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## STUDIES OF *PATELLA VULGATA* L.

### I. GROWTH, REPRODUCTION AND ZONAL DISTRIBUTION

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**Abstract:** A population of *Patella vulgata* L. from a sheltered coast at Robin Hood's Bay, North Yorkshire, has been studied. On alternate spring-tides (from September 1964 to December 1966) the population was sampled at seven stations along a transect line which extended from between M.H.W.S. and M.H.W.N. to between M.L.W.N. and M.L.W.S. The population was found to have a polymodal frequency distribution, the components of which were dynamically maintained. Each component represented a separate year group, the growth of which was maximal during the summer and was depressed over the winter. This pattern persisted from year to year but varied in degree, some years supporting higher growth rates than others. Animals five years old and over were few in number and had no measurable growth rate. The limpets matured for the first time in their second year as males. Females first appeared in the third year and thereafter were present in increasing numbers. Gonad maturation coincided with the period of maximum increase in body size. The settlement of the young limpets was usually first detected in January. The pattern of their settlement and subsequent survival was responsible for the zonal pattern of the total population.

#### INTRODUCTION

Of all the intertidal gastropods the common limpet, *Patella vulgata* L., is perhaps the most ubiquitous. It can be encountered on most shores providing that there is a stable substratum (Fretter & Graham, 1962). The degree of wave exposure experienced is not a critical limiting factor but under conditions of very high exposure it may be limited to the upper region of the shore, its place being taken below mean tide level by *P. aspera* Lamarck. (Ballantine, 1961a; Ebling, Sloane, Kitching & Davies, 1962.).

The widespread distribution of *P. vulgata* around the British Isles has undoubtedly been responsible for the numerous accounts already devoted to limpet biology and the production of yet another might seem superfluous. The present work however was designed to combine, within the one limpet population, the analyses of growth rates, distribution, and breeding cycle (and also tissue composition; Blackmore, in prep.). Though this resulted in some repetition of earlier work a detailed population analysis was considered to be an essential preliminary for the study of other aspects of the problem.

#### DESCRIPTION OF SITE AND GENERAL METHODS OF COLLECTION

The population of limpets studied came from the shore at Robin Hood's Bay, North Yorkshire. The whole region here is part of the Cleveland anticline which at

this point, due to a depression inland, is tilted back towards the land; this has resulted in the outcropping rocks of the shore producing a semicircular pattern. Erosion has enhanced this pattern and produced a number of seaward facing scars (see Colman & Segrove, 1955). A suitable collecting site was located in the bay immediately south of Mill Beck, which was easily accessible by road and yet far enough away from the village to avoid undue attention from the public. This section of the beach ran north-south for about 0.5 mile (800 m) and on Ballantine's (1961a) scale this region of the shore would be classified as 'sheltered'. Algae were sparse on the upper part of the beach but *Fucus serratus* L. became abundant 2 ft (0.6 m) below M.L.W.N. and was succeeded at lower levels by *Laminaria* spp. Faunistically this region was also poor.

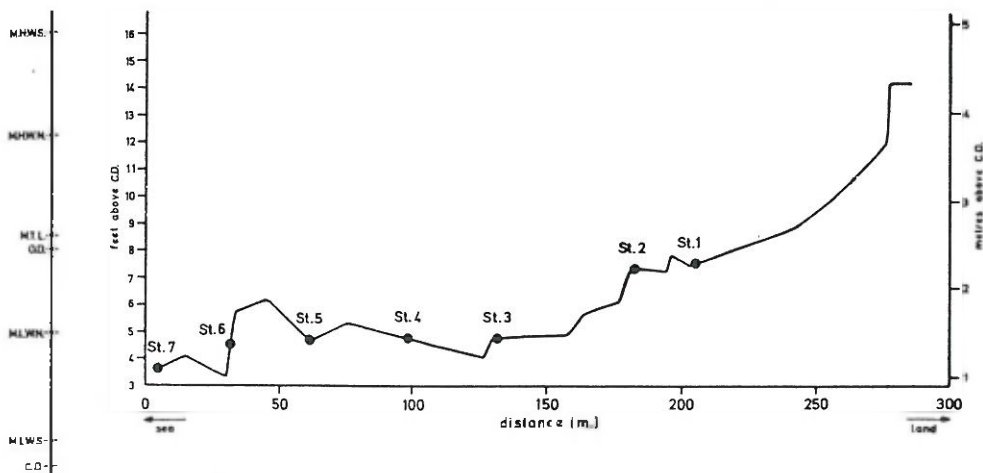


Fig. 1. *P. vulgata*. Profile of the shore along the transect at Robin Hood's Bay with the sampling stations shown.

Approximately 1 ft (0.3 m) below M.T.L. there was a narrow band (~ 12ft-3.63 m-wide) of *Balanus balanoides* L. Lower down the shore, at about the level of M.L.W.N., a zone of very small *Mytilus edulis* L. became established during the course of the work. The only other conspicuous animals present in any number were *Littorina littorea* L. and *Thais lapillus* L.

