The Biology of *Purpura lapillus*. I. Shell Variation in Relation to Environment.

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With 11 Figures in the Text.

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INTRODUCTION.

Purpura lapillus Linn., more strictly known as *Nucella lapillus,* and frequently also as *Thais lapillus,* is a common carnivorous gastropod living between about half-tide level and extreme low water. While it does not usually extend below this level, occasional specimens are taken in some places down to a depth of several fathoms. It is not tolerant of strongly estuarine conditions, and it becomes less abundant on rocks where high wave-exposure is combined with absence of adequate sheltering crevices. It is also said to be absent from rocks which hang vertically over deep water (Agersborg, 1929).

Its geographic range on the east side of the Atlantic is from the west coast of Spain where it is locally plentiful, and Portugal where it is rare, throughout the coasts of the British Isles, France, Belgium, and Norway to the Murmansk coast and to one locality in Novaya Zemlaya, its extreme northern limit. These records have been assembled by Cooke (1915). It is absent from the Mediterranean, the Baltic and the White Sea. It is absent also from Spitzbergen and Jan Mayen Island, but occurs in the Faroe Islands and on the west and south coasts of Iceland. It is absent from the east coast of Greenland, and the records from the west coast seem doubtful. In North America it ranges from the southern coast of Newfoundland to about New York. Figure 1 shows this distribution, together with the positions of the summer and winter isotherms as given by Schott (1912). The northern limit of the species agrees fairly closely with the −1° C. winter isotherm, except on the American side, where it extends somewhat further north, and the limiting factor here seems to be the presence of regular winter ice on the shore. The southern limit lies closely along the 19° C. summer isotherm. These figures refer to oceanic water, and conditions would be more extreme on the shore. On the other hand, in winter at any rate, the Purpura tend to creep into sheltered crevices where their temperature probably does not fall much below that in the sea.

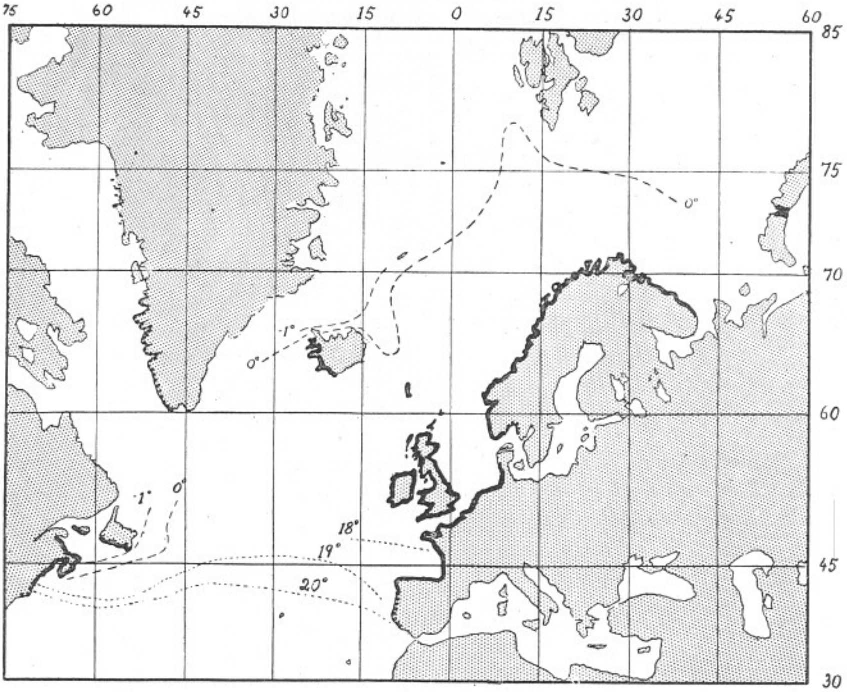

FIG. 1.—Geographical distribution of *Purpura lapillus*. The heavy lines show where it is abundant, and the dotted areas of coast where it is sporadic. The winter and summer isotherms are shown as discontinuous and dotted lines respectively.

Purpura lapillus, which is notoriously a very variable species, is for several reasons specially suitable for a study of variation in relation to environment. In the first place, the fact that it does not have a pelagic larva, and that the adults do not readily cross a barrier of either sand or deep water, renders each local community more or less self-contained, and the young of successive generations tend to disperse over the same area from which their parents were drawn. Variations would thus have a good opportunity of being perpetuated and becoming a characteristic of the community as a whole. In the second place it is very abundant, and can readily be collected in large numbers, and for this reason also it fits in with a survey in progress of the biology of the important littoral animals. Finally, as shown below, the obvious differences between populations from adjacent localities cover quite as wide a range as do the differences in populations from the extremes of the animal's geographical range.

