight size) is positively related to growth rate. The mean size is a fairly important biological quantity - it is the size of the limpets which are doing most of the grazing in the population - but its main significance lies in the fact that it can be easily and accurately measured on a single sample of the population. Other points that vary with the mean size and the growth rate are the rate of gonad development, the number of eggs produced, the radula ratio and the shell shape.

Using mean size the populations of *P. vulgata* can be arranged in a sequence. At one end of this series there are populations like Population 1 at Mount Batten. They have a very high growth rate, high recruitment and mortality rates and a short life span. The reproductive efficiency is high, they have low radula ratios and flat shells. The density of these populations is not necessarily very high, even when estimated as weight per occupied area, and the limpets are frequently confined to small rare clearings amongst the large areas of fucoid
covered rock. All the *F. vulgata* populations inside the fucoid community are of this type, although there is some variation in mean size. At the edge of the fucoid community there is a sharp change in population type. The mean size and growth rate is lower, but the density is very high indeed. Beyond the fucoid community, out on the open barnacled rocks the populations have a much lower mean size, growth rate and density. On shores too exposed to have fucoids, except a little *Fucus serratus* at low level, there is a steady increase in mean size downshore. At the top of such shores the mean size may be as little as 16 mm., rising to about 35 mm. at the lowest level. The smallest mean size at Mount Batten was 30 mm. and it is not known for certain if the correlations with growth rate etc. extend to these populations on exposed shores. Such evidence as there is suggests that they do.

The timing of sexual maturity and the process of sex change appear to be independent of growth rate. All specimens are male in the 3rd year, although proper spawning does not seem to take place until the 4th year. Between the 3rd and 5th year about 40% of the individuals become female. A survey of sex proportions in a wide variety of habitats showed that the size at which 40% of the specimens were female was always slightly below the mean size. Unless both correlations are wrong this seems to confirm both the connection between mean size and growth rate and between age and sex-change.
Savilov (1953) working on *Mytilus edulis* in the White Sea area, showed that maximum size, rapidity of gonad development, reproductive efficiency (egg production per gm. in an individual), and shell shape were all related to growth rate in the same way as they are in *P. vulgata* at Plymouth. Savilov used annual rings to determine age, and did not record population structure. It seems possible that the correlations established for *P. vulgata* have a wide significance.
References

Ballantine, W.J. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. Field Studies 1. (reprint enclosed with this thesis)


Harding, J. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. 28, 141.


Jones, N. S. 1948. Observations and experiments on the biology of
**Patella vulgata.** Proc. Lpool bio. Soc. **56.** 60.


Plymouth Marine Fauna.


Addendum

Appendix A  The specification of the drill used to mark individual limpets.

Power: Two 6 volt, lead/acid, leak-proof batteries, the type supplied for motor scooters, cases of heavy duty rubber, connected in parallel.

Motor: Ex-service, 12 volt, developing 1600 r.p.m. under light load, light alloy case diameter $1\frac{1}{2}$", length $4\frac{1}{2}$".

Chukk: Specially made brass cylinder, fitting directly on to the motor spindle.

Drill: 'Mash' bur, wheel plain cut No. 5 (Dentists' drill).

Cable: 10 feet, heavy duty plastic sheath.

Came: Dexion frame to carry all the equipment and hold the batteries while in use.

Total weight approximately 10 lbs.
Appendix B

The growth rate of *Fucus vesiculosus* in the experimental areas at Mount Batten.

<table>
<thead>
<tr>
<th>Date</th>
<th>The average length of 15 dominant plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Group 2a area</td>
</tr>
<tr>
<td>July 1959</td>
<td>3 cm.</td>
</tr>
<tr>
<td>Sept. 1959</td>
<td>8 cm.</td>
</tr>
<tr>
<td>Feb. 1960</td>
<td>22 cm.</td>
</tr>
<tr>
<td>May 1960</td>
<td>34 cm.</td>
</tr>
<tr>
<td>Sept. 1960</td>
<td>-</td>
</tr>
<tr>
<td>Nov. 1960</td>
<td>42 cm.</td>
</tr>
</tbody>
</table>

The *F. vesiculosus* in the *Ascophyllum* cleared areas reached
25 cm. by Feb. 1960

35 cm. by May 1960

The growth rate of *Himanthalia* (Natural conditions) in the Population 1 area.

<table>
<thead>
<tr>
<th>Date</th>
<th>The average length of 15 dominant plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan. 1960</td>
<td>9 cm.</td>
</tr>
<tr>
<td>Feb.</td>
<td>19 cm.</td>
</tr>
<tr>
<td>March</td>
<td>48 cm.</td>
</tr>
<tr>
<td>May</td>
<td>160 cm.</td>
</tr>
<tr>
<td>July</td>
<td>250 cm.</td>
</tr>
<tr>
<td>Sept.</td>
<td>260 cm.</td>
</tr>
</tbody>
</table>
Appendix C

The numbers of free-roaming molluscs in an area of unaltered Population 2 equal to that of Group 2a.

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>July</th>
<th>Sept.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monodonta</td>
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<td>28</td>
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The numbers of free-roaming molluscs in the Group 2a area.

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The number of free-roaming molluscs in the Group 4a area.