The selected transect line ran almost due east-west for about 300 yd (273 m) and extended from midway between M.H.W.S. and M.H.W.N. to between M.L.W.N. and M.L.W.S. Along this line seven collecting stations were marked (Fig. 1). The first (upper) collecting station was just below mean tide level. Immediately above this level a shifting belt of sand prevented the establishment of a permanent limpet population. The lowest station was positioned midway between M.L.W.N. and M.L.W.S. at a point immediately above the *Fucus serratus* zone.

The population was sampled from all accessible stations, approximately once a month on alternate spring tides. At each station and on each occasion, not less than

125 animals were collected by removing all the limpets from a number of unit areas, each of 0.5 m<sup>2</sup>, until this number had been exceeded. At the time when spat settled the young limpets were independently sampled by collecting from an area of 0.03 m<sup>2</sup>.

After collection the limpets were stored in polythene bags at 12 °C where they remained alive until required for the population and breeding cycle analyses. All individuals were examined within 5 days of collection.

In analysing the results, differences between samples have been considered significant at a level of  $P \leq 0.05$ .

#### POPULATION STRUCTURE AND GROWTH

Shell length was selected as the most convenient index of growth. All shells were measured to the nearest 0.5 mm. and then assigned to whole millimetre groups, *e.g.* a shell in the range 20.50–21.49 mm was classified as 21.00 mm.

#### ANALYSIS OF THE POPULATION

Graphical representation of the data showed that for any month's collection the population was polymodal. The separate modes were identified by the use of arithmetical probability paper, the method employed being a slightly modified version of that described by Harding (1949). For each component population the mean length, its standard deviation, and the percentage of the total population that it formed were calculated; each month, four or five component populations could be distinguished and recognized. Identification of more than five sub-populations was not possible and there remained a residuum composed of large, old, slow growing limpets from different year groups.

#### GROWTH RATES

The mean lengths of the component populations for each monthly collection, are plotted as growth curves in Fig. 2. Since spat was usually first found on the beach in January it is possible to identify each year group by the year in which it first appeared on the beach. If spat settlement did not occur in January then for the present purposes it was designated as though it had settled in the January nearest to the month in which settlement actually occurred. Thus the spat of November 1966 is termed the 1967 year group. Those year groups already present on the beach at the start of the survey were assigned successively to those years preceding that in which spat settlement was first observed; thus the four years groups present in September 1964 were successively labelled as the year groups of 1964–1961.

For comparison of the growth of various year groups, regression lines were fitted to the growth curves. When the growth curve exhibited a marked change of slope a new regression line was fitted; although this method was subjective, the resulting lines are considered suitable indicators of seasonal growth rates.

As has been already indicated, the young limpets were first found on the beach

during the winter. The exact month of settlement varied from year to year and depended upon the time at which the adult population reached maturity in the previous autumn. When first detected the limpets were of about 1 mm shell length and still had the coiled larval shell. Smith (1935) considers that the post-larva settles on the rocks at a shell length of 0.2 mm. This would indicate that at the time it was first noticed at Robin Hood's Bay, the spat had already been on the beach some weeks. The free swimming larval stage is limited to about two weeks (Smith, 1935; Dodd, 1957) and from the data on the breeding cycle it would seem that the spat was about five to six weeks old when first detected. Since collections were taken at monthly intervals it is probable that the spat had settled a month earlier. If this were the case these minute stages were overlooked.

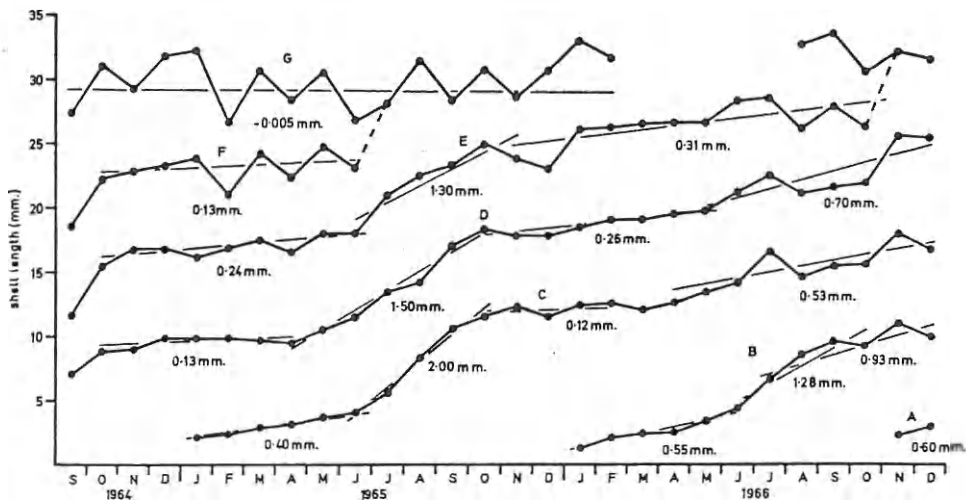


Fig. 2. *P. vulgata*. Growth curves of the various year groups throughout the period of study: A = 1967 yr group; B = 1966 yr group; C = 1965 yr group; D = 1964 yr group; E = 1963 yr group; F = 1962 yr group; G = 1961 yr group: the regression lines indicate the mean monthly rate of growth.