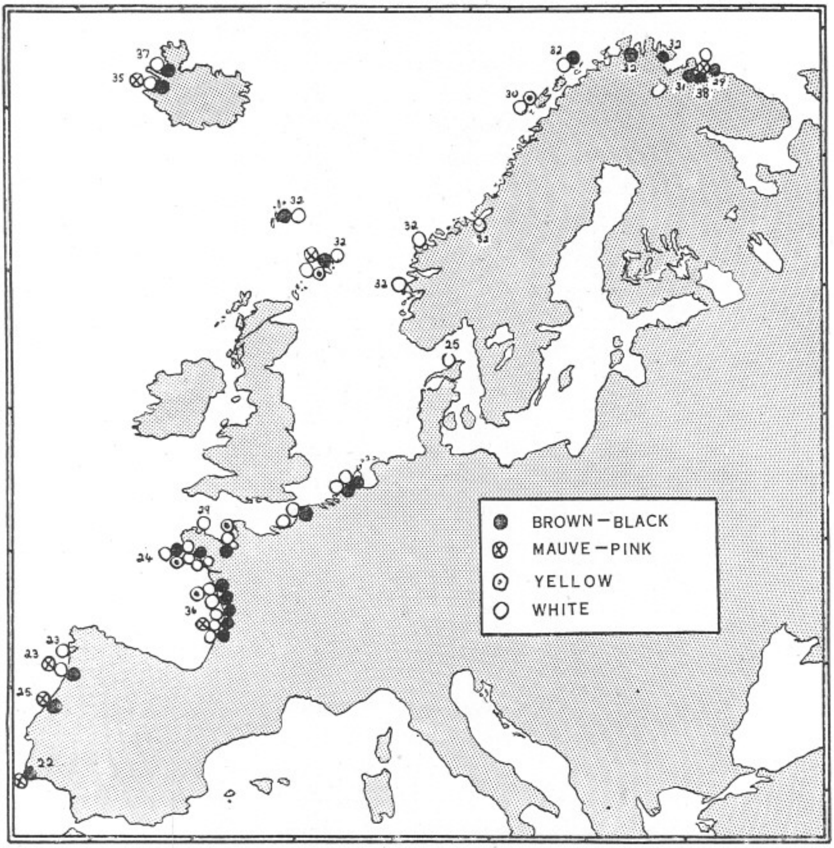

FIG. 2.—Distribution of localities from which coloured Purpura are recorded, and maximum heights (in mm.). Localities in the British Isles are shown in Fig. 3.

By the courtesy of the trustees of the British Museum it was possible to examine specimens of Purpura from a very large number of localities in the A. H. Cooke and other collections. Owing to the small size of the samples it was possible to make only a rough measure of a few characters, but this was sufficient to make clear one or two points. Although no actual measurements were made on shell angles, it was clear that there was no marked geographical trend of the apical angle θ (see p. 72). Colour, as is shown later (p. 79), is an index of the diet of the Purpura, and is therefore an important character. A note was taken of the presence or absence of the three principal colour types—brown-black, mauve-pink and yellow—in the sample from each locality. Since there is no evidence as to the degree of selection used in collecting these samples, deductions may only be drawn from a consideration of the general trend of the whole material. The colour distributions found in these collections, together with those from Mr. R. Winckworth's collections and that of the author, are shown in Figures 2, 3 and 4. In the latter, based on the author's own material, the actual percentages of brown-black specimens in the populations are shown. It will be seen that, although some localities, and even some limited areas such as the west of Scotland lochs, seem to contain only white shells, yet colour is generally distributed throughout their entire range from Portugal to Murmansk and Iceland, and to the American coasts also. Such local variation justifies the intensive study of a relatively small area of coast in an attempt to relate some of the observed variations to the environmental conditions supposed to produce them.

The size of the shells was the only character which showed any general geographical trend. The samples were of course inadequate for the determination of the mean size of the population, so in each case the height of the largest shell present was measured, and by grouping together all the results for a large area, significant results could thus be obtained. These maximum heights, wherever available, are shown in Figures 2 and 3. Three regions were taken, the first being the coast south of Cape Finisterre; the mean value for the maximum height in this region was twenty-six millimetres, obtained from six localities. In the second region from Cape Finisterre north to latitude 60° N., which is just south of Bergen, the mean value was thirty-five millimetres, obtained from ninety-five localities; while in the third region from 60° northwards the mean value was thirty-two millimetres from fourteen localities. Here therefore there seems to be a definite decrease in size towards the southern limit of the animal's distribution, and possibly a slight decrease also in the northern part of its range.

It seems to be a generally accepted theory that wave-exposure is the environmental factor responsible for most of the variations observed in Purpura. Cooke, for example (1895, p. 90), states: "Forms occurring in very exposed situations, e.g. Land's End, outer rocks of the Scilly Is., coasts of north Devon and Yorkshire, are stunted, with a short spire and relatively large mouth, the latter being developed in order to increase the power of adherence to the rock, and consequently of resistance to wave force. On the other hand shells occurring in sheltered situations, estuaries, narrow straits, or even on open coasts where there is plenty of shelter