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A BIOLOGICALLY-DEFINED EXPOSURE SCALE
FOR THE COMPARATIVE DESCRIPTION OF ROCKY SHORES

By W. J. BALLANTINE
Zoology Department, Queen Mary College, London

Wave action on the shore varies greatly even over quite small distances. Some shores are almost landlocked, so sheltered that no waves larger than ripples ever reach them, while others are buffeted on most days by great rollers or the breaking swell from storms far out to sea. Every kind of intermediate condition exists between these extremes.

A scale which could measure the relative exposure of shores to wave action would be very useful. The biologist constantly finds himself saying that one shore must be considered more exposed than another, but he may find it difficult to justify his statement. A physical scale, derived from measurements of the amount of wave-action on different shores, would be one way of solving this problem.

A different and more biological approach is another possibility. This approach would define the problem in slightly different terms. The shore ecologist needs a frame of reference, preferably a simple scale, in which different shores can be directly compared. It is not necessary that the scale should be an exact or direct measure of wave action provided it allows biological data to be related in an orderly and understandable way.

Biological measurements made of the abundance and levels of growth of the common animals and plants could be used as the basis of the scale. This scale would be closely related to the amount of wave action, although not a precise measure of it. Different species growing on rocky shores require different degrees of protection from certain aspects of the physical environment, of which wave action is often the most important. They can survive and flourish in different degrees of exposure to these forces. Thus the scale is an exposure scale in the broad everyday sense of that word.

PROBLEMS IN THE USE OF PHYSICAL MEASUREMENTS

Few attempts have been made to measure wave action or to compare its strength at different points. Moore (1935) determined the “number of days per hundred days in which any wind blew into the area over more than three miles of sea”, but in doing so he ignored wind speed, fetch and any swell. Southward (1953) measured the height of swash above predicted tide-levels under known wind conditions. Some account was taken of wind speed but not of fetch or swell. Most workers have relied upon subjective estimates. These may be useful in purely local studies but, in the absence of any measurements, comparisons with other areas or the results of other workers are unrewarding.
“Very exposed” shores in the Isle of Man (Burrows and Lodge, 1951) and the Plymouth area (Evans, 1947) are very different from one another and the same phrase applied to an open Atlantic shore might imply yet another set of conditions.

The dimensions and energy of free water waves depend on the speed of the wind, its duration and the distance of open water over which it can blow (fetch), and these factors have to be known if the dimensions of the waves are to be calculated. This information is often not available even for local winds and rarely if ever for distant storms which give rise to swell.

Continuously recording instruments, placed below low water, can measure the height of the waves passing over them. Such instruments are, however, expensive, difficult to install and maintain, and must be run for long periods to provide useful information.

Waves are often refracted and their form altered as they approach a shore, and the distribution of their energy on the shore itself is governed largely by the slope and detailed configuration of the rocks.

Finally, it is by no means obvious how even perfect data for different shores should be compared. For example, what amount of continuous moderate wave action on one shore is equivalent to the infrequent heavy storms which attack another.

Thus, although considerable progress is being made in the measurement of waves and wave action (see King, 1959, for review), the present state of knowledge is not very helpful to ecologists engaged in shore surveys.

Problems in the use of biological measurements

It has long been recognized that wave-beaten shores have a characteristic pattern of communities and that sheltered shores have a very different pattern. The argument for a biological scale of exposure requires that between these two extremes the community patterns fall on to a roughly linear sequence or trend. Intermediate linking patterns do exist, but it can be objected that some shores do not fall neatly into this trend.

This is the first limitation of the biological scale. The shores considered must be moderately uniform slopes of bedrock. Very uneven shores with large stacks and jagged reefs cannot be considered as a whole, although one slope of a very large stack or reef could be considered on its own. Furthermore, gullies, pools, caves, boulders (unless very large and never moved by the waves) and shingle beaches must be excluded. Since these features would produce anomalies on almost any scale this limitation should probably be accepted with patience. When more information is available, modifications might be derived to cover some of these situations.

The second major difficulty arises when a physical factor other than wave-action and topography begins to have an over-riding influence. For example, what happens when decreased salinity becomes more important than freedom from wave action. No one seems to know exactly where, or under what conditions this takes place, although the situation must occur in the estuary of every river. I would suggest that the exposure scale, or some modification of it, can be used to investigate such problems. The exposure scale represents a standard trend of community patterns correlated with a continuous decrease
A Biologically-defined Exposure Scale for Rocky Shores

of the major limiting physical factor (wave action). Where this situation
does not obtain, the application of the scale will produce anomalies. However,
because the scale is biological and quantitative, these anomalies will be quickly
apparent, interesting in an ecological sense, and definable in trend and amount.
This should make it easier to discover where the salinity drop (for example)
begins to have its effects and what kind of effects, in community terms, they
are. The discussion provides examples of such anomalies and shows how
information can be gained from them.

Other major criticisms of the exposure scale aim at the basic theory.
They may be summarized as follows:

(a) It is not clear what, if anything, is being measured by the scale.
(b) The scale is based on a circular argument: a shore is exposed because
it has a certain community pattern and it has this pattern because
it is exposed.
(c) The scale is a tautology. It merely states that a shore with a certain
pattern of communities is equivalent to one with the same pattern.