Once the spat had been identified on the beach its subsequent growth was easily followed because it formed a complete and separate component within the total population. After eight or nine months the higher rate of growth of the spat as compared with the second year limpets resulted in the first year group beginning to overlap on the second. The degree of overlap increased with increasing age.

Growth of the spat during the first six months was steady and relatively slow, of the order of 0.40 mm/month in 1965 and 0.55 mm/month in 1966. In both years this rate of growth continued until June when the limpets had a mean shell length of  $\sim 4.0$  mm. Between June and October (1965 and 1966) the first year group showed a marked increase in growth which in 1965 was of the order of 2.00 mm/month but in 1966 only 1.28 mm/month. After October 1964, 1965 and 1966 the growth rate of

the young of each year was reduced to give a mean shell length, by December, of 9.8 mm, 11.5 mm and 9.8 mm respectively. Reduced growth continued throughout the winter at the rate of 0.13 mm/month in 1964-65 and 0.12 mm/month in 1965-66 until the following April, when a marked increase was again detected. The 1964 year group then increased 1.5 mm/month until October 1965 and the 1965 year group 0.53 mm/month until December 1966. By the end of the second year these two populations had mean shell lengths of 17.8 mm and 16.7 mm respectively. The length of the 1965 year group (16.7 mm) after two years was almost identical with that obtained for the 1963 year group (16.8 mm) over a similar period. The same growth pattern is maintained in older animals but the rate of growth progressively diminishes. This is well illustrated in 1965 when the first year limpets increased by 2.00 mm/month, the second year limpets by 1.50 mm/month and the third year limpets by 1.20 mm/month. After three years on the beach the limpets had attained a mean shell length of approximately 25.00 mm but subsequent growth was slow (from November 1965 to October 1966, the 1963 year group added only 0.31 mm/month). By the end of the fifth year identification of the component populations was impossible. The growth rates of limpets over five years old could not be detected within the period of investigation.

In different years each year group may exhibit different growth rates; for example, the increase in shell length of the first, second, and third year groups during the summer of 1965 was about twice that of the corresponding populations during 1966. As a result of this reduced rate in 1966 the means of the component populations by December 1966 were very similar to those of December 1964. Whether the yearly fluctuations of growth rate resulted from changes in environmental conditions or whether it was endogenously controlled (*i.e.* faster growth in one year being necessarily followed by slower growth the following year) cannot be determined from the present data.

## BREEDING CYCLE

### DETERMINATION OF SEX AND GONADAL ACTIVITY

*Patella vulgata* possesses no known secondary sexual characters and therefore sexing and measurements of gonad activity were made directly upon the gonad. The gonad of the limpet is situated on the ventral side of the visceral mass, adjacent to the foot. For routine examination the foot was freed from the visceral mass by an incision passing from the left side of the head, around the body, to the right hand side of the head, so enabling the foot to be turned back over the head of the animal whilst leaving the remainder of the body within the shell and to expose the gonad (see Orton, Southward & Dodd, 1956). The sex and state of the gonad were then determined by the method described by Orton *et al.* (1956).

From these analyses a mean gonadal condition (M.G.C.) calculated as follows was determined for the population. The number of limpets in each gonad stage was mul-

multiplied by the number allotted to the stage (*i.e.* 0-V) and the values so obtained were added together. This grand total was then divided by the number of individuals in the whole sample to give the M.G.C. This was determined for limpets in two size groups, namely, those with a shell length between 15-25 mm (15-25 mm group) and those with a shell length greater than 30 mm (> 30 mm group) and taken from the collections from stations 1 and 7 (*i.e.*, the highest and lowest). In each group males and females were treated separately. The smaller size group included most of those animals maturing for the first and second time while those in the larger size group were maturing for the third or subsequent time.

Stage	Brief description of gonad
0(or N)	Inactive or neuter; either rudimentary virgin stage or resting after discharge of gametes.
I	Beginning to develop and sex detectable but only slight increase in size.
II	Developing to one-third full size.
III	Between one-third and two-thirds full size.
IV	Two-thirds full size.
V	Fully developed.

#### THE BREEDING CYCLE

At maturity the whole population consisted of about 20 % neuter, 60 % male and 20 % female animals.