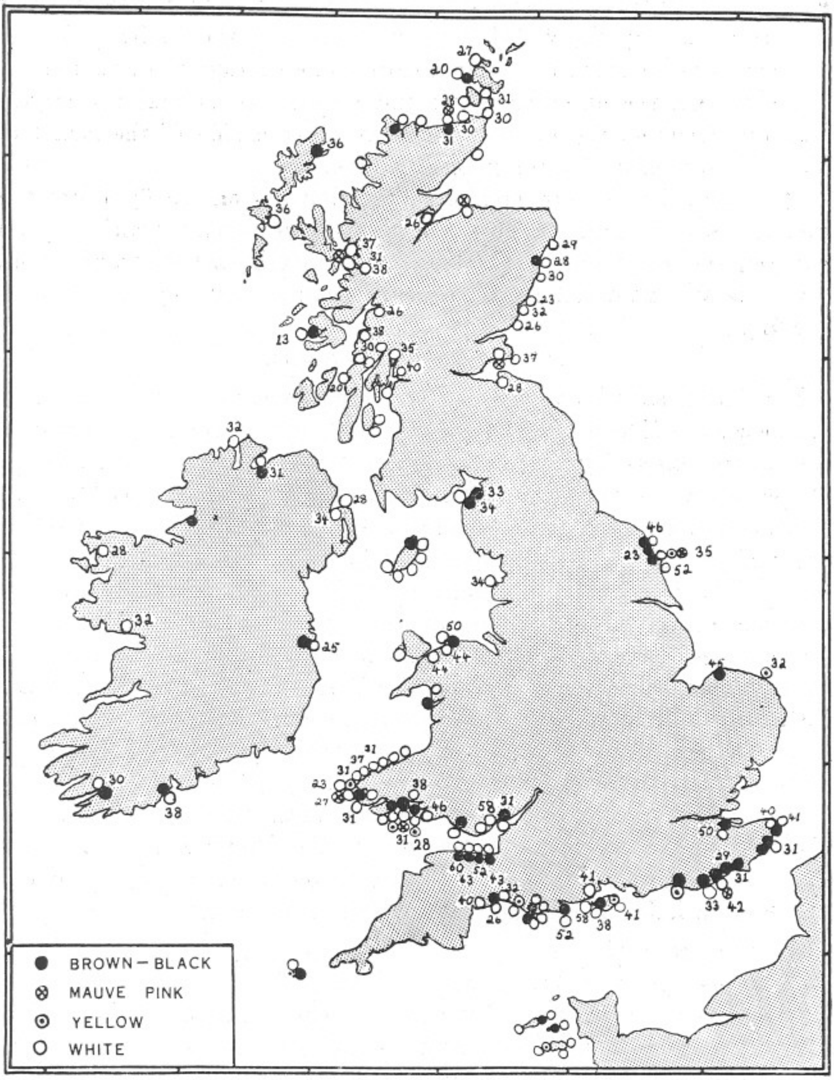

FIG. 3.—Distribution of localities from which coloured Purpura are recorded, and maximum heights (in mm.). Localities in the west of England are shown in Fig. 4.

from the waves, are comparatively of great size, with well-developed, sometimes produced spire and a mouth small in proportions to the area of shell surface." Wilkins (1934) confirms the belief that shells from a wave-exposed locality are stunted and have mouths large in proportion to their surface area. Agersborg also (1929, p. 47) records the tendency for the more acute shelled forms to occur in more sheltered, estuarine situations in Norway. On the other hand, Ökland (1933) records that the largest Purpura occur on the outer, more wave-exposed side of the island of Tromö, the salinity also being highest there.

With regard to colour, opinions differ, but Colton (1916) relates the abundance of coloured shells to the degree of wave action to which they are exposed, the colour being most abundant where there is most wave action. As will be shown later, none of these statements is a true representation of the facts.

MATERIAL AND METHODS.

Population samples were collected from seventy-six localities mostly on the coasts of Dorset, Devon and Cornwall. Over twenty-five thousand shells were collected, giving an average of 326 per sample, although, where Purpura was rare, the figures often fell far below this value (see Table I). The samples were made as representative as possible, their greatest error lying in the proportion of small shells which they contained. The latter tend to lie hidden in crevices, and hence to be inadequately represented in a sample, the extent of the error depending largely on the nature of the rock surface, and on the weather conditions prevailing at the time. Nearly all the samples were however collected in summer, when the young Purpura are most likely to be out on the open rocks, and only one characteristic (see p. 76) will be affected by this error. The material was preserved in formalin for later examination.

At the time of collection a note was made of the presence or absence of the two important barnacles on which the Purpura feed, *Balanus balanoides* and *Chthamalus stellatus*, and also of the degree of abundance of the mussel, *Mytilus edulis*. The latter was recorded under the following five categories :

—	Completely absent.
+	Either doubtfully present, or else absent in the immediate locality, but present in the neighbourhood.
++	Present in small numbers.
+++	Present in fairly large numbers.
++++	Present in very large numbers, and forming practically the whole diet of the Purpura.

Wave-exposure was measured by the method already applied in the study of barnacle distribution (Moore, 1935, p. 280). In this method the figure obtained represents the percentage of days throughout the year in which there is an onshore wind, and therefore sea, the aperture through which this can enter being taken at a distance of half a mile. While yielding adequate results for comparative studies, the method has not been used to compare localities outside the limited area of the west of England chosen for this study, nor can the method be used for a locality such as Tinside, Plymouth, which is sheltered from the open sea by a breakwater about two miles distant. The wind data used were ten-year means from the summaries published by the Meteorological Office for Portland Bill, Plymouth, Penzance and Newquay, each being applied to those localities nearest to it. On exposed headlands, and positions facing directly into the prevalent wind, very high values may be found, as for example at Pendeen Watch, Start Point and Hartland Point, each of which had a wave-exposure factor of seventy or over. In the first year's work, in which localities were chosen entirely at random, there was found to be a tendency for Mytilus to be most abundant on wave-exposed shores (apart from