Since the exposure scale is intended as a tool for research it should help
to uncover new information and order it in an understandable fashion. If it
does this, the objections listed above lose most of their force and become
relatively unimportant. The latitudinal trend discussed later was discovered
by the use of the scale and is, I believe, of some interest. Moreover, there is
already in existence an accepted system of comparison about which the same
criticisms could be (and were) made. No one is quite certain what the position
of the barnacle line measures in terms of physical conditions, or even that
they are the same conditions in every case. To say that the barnacle line in
one place is equivalent to the barnacle line in another may seem to be a
circular argument or tautological according to certain points of view. Never-
theless, the barnacle line (the upper limit of the barnacles in quantity) is
used as one of the major reference points in the Stephensons' scheme for the
comparison of vertical zonation (Stephenson and Stephenson, 1949). This
scheme is widely accepted and has proved more useful in comparisons than
physical measurements of tide-levels.

The exposure scale for horizontal comparisons is at a much lower stage of
development than the Stephensons' scheme for zonation, and it is not likely
to have such a wide application. The comparison between the two is made
simply to suggest that the theoretical criticisms stated above may not be so
devastating as they appear at first sight.

METHODS

Some species occurring on rocky shores are abundant only in wave-beaten
places—positive correlation with exposure; others are commonest in shelter—
negative correlation. The vertical ranges of the various species may alter with
the degree of wave action (Lewis, 1955), also the absolute levels (Evans, 1947);
however, with a few exceptions, the judging of range limits is a difficult and
subjective process. For comparable results between shores the abundance of
each species provides an easier, quicker and more reliable guide to exposure
than does their range.
MAP OF THE EXPOSURE
SURVEY STATIONS NEAR DALE.

Marloes Sands
Hoopers Point
West Dale Bay
Dale Village
Black Rock
Musselv Pc
Dale Roads
Dale Point
Watwick Point
Mill Bay
St. Anns Head
**A Biologically-defined Exposure Scale for Rocky Shores**

I have included notes on zonation where this provides extra information. The terminology of zonation used was devised by the Stephensons (1949). The following indicator species were selected (the correlation with exposure is given beside each species, positive or negative):

### Algae

<table>
<thead>
<tr>
<th>Algae</th>
<th>Fauna</th>
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<tbody>
<tr>
<td>Pelvetia canaliculata</td>
<td>Chthamalus stellatus +</td>
</tr>
<tr>
<td>Fucus spiralis</td>
<td>Balanus balanoides</td>
</tr>
<tr>
<td>Ascophyllum nodosum</td>
<td>Patella vulgata</td>
</tr>
<tr>
<td>Fucus vesiculosus</td>
<td>&quot;intermediate&quot;</td>
</tr>
<tr>
<td>Fucus serratus</td>
<td>&quot;intermediate&quot;</td>
</tr>
<tr>
<td>Laminaria digitata</td>
<td>Littorina littorea</td>
</tr>
<tr>
<td>Alaria esculenta</td>
<td>Littorina obtusata</td>
</tr>
<tr>
<td>Laminaria saccharina</td>
<td>Littorina saxatilis two forms*</td>
</tr>
<tr>
<td>Porphyra, high level form</td>
<td>Littorina neritoides +</td>
</tr>
<tr>
<td>&quot;Lithothamnia&quot;</td>
<td>Gibbula umbilicalis</td>
</tr>
<tr>
<td>Lichen</td>
<td>Monodonta lineata</td>
</tr>
</tbody>
</table>

* one form positive, the other negative.

A transect line was established at each of 28 stations in the Dale area (see Map and Table 2 for positions) and the abundance of each indicator species was recorded using the notation developed by Crisp and Southward (1958), see Table 1.

The stations were arranged in order by the abundance of each species separately at first. These orders were checked for consistency using rank correlation methods. The final order of stations (Table 2) was the average of the single species orders. The final order was divided up into convenient sections to provide the data for the exposure scale.

**Table 1.** The notation used to describe abundance

**Balanus balanoides and Chthamalus stellatus:**

- **A** More than 1 per sq. cm., rocks well covered.
- **C** 0.1 to 1 per sq. cm., up to one-third of the rock covered.
- **F** 0.01 to 0.1 per sq. cm., individuals never more than 10 cm. apart.
- **O** 10 to 1,000 per sq. metre, few within 10 cm. of each other.
- **R** Only a few found in 30 minutes' search.

**Limpets:**

- **A** Over 50 per sq. metre or more than 50% of limpets at certain levels.
- **C** 10 to 50 per sq. metre, or 10-50% at certain levels.
- **F** 1 to 10 per sq. metre, or 1-10% at certain levels.
- **O** Less than 1 per sq. metre, or less than 1% of the population.
- **R** Only a few found in 30 minutes' search.

**Top-shells and Nucella lapillus:**

- **A** Exceeding 10 per sq. metre generally.
- **C** 1 to 10 per sq. metre, locally sometimes more.
- **F** Less than 1 per sq. metre, locally more.
- **O** Always less than 1 per sq. metre.
- **R** Only one or two found in 30 minutes' search.
Littorina neritoides and the small form of L. saxatilis:
- A: Over 1 per sq. cm. at H.W.M., extending down the mid-littoral zone.
- C: 0.1 to 1 per sq. cm., mainly in the supra-littoral fringe.
- F: Less than 0.1 per sq. cm., mainly in crevices.
- O: A few individuals in most deep crevices.
- R: Only one or two found in 30 minutes' search.

Other Littorina:
- A: More than 50 per sq. metre.
- C: 10 to 50 per sq. metre.
- F: 1 to 10 per sq. metre.
- O: Less than 1 per sq. metre.
- R: Only one or two found in 30 minutes' search.