Orton *et al.* (*loc. cit.*) found that the time involved in maturation and spawning depended upon the locality: more northerly populations took longer to complete the cycle than did those in the south and therefore spent less time in the neuter condition. In the population at Robin Hood's Bay the breeding period was about nine months but was clearly dependent upon factors other than latitude. In 1965 there were only two months when the population could be classed as neuter, whereas in 1966 there were four months (Fig. 3). The emergence from the resting condition began during the summer, in 1965 in August but in July in 1966. In the larger animals maturation reached a peak after 3-4 months (November in 1965, September in 1966) at a M.G.C. between stages III and IV. Since no collection contained animals all at stage V a M.G.C. of V was never observed. After spawning, the population regressed to the spent condition which, in 1966, was attained by about March. In 1965, after a drop to stage I by December 1964, about four months elapsed before the spent condition was reached. The interval between the peak M.G.C. and the fully spent condition varied between 3 and 6 months. Two to three months after the peak M.G.C. the oocytes showed signs of degeneration indicating that, at least in the latter period of gonad regression, gamete release was unlikely. Prior to the period of degeneration the oocytes were generally much more loosely packed than in the period prior to the peak M.G.C. From the classification of Orton *et al.* (*loc. cit.*) this is indicative of a spawn-

ing gonad. Whether the gonad had spawned (Ballantine, 1961b) or was still spawning is not known. Since a few ovaries with loosely packed oocytes were present before the peak M.G.C. and some with closely packed oocytes after the peak, it is likely that the population as a whole did not release the gametes synchronously. The breeding cycle of *P. vulgata* at Robin Hood's Bay may then be regarded as beginning with the maturation of the gonad about July, subsequent to the coldest months of the year; it proceeds for about four months during a period of high temperatures and increased food supply<sup>1</sup>. Spawning occurs in the autumn followed by spatfall towards the end of the year. After spawning, the gonads, which may still contain gametes, probably resorb the remaining eggs and sperm. When resorption is complete a period of two to four months is passed without any visually recognizable gonad being present before maturation begins anew.

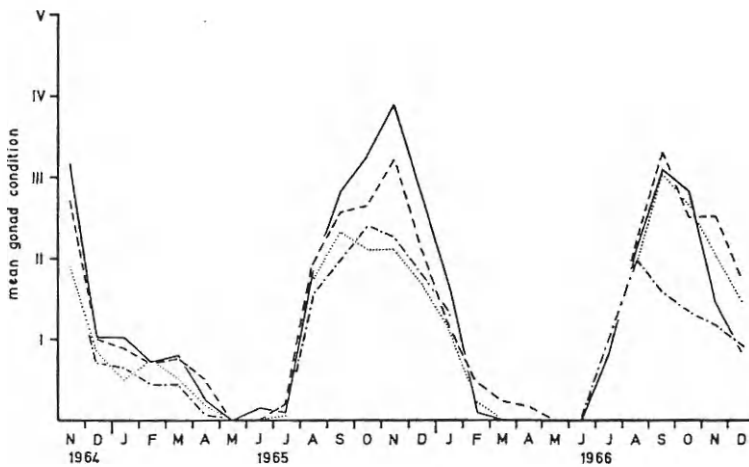


Fig. 3. *P. vulgata*. The mean gonad condition (M.G.C.) for limpets at Robin Hood's Bay throughout the period of study: limpets > 30 mm shell length from St. 1 ---; limpets 15-25 mm shell length from St. 1 ····; limpets > 30 mm shell length from St. 7 ———; limpets 15-25 mm shell length from St. 7 - · - · - ·.

A comparison of the gonad size of limpets in the 15-25 mm and > 30 mm groups shows that the mean size of the gonad of the larger limpets was generally relatively greater than that of the smaller animals, particularly about the time of maturity. This difference was noted by Ballantine (1961b) at Plymouth and he mentions that there young animals failed to spawn "properly" since there was no decrease in the relative volume of the gonad at the appropriate time. The rate of shrinkage of the gonad in limpets of the 15-25 mm group at Robin Hood's Bay tended to be less than in the larger limpets. The effect of sex on gonadal size was also apparent, but was less than that of size (age). Of those animals in the > 30 mm group the females tended to have smaller gonads than the males, this difference being more pronounced in limpets in the 15-25 mm size group. There appeared to be no difference between St. 1 and

<sup>1</sup> See page 210.

St. 7 (Fig. 3) with regard to the time the peak of maturation was reached or the size of the gonads at maturity. This is in contrast to the results of Williams (1964) who found that in *Littorina littorea* (over a similar tidal range) maturation proceeded more quickly on the upper than on the lower shore.