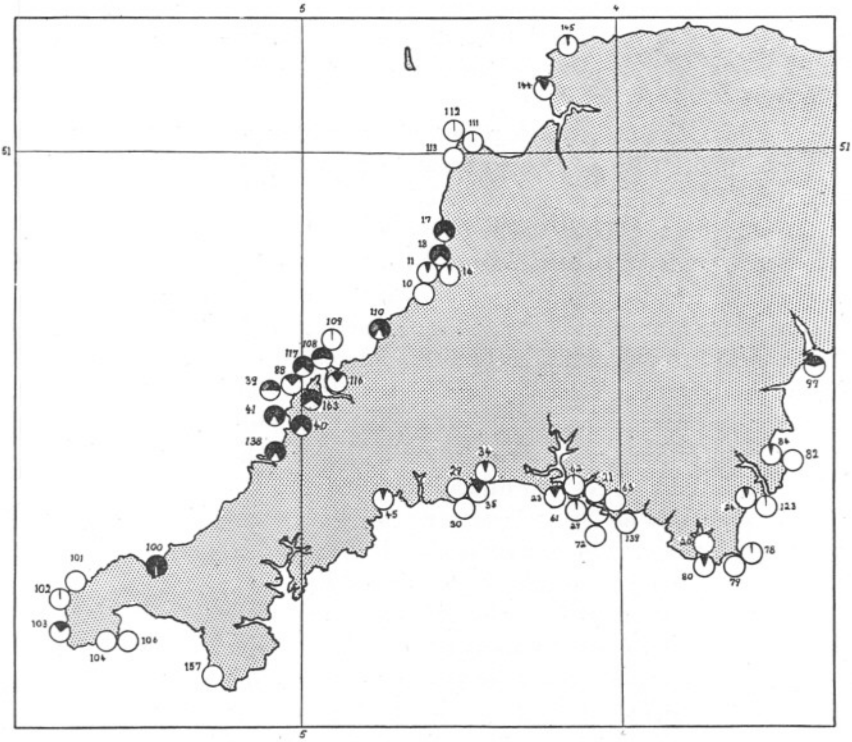

FIG. 4.—The localities in the west of England used in the present work and their reference numbers (see Table I). The percentage of brown-black shells in each community is represented by the black sector in the circle.

muddy estuaries where Purpura does not penetrate), and this made it difficult to distinguish whether the Mytilus or the wave-exposure was influencing the several variable characters. In the second year therefore, in addition to increasing the number of localities, an attempt was made to include some representative of the two sets of conditions previously poorly represented, namely high wave-exposure together with absence of Mytilus, and shelter from waves with abundant Mytilus. The latter proved much the harder to find since in most such localities other conditions such as silt and low salinity tend to appear and to exclude Purpura. However, some examples such as Trebarwith Sands (110) were obtained.

Colour of the shell, which refers here to the outer surface only, was recorded under three headings, brown including black, mauve including pink, and yellow. Where two colour types were mixed in one shell it was recorded under both headings. A strong diffuse brown or black pigment has a tendency to mask a more delicate mauve tint, so that, where the two occur together, the figures for mauve may be somewhat too low. Boring filamentous algæ are responsible for a greenish brown coloration of the shells in some localities, *Gomontia polyrhiza* and *Plectonema terebrans* being the commonest species,* but such coloration is usually patchy, and readily distinguished from true pigmentation of the shell. In cases of severe infection the algal coloration may mask the true pigmentation of the shell and make it very difficult to recognise.

P. lapillus is a mollusc whose immature and mature shell types differ very considerably. The immature shell is growing fairly rapidly by increments to the free edge of the lip, which remains thin and sharp. At the onset of maturity growth of the lip ceases, and instead the region near the lip thickens, sometimes to as much as five millimetres, while the lip itself becomes rounded and a series of rounded teeth develop on its inner side which still further occlude the opening. In some communities a

* Identified by Mr. T. G. Tutin.

FIG. 5.

A. Mature, thick type shell, with marginal teeth and greatly occluded aperture.
B. Immature, thin-type shell, with thin-growing edge and very wide aperture.
C. Very small mature thick-type shell. Height, 13·0 mm. Nat. size.
D. Large thin-type (sub-littoral) Purpura. Height, 58·9 mm. Nat. size.
E. Var. *imbricata*.
F. Colour change from Mytilus type (dark) to Balanus type (light) under natural conditions.
G, H, I. Three views of a shell which shows the relation of colour to diet. G shows the original dark colour when the animal was feeding on Mytilus, and the sudden change to light (arrow) when transferred to Balanus. H shows the same shell rotated to the right. On the right is the light, Balanus produced area. At the arrows the diet was changed back to Mytilus, and to the left of this there is gradual recovery of pigmentation. I, rotated still further to the right, shows eventual complete recovery of pigmentation.