Mytilus edulis:
- A: More than 20% cover at certain levels.
- C: 1 to 20% cover, zone well-defined.
- F: Many scattered individuals and small patches.
- O: Scattered individuals, no patches.
- R: A few seen in 30 minutes' search.

Lichens:
- A: More than 20% cover at some levels.
- C: 1 to 20% cover, zone well-defined.
- F: Large scattered patches, zone ill-defined.
- O: Widely scattered patches, all small.
- R: A few small patches seen in 30 minutes' search.

Fucoids, Laminaria spp. and Alaria:
- A: More than 30% cover.
- C: 1 to 30% cover.
- F: Less than 5% cover, but zone still apparent.
- O: Scattered individuals, zone indistinct.
- R: A few plants found in 30 minutes' search.

A = abundant, C = common, F = frequent, O = occasional, and R = rare; N is used for absent.

N.B. - The notation of abundance for each species should be applied only to the levels at which the species is normally found, e.g. for Ascophyllum, abundant is more than 30% cover near mid-tide level, not over the whole shore.

THE EXPOSURE SCALE

For each unit of the scale, the criteria by which it is defined and may be recognized are given in the following order:

(i) General comments
(ii) Barnacles
(iii) Laminaria and Alaria
(iv) The fucoids
(v) Other algae
(vi) Limpets
(vii) Littorinids
(viii) Top-shells
(ix) Other animals

Dominant in this scale means the most abundant species in the group (e.g. barnacles or fucoids) at the specified level.

(1) Extremely exposed (based on stations 1, 2 and 3)
(i) Heavy surf occurs more or less continuously. Many abundance trends may be reversed because the isolation of the localities prevents or reduces
A Biologically-defined Exposure Scale for Rocky Shores

Fig. 1

The changes in distribution and zonation of the barnacles and algae with exposure. Based on shores in the Dale area, Pembrokeshire, except the extremely sheltered shore. Vertical scale according to Stephenson's universal scheme. Horizontal scale of exposure (sheltered to the right) with the approximate positions of the exposure scale given.

\[ X = \text{Fucus vesiculosus f. vesiculosus,} \]

\[ \ldots = \text{upper limit of "Lithothamnia".} \]
colonization (e.g. the total absence of *Lichina pygmaea* on Grassholm). However, extremely exposed shores are rare, often inaccessible and quite distinctive.

(ii) *Alaria* is abundant and dominant in the infralittoral fringe; *Laminaria* spp. are rare or absent.

(iii) The only fucoid present is *Fucus vesiculosus* form *evesiculosus* which is frequent to abundant as very short erect tough bladderless plants with complete barnacle cover underneath.

(iv) The thick form of "lithothamnia" and *Corallina* are abundant under the *Alaria* and *Himanthalia* and *Gigartina* communities. *Porphyra* persists as a dense band above the barnacle line throughout the summer.

(v) *Lichina pygmaea* usually common, but see note (i). The lichens of the supralittoral fringe, which may extend up to 100 feet above sea-level, are all abundant and have very wide zones.

(vi) *Chthamalus* is abundant and dominant over the whole barnacle zone (the upper two-thirds of the midlittoral); *Balanus balanoides* is only frequent or less.

(vii) *Patella aspera* is abundant and dominant from amongst the *Alaria* to at least half way up the midlittoral; *P. vulgata* is common to abundant near the barnacle line, but all very small, 25 mm. max. shell-length except in crevices; *P. depressa* is usually common (always less common than *P. vulgata*).

(viii) *Littorina neritoides* and *L. saxatilis* common or abundant. *L. saxatilis* very small (max. shell-length 6-8 mm.) and *L. neritoides* nearly as large (max. 5-6.5 mm.). Other littorinids absent.

(ix) *Nucella* is confined to crevices and the individuals are all small (18-22 mm. max. shell-length) with thick shells, short spires and large apertures. *Mytilus edulis* is common in the lower midlittoral as tiny crowded individuals.

(2) Very exposed (based on stations 4, 5 and 6)

(i) The most exposed kind of shore to be found on the mainland, still very impressive physically and workable only on calm days.

(ii) *Laminaria digitata* common to abundant and always dominant; *Alaria* less, frequent to common.

(iii) *Fucus vesiculosus* f. *evesiculosus* rare to common, no other fucoids except possibly some *Pelvetia* on landward-facing slopes and scattered *Fucus serratus* just above the *Laminaria*.

(iv) A "lithothamnia": *Corallina: Gigartina* zone occurs at the base of the midlittoral zone. *Porphyra* persists in summer on *Fucus* and as scattered tufts above the barnacle line.

(v) *Lichina pygmaea* common at the top of the midlittoral; the supralittoral fringe lichens are normally abundant and have wide zones.

(vi) *Chthamalus* is abundant and dominant over the upper half of the midlittoral; *Balanus balanoides* frequent to common in the lower half and often dominant there.

(vii) *Patella aspera* is abundant and dominant in the infralittoral fringe and lower midlittoral zone; *P. vulgata* abundant and dominant over the rest of the midlittoral; *P. depressa* common amongst the *P. vulgata*. 

[8]
Diagrams of the main zonation on three shores of the exposure scale in the Dale Area, Pembrokeshire (midlittoral reduced to same vertical scale in each case).