#### THE EFFECT OF AGE ON SEX AND MATURITY

From August 1966 to December 1966 every animal that was collected (6 284) was sexed. The frequency of neuter, male, and female limpets was then correlated with size, and the peaks of distribution of each sex were related to the mean size of the various year groups obtained from the growth curves. The distribution of neuter, male, and female animals is correlated with the means of the various year groups. The results obtained were, however, somewhat at variance with others obtained later from

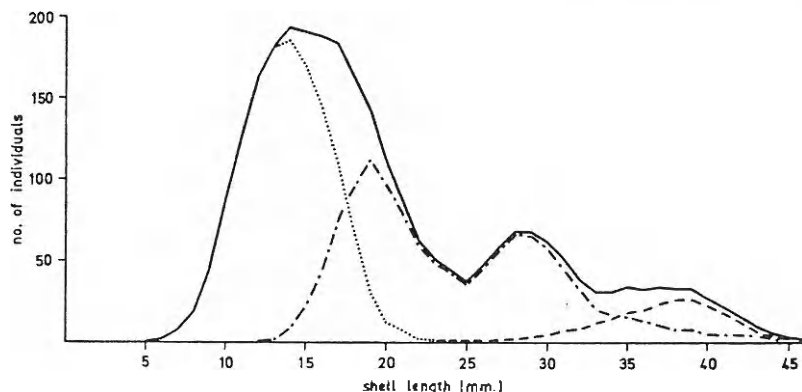


Fig. 4. *P. vulgata*. Size-frequency data for limpets collected from St. 7 on 30th November 1967: total population, ———; neuter, ····; male, - - - -; female, - · - ·.

analyses of limpets from only one intertidal level and it would seem that growth variations due to level masked the distributional pattern of neuter, male and female limpets within the total population. Analysis of limpets from a single level is more satisfactory (Fig. 4). The neuter population was distributed almost normally and corresponded with the first year group. The distribution of the male limpets consisted of two clearly defined peaks together with a tail. The first of these peaks corresponds to the second year group of limpets which was, therefore, pure male. The second male peak was equivalent to the third year group but associated with it was a very small population of female limpets. The number of these third year females was small but analyses indicated that they were third year animals. After the third year the numbers of female limpets form an increasingly greater proportion of the population, and by the fourth year males and females were present in about equal numbers. Older year groups were comprised of even greater numbers of females but no limiting size was reached above which males were not found. These results substantiate the view of Orton (1946) that individuals of *Patella vulgata* may undergo a sex change,

from male to female, during their lifetime. The belief that some male limpets may never change sex is supported by the presence of a male population within the oldest age group. No evidence was obtained to suggest that the higher incidence of female limpets within the larger size groups may be a result of a differential growth rate between the two sexes.

It can be concluded that in this locality limpets in their first year do not mature. During their second year maturation produces all male animals. Maturation in the third year again results in an almost complete population of males, together with a very few females and only in the fourth year are females at all abundant, having developed from limpets which, in previous years, were male.

#### ZONATION

From previous accounts it is clear that the normal range of *P. vulgata* can be regarded as extending from M.L.W.S. to M.H.W.S. but that this range is modified according to the degree of exposure. At Robin Hood's Bay the range of *P. vulgata* extended from just below M.H.W.S. to about M.L.W.S. At its lowest level the limpet population was a mixed one of both *P. vulgata* and *P. aspera*.

Analysis of zonal patterns within the population of limpets was made on those animals which had previously been collected for the analysis of population structure. The population could be satisfactorily divided into four groups. Size group I contained all limpets (19 629) with a shell length of 14 mm or less. The majority of these animals had been on the beach for a period of up to 18 months and were still virgin. Size group II contained all animals (7200) of shell length 15–21 mm. The maximum age of these animals, as determined from the growth curves, was 2.5 years; the majority of the limpets within this size group were males which had matured for the first time. Size group III contained animals (3048) of shell length 22–26 mm; at this size there was a marked degree of population overlap but essentially it contained limpets in either their 3rd or 4th year and thus contained a high proportion of females. Size group IV contained all animals (1906) of shell length 27 mm and over, the ages of which were indeterminate. The distributional patterns of each of the four groups, per m<sup>2</sup>, at each station throughout the sampling period are illustrated in Fig. 5.

The zonation of Group I animals results directly from that of the spat. Although no figures are available for the spatfall in the winter of 1964/65 it is apparent from the size and distribution of Group I animals that spatfall occurred more or less uniformly throughout the sampling area and that apart from minor variations there was a uniform decrease in the size of this group during the year. In marked contrast there was an increase of Group I limpets at St. 6 in January 1966 and a little later at St. 7. This was due to the appearance of that year's spat; there was no concomitant change in numbers at the upper five stations. Since this pattern virtually persisted for almost the next twelve months it seems clear that either the spatfall was restricted to the lower two stations, or that, after a uniform settlement, some unknown environmental

condition resulted in the destruction of the spat at St. 1-5 before it had reached a measurable size. The third settlement (Nov. 1966) was somewhat intermediate, spat settlement or survival reaching as far as St. 4. At the higher stations the spat was concentrated around the damper regions of the rocks. The lower stations, which did