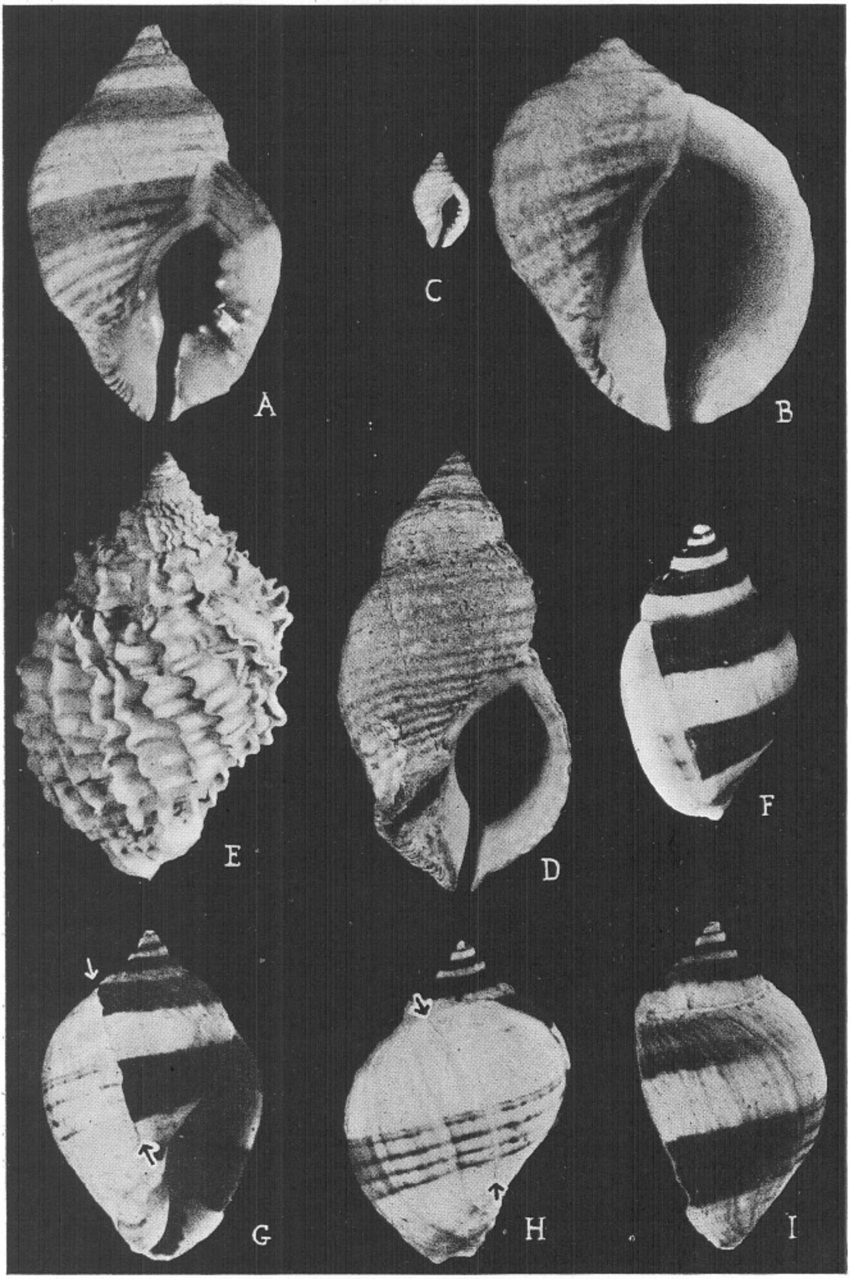

FIG. 5.

further tooth develops on the columellar margin of the aperture. Figures 5, A and B, show the great contrast between the relatively enormous area of aperture of an immature shell and the occluded opening of a mature one. In the two examples shown the area of the aperture of the immature shell (excluding the siphonal groove) represents 39% of the total projected area of the shell in the same plane, while that of the mature shell represents only 7% of that area, a difference of over five times. The fact that a Purpura can, on maturity, afford to reduce the size of its aperture to a fraction of its previous value surely indicates such a surplus of aperture size that the slight differences said to be observed between sheltered and wave-exposed communities could have no possible value in increased power of adherence to the rock. In any case the differences are shown later to have no connection with wave-exposure, but rather to be dependent on diet.

That increase of external size normally ceases completely when this lip thickening takes place has been demonstrated in numbers of individuals which were marked and released on the shore both at Plymouth and in the Isle of Man. When recaptured, even after a period of more than a year, these " thick " type shells showed no new increase whatever. Occasional specimens are taken in which the presence of a second set of teeth within the marginal ones indicates that the original stoppage of growth was followed by a second slight growing period, this in turn being replaced by a second period of thickening and growth stoppage, but such specimens are too rare to be a serious source of error. Owing to the great dissimilarity in the nature of the shells of the thin and thick types, it is necessary to treat them separately in certain of the measurements, as for example in estimating shell weight, and where this is done the two types are referred to as " thin " and " thick " types of shell respectively. Since growth ceases when the thickening occurs, the mean height of the " thick " type shells for any community is a measure of the mean size at which they matured (see p. 77), and is an important characteristic of the population. The figure varies greatly, " thick " type shells were recorded as small as 13 millimetres in height, and " thin " type as large as 63 millimetres (Fig. 5, C and D).