Fig. 2
An extremely exposed shore

Fig. 3
A semi-exposed shore

Fig. 4
A very sheltered shore

- Fucus vesiculosus
- Chthamalus stellatus
- Himanthalia
- Alaria
- Laminaria
- Porphyra

- Mytilus patches
- Patella aspera
- Patella vulgata
- Fucus vesiculosus
- Fucus vesiculosus f. esculentus
- Chthamalus stellatus
- Balanus balanoides
W. J. BALLANTINE

(viii) Littorina neritoides and L. saxatilis common in the supralittoral fringe and amongst barnacles; other littorinids absent.

(ix) Top-shells absent.

(x) Nucella common and occurs on the open rock in places. Mytilus usually only in crevices but on isolated stacks may cover much of the lower mid-littoral zone.

(3) Exposed (based on stations 7, 8, 9 and 10)

(i) Shores of this unit are fairly common on the west coast. They occasionally receive almost the full force of Atlantic storm waves.

(ii) Laminaria digitata common or abundant, dominant; Alaria rare or absent.

(iii) Pelvetia rare on seaward slopes; Fucus vesiculosus f. vesiculosus rare or occasional; F. serratus occasional. Other fucoids absent.

(iv) "Lithothamnia" and Corallina common; no high-level Porphyra in summer.

(v) Lichina pygmaea common or abundant; supralittoral lichens common.

(vi) Chthamalus abundant and dominant in the upper midlittoral; Balanus balanoides abundant and dominant over rather more than half (lower half) of the midlittoral zone.

(vii) Patella aspera common in the upper part of the infralittoral fringe and in "lithothamnia"-lined pools; P. vulgata abundant and dominant over the whole of the midlittoral; P. depressa frequent or common.

(viii) Littorina neritoides and L. saxatilis common or abundant. Other littorinids absent.

(ix) Top-shells absent except perhaps for a few Gibbula umbilicalis in deep pools.

(x) Nucella common on the open rock. Mytilus confined to cracks except on small isolated stacks where it may be abundant.

(4) Semi-exposed (based on stations 11, 12, 13, 14 and 15)

(i) Shores in this unit occur commonly. The reduction in wave action from the full possible force is at once apparent to the critical observer.

(ii) Laminaria digitata common or abundant; Alaria absent.

(iii) Pelvetia occasional to common, but rarely forming a distinct zone; Fucus vesiculosus rare, plants without air-bladders, but larger than the typical f. vesiculosus; F. serratus occasional to common, usually forming a definite zone above the Laminaria; F. spiralis and Ascothyllum absent. No fucoid invasion of the main midlittoral zone, which is barnacle and limpet dominated.

(iv) "Lithothamnia" and Corallina common in pools and damp places beneath Fucus serratus and Laminaria.

(v) Lichina pygmaea common only on south-facing rock at the top of the midlittoral. Supralittoral lichens common, but zones now only a few feet in vertical extent.

(vi) Chthamalus common or abundant, dominant for a few feet at the top of the midlittoral; Balanus balanoides abundant and dominant over the remaining midlittoral zone (75% of the total population, 100% of the lower half).
A Biologically-defined Exposure Scale for Rocky Shores

(vii) Patella aspera occasional to common, largely confined to pools; P. vulgata abundant and dominant over the entire midlittoral zone; P. depressa frequent.
(viii) Littorina neritoides and L. saxatilis usually common; L. littorea absent or rare; L. obtusata absent.
(ix) Monodonta rare or absent; Gibbula umbilicalis occasional to common in pools or damp places.
(x) Nuella common or abundant on the open rock; Mytilus rare or absent.

(5) Fairly sheltered (based on stations 16, 17 and 19)
(i) Shores in this unit are common. Large stones present are rarely moved; by the waves and develop a semi-permanent flora and fauna.
(ii) Laminaria digitata abundant and dominant; L. saccharina rare or absent Alaria absent.
(iii) Pelvetia frequent to common, forming a definite zone; F. spiralis absent or at most a few scattered plants; Ascophyllum usually present as isolated short plants; Fucus vesiculosus often present on the smaller rocks, plants with some air-bladders; F. serratus frequent to common, forming a dense zone.
(iv) "Lithothamnia" and Corallina only under dense seaweed or in pools.
(v) Lichina pygmaea rare to frequent on rough rock in sunny places.
(vi) Chthamalus frequent to common, with a very narrow zone of dominance at the barnacle line; Balanus balanoides common to abundant, but although it dominates almost all the barnacle area, fucoids are regularly present as isolated plants in the midlittoral.
(vii) Patella aspera absent or confined to pools; P. vulgata abundant over most or all the midlittoral; P. depressa frequent only on sunny slopes.
(viii) Littorina neritoides occasional to common in supralittoral fringe only; L. saxatilis common (max. shell-length 8-12 mm.); L. littorea occasional in pools; L. obtusata rare to frequent on the fucoids.
(ix) Monodonta rare to common; Gibbula umbilicalis common to abundant.
(x) Nuella common; Mytilus rare or absent.