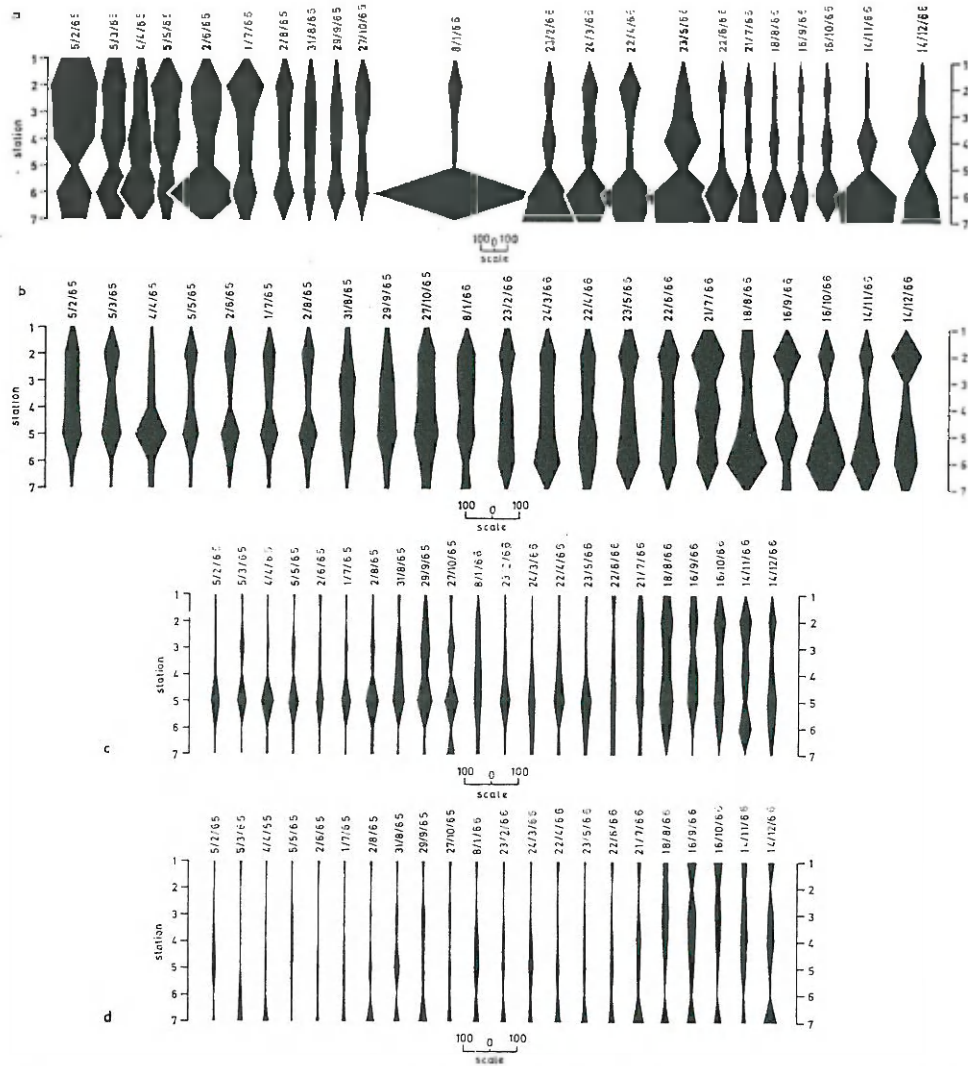


Fig. 5. *P. vulgata*. Zonal pattern of limpets at Robin Hood's Bay from 5th February 1965 to 14th December 1966: a, Group I individuals of shell length  $\leq 14$  mm; b, Group II individuals of shell length 15-21 mm; c, Group III individuals of shell length 22-26 mm; d, Group IV individuals of shell length  $\geq 27$  mm.

not dry out for very long, had a more uniform distribution. Apart from the high numbers at St. 6 and 7 there was a tendency for persistently higher numbers of Group

I at St. 2 which may be attributed to a lower growth rate of the limpets at this station and occasioned by the presence of barnacles (see Fischer-Piette, 1948).

The distribution of limpets in Groups II, III, and IV was subject to much less variation than those in Group I, though numbers were higher at some stations than at others. Limpets in Group II exhibited two peaks of population density. One was at St. 2, no doubt as a result of the association of barnacles, and another at St. 5. This latter peak is believed to be related to the smaller numbers of Group I at this station. Though the cause of this is uncertain it may have resulted from the adverse effect of a persistent thin covering of sand on spat settlement and/or survival. Group III individuals also showed their highest numbers at St. 5 a further reflection of the suitability of this station for the larger limpets. The greatest concentration of Group IV limpets occurred at St. 7. This is believed to be the outcome of increased growth as a result of the proximity of *Fucus* (see Fischer-Piette, 1948).