The size distribution of the entire population was estimated separately in millimetre groups for the thick and the thin type shells. The results were used in obtaining the mean thick type height, and also the percentage of thick type in the population. From the size-grouped material sets of twenty shells were taken, as far as possible at millimetre intervals, for shell weight and shape determinations. The height of each shell in the set was measured to the nearest 0·1 mm. They were then dried for forty-eight hours in a boiling-water oven, and weighed in group. As the tissue was left *in situ*, a correction had to be made to obtain the weight of the shell

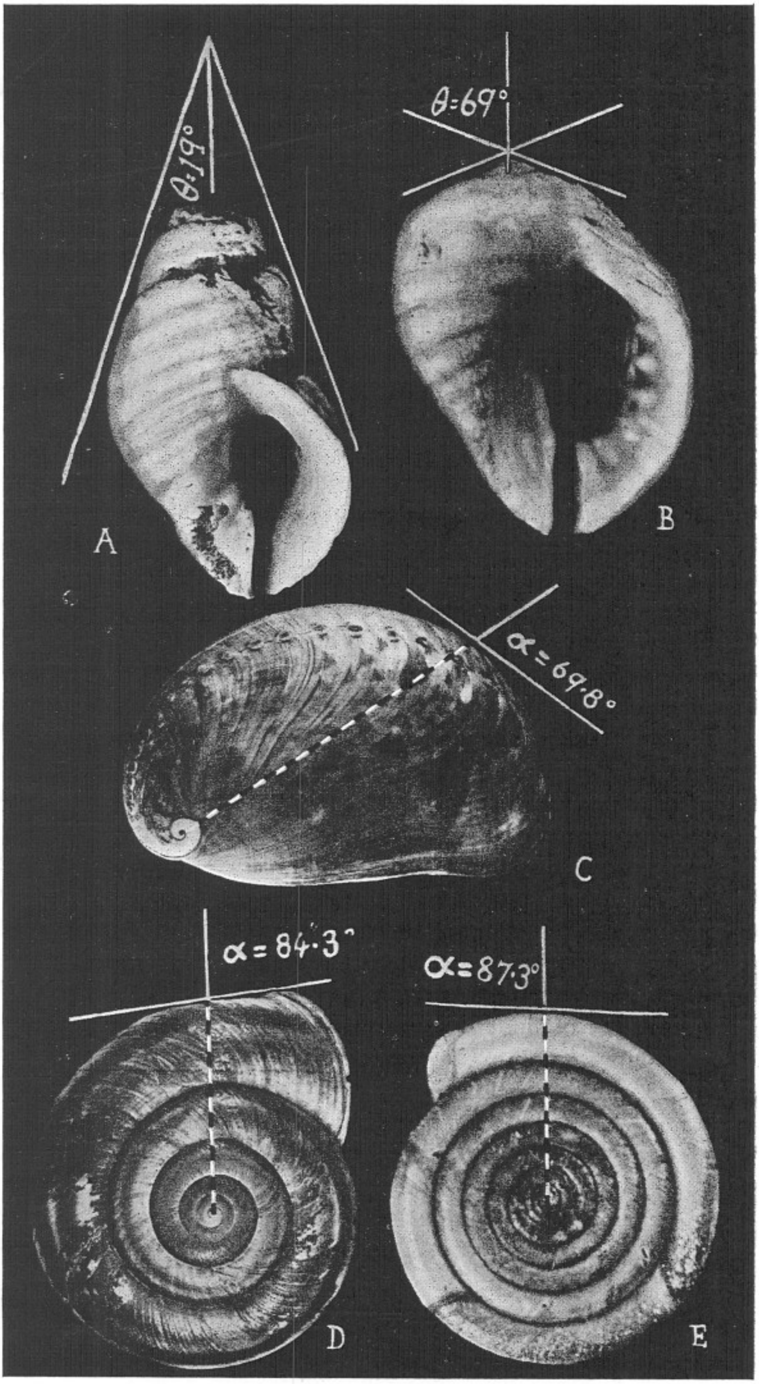

Fig. 6.

A, B. Extremes of variation in the apical angle θ in *P. lapillus*.
C, D, E. A series of shells, all viewed along their vertical axis (C and D from above, E from below), and illustrating the relation of the shape of the spiral to the spiral angle α. C, Haliotis. D, Helix. E, Planorbis.

alone, by multiplying by 0·956 for thin type shells, and by 0·960 for thick type. These factors were obtained from independent tissue-weight estimations on a number of samples. From the smoothed curves relating shell weight to height in each population, figures were obtained for the thick type shell weight at a height of 2·75 cm., a height at which the greatest number of populations could be included. Similar figures were obtained for both thick and thin types at a height of 2·3 cm., and the ratio of the latter two values was taken as a measure of the amount of thickening which had taken place at maturity, the figures so obtained ranging from 1·0, or no thickening, to 1·5, or an increase of 50% in weight.

As an expression of the shape of the shell, two characters have been taken, θ the half-apical angle, and α the angle of the logarithmic spiral of the shell. Both these values vary during the life of an individual, and the measurements taken refer to the last two whorls of the shell to be formed. The two angles can vary independently, although in Purpura a slight correlation was found between them due to their mutual correlation with a controlling factor, diet (p. 73). A low value of the apical angle θ corresponds to a tall spire such as that of Turritella. In an extreme case, *Terebra triseriata* Gray, θ is as low as 2·5°. In Purpura it usually lies between 35° and 40°, although extreme individuals vary much more widely. In a flattened shell like Planorbis, θ may be 90° or more. The effect of variation of α is less readily visualised. In Figure 6 are shown a series of shells illustrating variation of both θ and α. A low value of α represents an open spiral such as that of Haliotis (Fig. 6, C), a higher value of α represents a closer spiral like Planorbis (Fig. 6, E). Finally, on a very tall spire like *Terebra triseriata* it is possible to have a value of α as high as 89·2°, which, on a flatter shell would lead to impossibly tight packing of the whorls. Other things being equal, then, a decreased value of α means fewer whorls per unit height of shell. It must be realised that a very small change of α produces a very considerable change in the shape of the shell. Although there is a range of only about 3° between the extremes in all the populations of Purpura, this is as great as the difference in α between the Planorbis and the Helix shown in Figure 5.