(6) Sheltered (based on stations 21, 22, 23 and 24)
(i) Shores in this unit are normally "good collecting shores". They are sheltered enough to have a considerable permanent fauna beneath stones, but not so sheltered that mud and silt are deposited in quantity.
(ii) The infralittoral fringe often consists of stone and shingle, but Laminaria digitata and L. saccharina may be common.
(iii) Pelvetia abundant, forming a dense zone of large plants; Fucus spiralis frequent to common forming a distinct zone; Ascophyllum occasional to common, forming dense patches on the more jagged bedrock; Fucus vesiculosus common, typical plants with paired air-bladders, on stable shingle and small rocks; F. serratus common or abundant on bedrock or stones.
(iv) "Lithothamnia" (thin form) and Corallina are present under thick fucoids.
(v) Lichina pygmaea is absent; the supralittoral fringe lichens are not more than frequent.
(vi) *Chthamalus* occurs only at or above the barnacle line; *Balanus balanoides* common or locally abundant in the central midlittoral, but even here fucoids predominate if the rock is not suitable for continuous limpet grazing.

(vii) *Patella aspera* absent; *P. vulgata* abundant throughout the midlittoral except in the densest fucoid patches; *P. depressa* occasional or absent.

(viii) *Littorina nerioides* rare to occasional; *L. saxatilis* common, small in the supralittoral fringe, but a large form (12-18 mm. shell-length) present in the *F. spiralis* zone; *L. litorea* occasional to frequent on fucoids and in gullies; *L. obtusata* common on the densest fucoids.

(ix) *Monodonta* and *Gibbula umbilicalis* common or abundant.

(x) *Nucella* occasional to common. *Mytilus* rare or absent.

(7) Very sheltered (based on stations 26, 27 and 28)

(i) Rocky shores of this unit are not common since where wave action is so reduced sand and mud are usually deposited in quantity.

(ii) The infralittoral fringe was sandy at all the stations visited in the Dale area. *Laminaria saccharina* occurred on the few small stones.

(iii) All the fucoids are common or abundant, and form a continuous cover over most of the shore. The zones of *Pelvetia* and *F. spiralis* are very narrow and consist of very large individual plants. *Ascophyllum* covers most of the midlittoral bedrock, and *Fucus vesiculosus* covers the stones and shingle down to the *F. serratus* zone.

(iv) The thin form of "lithothamnia" and some *Corallina* exist under the lower fucoids.

(v) *Lichina pygmaea* is absent. The supralittoral fringe is at most only a few feet in vertical extent and the lichens growing there are occasional or rare.

(vi) *Chthamalus* is rare or absent; *Balanus balanoides* is frequent to common, but only on the steepest pieces of bedrock.

(vii) *Patella aspera* and *P. depressa* are absent; *P. vulgata* grows very large (50 mm. or more shell-lengths are common), but it is confined to small areas of well-drained rock beneath the fucoids and the few barnacled slopes.

(viii) *Littorina nerioides* is absent; *L. saxatilis* (almost entirely the large form 16-22 mm. max. shell-length) is common amongst the upper fucoids; *L. obtusata* is abundant; *L. litorea* common amongst fucoids, locally abundant.

(ix) *Monodonta* and *Gibbula umbilicalis* are common or abundant.

(x) *Nucella* is occasional, the shells are long and thin and taper gradually to a fine point; *Mytilus* may be common as groups of large specimens in the shingle.

(8) Extremely sheltered

(i) No rocky shores of this unit exist in the Dale area, but they are common in south-west Ireland and some other regions. They occur at the heads of intricate rocky inlets which receive no silt and where fetch is reduced to a few yards. Wave action and tidal currents are absent.

(ii) The infralittoral fringe is not usually present, but if the rock at this level does occur it is dominated by *Laminaria saccharina.*
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(iii) All the fucoids are present and develop 100% cover even on vertical faces. Unattached fucoids such as Ascophyllum nodosum f. mackii are very common.

(v) Lichina pygmaea absent; the supralittoral fringe scarcely exists and grass and other land plants grow within a foot of the Pelvetia.

(vi) Chthamalus and Balanus balanoides are absent or rare.

(vii) Patella vulgata is at most rare; other limpets absent.

(viii) Littorina neritoides absent; L. saxatilis (large form only) common in upper fucoids; L. obtusata and L. littorea abundant.

(ix) Monodonta rare; Gibbula umbilicalis common.

(x) Nucella absent or rare.

The use of the exposure scale

To find the position of a shore on the exposure scale, the following procedure is recommended:

(a) Fix the position of the transect line.

(b) Measure the slope along the line. If this varies considerably the exposure of each section may have to be measured separately.

(c) Measure the abundance of the indicator species in the transect area, using the notation given in Table 1.

(d) Note the general features of the zonation, the physical configuration of the shore, its aspect and exact geographical position.

(e) Determine the approximate position of the shore on the exposure scale by examining Figures 1 to 4.

(f) Make a detailed comparison between the notes taken on the shore (under e and d) and the units of the scale to decide the precise position of the shore.

A test of the biological scale of exposure against physical estimates of wave action

The shore survey work on which the exposure scale is based was carried out during June 1958 and June 1959. Most of the stations were visited in both years and no significant change was seen. All the mainland stations can be included within a circle of 14 miles radius and even the island of Grassholm is only 14 miles from Dale. The rock at all the stations (except Grassholm and Skomer) is uniformly sandstone or mudstone. There is no evidence of any significant variation in tidal range, pattern or timing within the survey area.

The aspect of the stations does vary, but south or south-west facing stations occur in all units of the scale. Most of the stations are of a uniform and moderate slope of bedrock. There was no noticeable pollution or other human interference at the time of the survey.