#### DISCUSSION

A seasonal variation in growth rate has been demonstrated in all but the larger limpets and this can be related to changing conditions within the environment. During the early months of the year, at a time when sea and air temperatures are low there is little growth. The marked increase in growth which occurs about June is later than would be expected if the limpet responded immediately to an increase in temperature and food with an increase in shell length. It could, however, be argued that increase in shell length does not occur earlier because the temperature is too low for active growth, but this seems unlikely in view of the results on the accumulation of food reserves and variation in body dry weight (Blackmore, in prep.) which indicate that the limpets do respond, as regards their metabolism, to the environmental conditions in about April; these include an increased food supply associated with the spring diatom increase but this does not appear to be reflected in the shell length until June. During the winter the body dry weight of the limpet of unit size is at its lowest level. The weight, together with food reserves, increases during the spring and early summer and it is therefore suggested that the increase in shell length does not occur until the weight of the body reaches a certain level. This level is clearly not solely dependent upon food reserves because limpets of < 10 mm shell length showed a similar growth pattern but no seasonal pattern in food reserves was observed. It is therefore considered that it is an increase in weight which is necessary and that this probably acts by increasing the relative volume of the animal within the shell so allowing the mantle to spread further out to give an increased shell deposition.

The high summer growth rate continues until after spawning when lower temperatures, and also probably decreased food supply, result in a much lower rate of growth. Cessation of feeding at this time appears unlikely since the guts of the limpets are full, whereas in experimentally starved limpets they are empty. Barry & Munday (1959), after measuring the levels of glycogen and blood glucose of limpets in various conditions, believe that the very low levels in the winter, which correspond with those in

starved animals, are an indication of cessation of feeding. It seems probable, however, that the food intake at this time was so low that all the ingested food was immediately utilized. The very low, but measurable, growth rate is consistent with this suggestion.

The seasonal variation in growth rate which is evident in the limpets at Robin Hood's Bay seems to be characteristic of limpets on British shores (Russell, 1909; Orton, 1928a, b) although studies in France by Hatton (1936) and Fischer-Piette (1941, 1948) indicate that there no arrest of growth occurs during the winter. At Robin Hood's Bay the number of five-year old limpets was small and growth was not measurable. Fischer-Piette (1948) considers that (in limpets with a growth rate similar to those at Robin Hood's Bay) growth continues for 9 or 10 years before death ensues. He does not indicate what proportion of the population was comprised of these old limpets but, from the present results, if the limpets do reach this age they must form a negligible proportion of the total population.

The maximum rate of growth of limpets at Robin Hood's Bay coincided with the period of gonad maturation. Orton (1928b) considered, however, that shell growth is depressed in midsummer as well as in the winter probably as a result of a diversion of food material to the developing gonad or even due to a cessation of feeding (Orton *et al.*, 1956). During the present study there was no evidence for such a decrease in growth during the summer; on the contrary, at this time of the year growth was at its maximum. The absence of any reduction in growth rate during maturation can be related to the presence of food reserves which are formed prior to shell growth and maturation (Blackmore, in prep.). These reserves are sufficient in themselves to provide for gonad formation, so that providing that food is available during maturation it may be utilized mainly for increase in shell length. No indication has been found that feeding was reduced during the summer. The gut, rather than being empty, was filled with more organic material than at other times of the year. It has been observed that in *Littorina littorea* the growth rate is reduced during maturation (Williams, 1964) but this animal matures during the winter months and so the effects of decreased temperature cannot be eliminated.

The peak M.G.C. of the population has been considered to be the approximate time of spawning but due to the time interval between collections peak spawning could have occurred within a two month period. The method employed in distinguishing the state of maturity of the limpets does not enable one to say just when a limpet had spawned and also if it had stopped spawning. The presence of some individuals which had gonads in the spawning condition at the collection prior to that in which the peak M.G.C. was observed and also some with apparently developing gonads after the peak suggests that the spawning period may extend over a longer time than two months; however, the number of such limpets was comparatively small and it is considered that the majority of limpets spawned over the peak M.G.C. The present results are not conclusive on this point, but it seems unlikely that in this locality spawning continues until no gametes remain as Orton *et al.* (1956) imply. From

the present data it seems as though spawning is somewhat intermediate between the prolonged spawning as suggested by Orton *et al.* (1956) and the sudden spawning as suggested by Ballantine (1961b).

After spawning the distribution over the beach of the young limpets is subject to wide variation. The 1965 year group showed an even distribution over the whole range studied whereas in January 1966, spat was confined to the lowest stations. In November 1966 the distribution was somewhat intermediate. During 1965 subsequent mortality was no greater at the upper end of the beach than at the lower. The preponderance in 1966 of spat at the lower stations was either the result of a localized spatfall or the result of an enormous mortality which affected the upper shore spat before it reached a measurable size. Whatever the reasons for the variation in spat distribution it seems clear that the effect of localized settlement influenced the zonation of the adult limpets. On the upper shore the population tended to be composed of larger limpets than at the lower stations, a situation similar to that described by Das & Seshappa (1948) and Jones (1948). The suggestion that this zonation is a result of movement after settlement, as Das & Seshappa think, seems unlikely and certainly it was not detected at Robin Hood's Bay. The greater proportion of large limpets at the higher stations can be accounted for purely on the settlement-survival pattern of the spat. The migration of limpets at various seasons which was noted by Lewis (1954) at Aberystwyth has not been detected during the present investigation; however, conditions in the two habitats are somewhat different. At Aberystwyth the population was present on a breakwater and thus any upward movement would represent a similar movement in the tidal range while at Robin Hood's Bay an upshore movement of many yards would be necessary for any appreciable increase in vertical height. It therefore seems that the vertical movement observed by Lewis occurred solely because it was in the range of the limpets normal movements.