θ was measured directly by means of a protractor somewhat similar to that illustrated by Thompson (1917, p. 529). α is not easy to measure directly except on a flat shell, and is more readily calculated from the formula :

$$\text{Tan } \alpha = \frac{2{\cdot}72 \text{ Sin } \theta}{\text{Log R}}$$

where θ is the observed half-apical angle, and R is the ratio of the diameters of two successive whorls (Thompson, 1917, p. 557). θ is introduced into the formula since the desired value of α is that for a plane spiral, and in the case of a shell it is projected on to a cone whose half-apical angle is θ. The fact that this method does not allow α to be calculated for the extreme lip of the shell introduces a slight lag in the observed values of α relative to the height of the shell (see p. 77). Since cessation of growth occurs when the shell commences to thicken, it does not matter whether the measurements of θ and α are made on thick or thin type shells, but in practice the latter were usually chosen as being cleaner and less corroded.

The individual measurements, about sixty thousand in all, are too numerous to publish, even as group means, but the characteristic values for each population, so far as they could be determined, are given in Table I. The resulting indications of relationships between the different characters are discussed in the following sections.

THE INFLUENCE OF DIET AND WAVE-EXPOSURE ON THE SHELL.

Despite the assertions of various authors that wave-exposure influences both the shape and size of the shell, as well as its colour, detailed analyses of our results failed to show a single case of such a relation, with the possible exception of the abundance of yellow shells. As has already been stated, there is a tendency, in a random sample of localities, for those with the higher wave-exposure to have also a higher proportion of Mytilus replacing barnacles in the diet of the Purpura. But either an examination of the relative degrees of correlation of any character with abundance of Mytilus and with wave-exposure, or else a study of those localities where Mytilus is absent, show clearly that there is no direct correlation with wave-exposure. A detailed account of this is unnecessary, and it is sufficient to say that in every case such a correlation was tested for and found to be non-existent.

Since *Mytilus edulis* when abundant replaces either *Balanus balanoides* or *Chthamalus stellatus* in the Purpura's diet, the abundance of Mytilus may be taken as a rough measure of the proportion of mussels to barnacles in the diet.

THE RELATION OF SHELL-SHAPE TO SHELL-SIZE AND TO DIET.

The curves relating spiral angle α to height (Fig. 7)—height being used here as a measure of size—show a considerable variation, although a general pattern runs through most of them. Not all populations offer a sufficient range of size to yield a complete curve, but where this is obtained there is generally a fairly steady rise of α to a peak, followed, with increasing shell size by a drop in α, frequently to a level at which it thereafter remains constant (see Aberystwyth, Fig. 7). Where sufficiently small specimens were available, the rise to the peak was sometimes found to be preceded by a drop. Figure 7 shows four types of curves from different localities. The peak was found to be the most constant characteristic of these curves, so the value of α at the peak, and the shell height at which it occurred were taken as the two characteristics of the spiral angle.

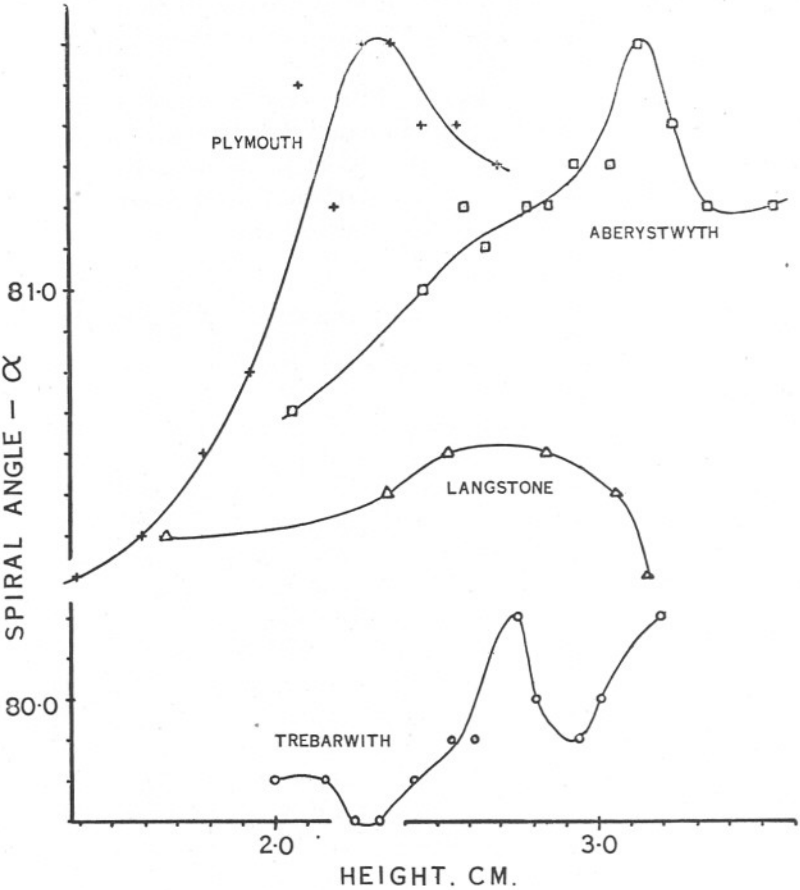

FIG. 7.—Curves relating spiral angle (α) to shell height for *P. lapillus* from four typical localities. For localities, see Table I.