The action of such variables as season, year, geology, geographical region, tidal regime, aspect to the sun, slope and pollution was thus minimized or at least randomly distributed relative to exposure. This leaves wave action as the only remaining variable likely to influence large changes in the composition of the shore communities.

In the Dale area all fetches fall into three groups: (a) more than 5,000 miles; (b) between 50 and 150 miles; (c) less than 10 miles. Moreover, the majority
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of gales acting on the coast (70°, 90°) blow from the same direction (SSW. to W.) as that of the greatest fetch. Because of this fortunate geographical accident, it is possible to divide shores in the area into three groups of greatly different wave action. When the open angle of the shore to its maximum fetch is considered and refraction taken into account, the shores can be graded into a series of relative wave action. Wind speeds and frequency may be ignored only because of the great differences between the three classes of fetch and the coincidence of the direction of high winds and long fetch in the Dale area.

Table 2 lists the stations of the exposure survey in order of exposure as given by the biological data. The physical data for the estimation of wave

<table>
<thead>
<tr>
<th>No.</th>
<th>Station: Name</th>
<th>Aspect in ° from True North</th>
<th>Biological Exposure Scale Unit</th>
<th>Physical Data for the Estimation of Wave Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Grassholm</td>
<td>225</td>
<td>extremely exposed</td>
<td>Shores open over 67° to fetches of more than 2,000 miles; refraction concentrates waves on to these shores. Headlands on off-shore islands.</td>
</tr>
<tr>
<td>2.</td>
<td>Skokholm</td>
<td>225</td>
<td>very exposed</td>
<td>Shores open over 40°-50° to fetches of more than 2,000 miles; refraction reduces this open angle slightly. Headlands on the mainland.</td>
</tr>
<tr>
<td>3.</td>
<td>Skomer</td>
<td>185</td>
<td>exposed</td>
<td>Shores nearly open to fetches of more than 2,000 miles; refraction of about 10° required to bring waves from this direction to bear.</td>
</tr>
<tr>
<td>4.</td>
<td>Hooper's Point</td>
<td>175</td>
<td>exposed</td>
<td>Shores open over more than 20° to fetches of 50-150 miles; refraction of 90° required to bring waves of 2,000 miles fetch to bear.</td>
</tr>
<tr>
<td>5.</td>
<td>St. Ann's Head</td>
<td>195</td>
<td>exposed</td>
<td>Shores with less than 10° open angle to fetches of 50 or more miles, and even this reduced by refraction.</td>
</tr>
<tr>
<td>6.</td>
<td>West Dale Bay</td>
<td>160</td>
<td>sheltered</td>
<td>Shores open to fetches of less than 10 miles over at least 60°; refraction of 90° required to bring waves of 50 or more miles fetch to bear.</td>
</tr>
<tr>
<td>7.</td>
<td>Mill Bay</td>
<td>180</td>
<td>exposed</td>
<td>Shores open to fetches of less than 10 miles over less than 60° and even this reduced by refraction; refraction of more than 90° required to bring waves of 50 miles fetch to bear.</td>
</tr>
</tbody>
</table>
action is also shown. These two things correlate well, and so the biological exposure scale does appear to give a good estimate of wave action.

It is important to note that this does not imply that there is a direct causal relationship between the existence of individual species on a shore and the size or frequency of the waves.

**DISCUSSION**

(1) *The nature of the exposure scale and its implications*

The exposure scale given above is not a simple mathematical scale. The intercepts are not necessarily equal, they are merely at convenient intervals. It is not possible to say that one shore is twice as exposed as another.

Exposure as measured on the scale includes the effects of other factors besides incident waves. The same waves breaking on a gentle slope will produce less “exposure” than on a steep shore.

At present we know relatively little about the nature of waves which break on rocky shores, and still less about the way they affect individual organisms and communities. Thus, although some method of systematizing shore description and comparison is needed, it is important that this should not include assumptions which may prove misleading. Any physical method of describing and comparing shores assumes that it is known which physical factors are important; it must do this or become cumbersome by recording everything. The biological scale avoids this by starting at the other end of the problem. It states that the shores of an area, for all their variety and complexity do not have random collections of organisms on them. There is a pattern, a trend, in the communities. To take a simple example in the Dale area—if a shore has *Alaria* abundant and dominant in the infralittoral fringe and *Porphyra* exists as a dense band above the barnacles in midsummer, then, without seeing it, one can say that the majority of the barnacles will be *Chthamalus* and that *Patella aspera* will be abundant. No causal relationships are implied in this deduction. It is simply a correlation with a very high degree of probability. This idea is implicit in much of the literature. Most local shore survey reports describe a “typical exposed shore” and a “typical sheltered shore” as a shorthand for the whole area and then fill in the detail. However, I have not been able to find the implications of this discussed fully. The exposure scale merely describes the main trend or pattern of communities and divides it up into convenient but arbitrary sections. The scale is flexible and can easily be modified, improved and refined to suit particular regions or problems. At the same time, since it is based on quantitative measurements, it enables strictly accurate comparisons to be made from shore to shore.