Movement is, however, believed to occur at Robin Hood's Bay, not seasonally, but as a result of population pressure. This occurred at St. 6 which was situated on the face of a steep scar and always had a good spatfall (*e.g.*, in January 1966,  $\sim 880/m^2$ ). Rough seas are believed to induce spat settlement (Fischer-Piette, 1948) and it seems likely, therefore, that the more turbulent conditions associated with this scar face, together with its low level, may have resulted in the high spatfall. This very high density of limpets probably caused a population pressure which produced a migration of a few feet to the top and bottom of the scar (where spatfall was less) and thus gave rise to the lower numbers for Groups II, III and IV (see Fig. 5) at this station as compared with others.

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## REFERENCES

- BALLANTINE, W. J., 1961a. A biologically defined exposure scale for the comparative description of rocky shores. *Fld Stud.*, Vol. 1, pp. 1-19.
- BALLANTINE, W. J., 1961b. The population dynamics of *Patella vulgata* and other limpets. Ph.D. thesis, Queen Mary College, London University, 236 pp.
- BARRY, R. J. C. & K. A. Munday, 1959. Carbohydrate levels in *Patella*. *J. mar. biol. Ass. U.K.*, Vol. 38, pp. 81-95.
- COLMAN, J. S. & F. Segrove, 1955. The fauna living in Stoupe Beck sands, Robin Hood's Bay (Yorkshire, North Riding). *J. Anim. Ecol.*, Vol. 24, pp. 426-444.
- DAS, S. M. & G. Seshappa, 1948. A contribution to the biology of *Patella*: on population distribution and sex proportions in *P. vulgata* Linnaeus at Cullercoats, England. *Proc. zool. Soc. Lond.*, Vol. 117, pp. 653-662.
- DODD, J. M., 1957. Artificial fertilisation, larval development and metamorphosis in *Patella vulgata* L. and *Patella coerulea* L. *Pubbl. Staz. zool. Napoli*, Vol. 29, pp. 172-186.
- EBLING, F. J., J. F. SLOANE, J. A. KITCHING & H. M. DAVIES, 1962. The ecology of Lough Ine. XII. The distribution and characteristics of *Patella* species. *J. Anim. Ecol.*, Vol. 31, pp. 457-470.
- FISCHER-PIETTE, E., 1941. Croissance taille maxima et longévité possible de quelques animaux intercotidal en fonction de milieu. *Annls Inst. océanogr.*, Monaco, T. 21, pp. 1-28.
- FISCHER-PIETTE, E., 1948. Sur les éléments de prospérité de Patelles et sur leur spécificité. *J. Conch.*, Paris, T. 88, pp. 45-96.
- FRETTER, V. & A. GRAHAM, 1962. *British prosobranch molluscs*. Ray Society, London, 755pp.
- HARDING, J. P., 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 141-153.
- HATTON, H., 1936. Observations sur l'habitat et sur la croissance de *P. vulgata*. *Bull. Lab. marit. Dinard*, T. 15, pp. 17-20.
- JONES, N. S., 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proc. Trans. Lpool biol. Soc.*, Vol. 56, pp. 60-77.
- LEWIS, J. R., 1954. Observations on a high level population of limpets. *J. Anim. Ecol.*, Vol. 23, pp. 85-100.
- ORTON, J. H., 1928a. Observations on *Patella vulgata*. Part I. Sex phenomena, breeding and shell growth. *J. mar. biol. Ass. U.K.*, Vol. 15, pp. 851-862.
- ORTON, J. H., 1928b. Observations on *Patella vulgata*. Part II. Rate of growth of shell. *J. mar. biol. Ass. U.K.*, Vol. 15, pp. 863-874.
- ORTON, J. H., 1946. Biology of *Patella* in Great Britain. *Nature, Lond.*, Vol. 158, pp. 173-174.
- ORTON, J. H., A. J. SOUTHWARD & J. M. DODD, 1956. Studies on the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 149-176.
- RUSSELL, E. S., 1909. The growth of the shell of *Patella vulgata*. *Proc. zool. Soc. Lond.*, Vol. 79, pp. 235-252.
- SMITH, F. G. W., 1935. The development of *Patella vulgata*. *Phil. Trans. R. Soc. Ser. B*, Vol. 225, pp. 95-125.
- WILLIAMS, E. E., 1964. The growth and distribution of *Littorina littorea* L. on a rocky shore in Wales. *J. Anim. Ecol.*, Vol. 33, pp. 413-432.