The community trend described in the exposure scale is not by any means the whole story; innumerable other trends and effects occur which tend to confuse the main pattern. There are pools and crevices, the communities on boulders, the effects of sand abrasion and shade to mention only a few. The main pattern itself is likely to change with time and in different geographical regions. Nevertheless, if a pattern can be established for even one area and time these modifications can be dealt with separately. Attempts to deal with the whole complex web of communities at once are unlikely to succeed.
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(2) The use of the exposure scale in south-west Britain

The exposure scale has been tested in south-west Ireland and in the Plymouth
area. In both regions it worked well and the shores could be quickly classified
and so were at once comparable to those at Dale. One or two anomalies were
immediately apparent. *Patella depressa* was absent from Ireland, although
many shores seemed identical in other respects with those at Dale where the
species was common. At Plymouth the relative abundance of *Chthamalus*
*stelatus* and *Balanus balanoides* was consistently out of phase with the other
indicator species, *Chthamalus* penetrating much further into shelter than at Dale.

Several important points arise from this work. Firstly, the scale works well
up to 100 miles or so from Dale where it was derived. Secondly, the anomalies
that do occur are as nothing compared to geographical geological anomalies
which render a scale based on physical measurements so unsatisfactory.
Thirdly, the biological anomalies are of considerable direct interest and signi-
ficance to the shore biologist (see Crisp and Southward, 1953, and Southward
and Crisp, 1956), and the use of the exposure scale enables them to be defined
in a concise and accurate manner.

(3) The fate of the exposure scale further afield

During 1959 I made some observations on shores in Norway (Bergen to
Hammerfest) and at Santander in north Spain. These span a difference of
latitude of some 2,000 miles. The scale produced in the Dale area proved
unworkable so far away, but the attempts to use it gave some interesting data
which are summarized in Fig. 5. The principle conclusion to be drawn from
this is the existence of a latitudinal trend down the coast of western Europe
similar to the local trend at Dale from sheltered to exposed shores. Thus, if
the Dale exposure scale is applied rigorously, one would be led to believe
that there are no exposed shores in Norway and no sheltered shores in Spain.
In fact it seems that many species show a progressive change in their exposure
tolerances from north to south.

Like the exposure trend, this latitudinal trend is mainly concerned with the-
fucoid : limpet : barnacle balance. Limpets graze fucoid sporelings; fucoids
tend to smother barnacles and barnacles compete with limpets for space and
reduce their feeding efficiency (Lodge, 1948; Southward, 1956). Although
barnacles and fucoids are directly affected by wave action, the competition
between the three groups of organisms may be just as effective a control on
the distribution and abundance of any of them. The relative efficiency of all the
species changes with latitude, but at different rates. *Balanus balanoides* holds
the barnacle field alone in Norway, shares it with *Chthamalus* at Dale, and
is completely eliminated by the latter in Spain. Fucoids are dominant on most
shores in Norway, but at Santander they are confined to sheltered places
and common only in considerable shelter. *Patella vulgata* is an animal which
thrives best on the edge of the fucoid : barnacle boundary and follows this in
its movement from exposure towards shelter as one goes south. As the number
of *Chthamalus* dominated shores increases *Patella depressa* becomes the commonest
limpet. It should be observed that all the species behave in the same way,
occupying increasingly sheltered shores towards the southern end of their
range.

[16]
Fig. 5
Diagrams showing the changes in the barnacle: fucoid balance from north to south (top row) and the associated changes in distribution of Patella spp. (bottom row). Each diagram represents a series of shores in the area stated, exposed to the left and sheltered at the right. The top of each diagram represents the top of the midlittoral zone and the bottom passes into the infralittoral fringe. Cysto.—Cystoseira zone.
Alternative explanations for this phenomenon might be:

(a) That there is a trend in gradually increasing complexity of coastal configuration from south to north and that the resulting wave refraction reduces exposed shores in the north to theoretical points, i.e. that only submerged off-shore reefs and tiny islets receive the full wave action.

(b) That the far greater proportion of sheltered shores in the north may produce a recruitment advantage to sheltered shore organisms and push the exposure-loving species further towards exposure or even eliminate them altogether.

(c) That there may be a relationship between exposure and latitude (of a climatic nature) which produces similarities between northern exposed and southern sheltered shores. At any latitude exposed shores are not so warm in summer and not so cold in winter as are sheltered shores; and this may imply a higher mean annual temperature in exposure. South-west Ireland with its cool summers and relatively warm winters is a more favourable place for sub-tropical land plants than the south-east of England which has much higher summer temperatures but much lower winter ones. Exposed shores may be more temperate in a similar way.

I believe that there is some truth in each of these explanations, but that (c) is probably the most important. It may be possible eventually to produce a latitudinal correction for the exposure scale, but as I have described it here its use should be restricted to south-west Britain.

ACKNOWLEDGEMENTS

Many people have given me assistance, advice and encouragement during this work; I would like to express my appreciation to them all and especially to Mr. J. H. Barrett, Warden of Dale Fort Field Centre, without whose continuous interest and help this work could not have been done.

SUMMARY

(i) Wave action on rocky shores and the concept of exposure are discussed. The advantages of using a purely biological exposure scale rather than physical estimates of wave action for comparing shores are assessed.

(ii) Exposure is considered as a trend in the composition of the shore fauna and flora. The abundance of the common species is used to produce a scale of exposure in the Dale area, Pembrokeshire.

(iii) The scale enables rocky shores consisting of moderate slopes of bedrock in south-west Britain to be directly compared with one another. Further away from Dale, and in certain conditions, modifications of the scale will be required.

(iv) Using experience on shores in Norway and north Spain, the nature of some of these modifications is discussed. A change in the exposure tolerances of many species from north to south is postulated.

REFERENCES


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(Received January 1961)