That the value of α attained at the peak is not simply a function of the height at which the peak occurs is demonstrated by the absence of correlation when α is plotted against height at peak α.

The apical angle θ, when plotted against shell-height (Fig. 8), also tends to rise to a peak and then fall, but the peak is not always found, and here the drop in θ usually continues up to the largest sizes. Owing to the comparative steadiness of the drop it is possible to compare the value of

θ at a constant height (2·75 cm.) in different populations, a proceeding not possible with the more irregularly dropping α. A series of typical curves from four different localities is shown in Figure 8.

Taking these values of θ at H=2·75 cm. and peak α, and using all the populations for which such values are available, we find that both show

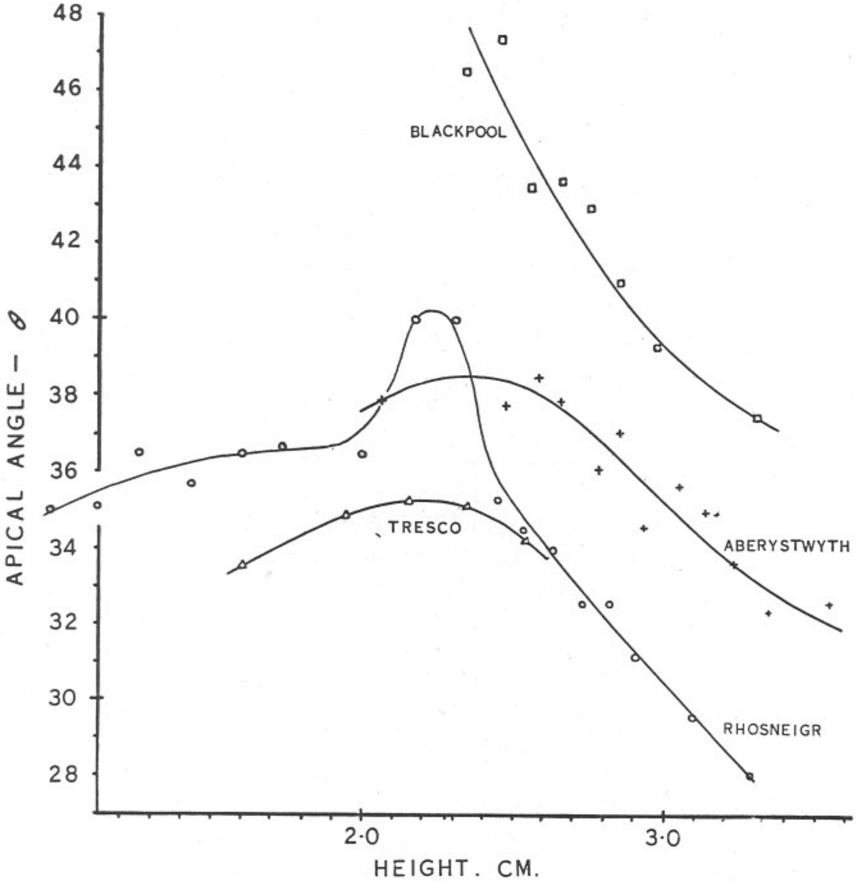

Fig. 8.—Curves relating apical angle (θ) to shell height for *P. lapillus* from four typical localities. For localities, see Table I.

a definite correlation with abundance of Mytilus but none with wave-exposure, nor is one found with wave-exposure when all Mytilus-fed communities are eliminated. The correlation* is good, $-0{\cdot}51 \pm 0{\cdot}12$ in the case of α and $+0{\cdot}51 \pm 0{\cdot}11$ in the case of θ. A slight secondary

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[*] A correlation coefficient of 1·0 represents complete correlation, and a lesser value down to 0·0, a lower degree of correlation. Any value obtained can be regarded as significant if it exceeds twice its standard error. A positive sign indicates variation in the same direction, and a negative sign variation in opposite directions.

correlation of $-0{\cdot}27$ between the values for θ and α is due to their mutual dependence on Mytilus. Figure 9 is intended to show diagrammatically the relations between the various shell characters and the factors influencing them. Correlations are represented in it by whole lines if they are judged to be direct, and by dotted lines if they are secondary. Arrows indicate the directions in which the causes of the correlations are inferred to operate.

THE RELATION OF SHELL-WEIGHT TO SHELL-SHAPE.

It is obvious that, for a given height of shell, a bigger value of θ means a fatter, and therefore heavier shell. In the present work, correlation coefficients of $+0{\cdot}29$ and $+0{\cdot}32$ were found between the weights of the thin and thick types of shell respectively and θ. Similarly a change in α will affect the weight of the shell, a higher value corresponding to a shell with more whorls per unit length, and hence more connecting wall between the outside of the shell and the columella. The observed correlations here were $+0{\cdot}36$ and $+0{\cdot}45$ with the thin and the thick types respectively. Thus the diet influences the shape of the shell, and this in turn influences its weight; but while increase of Mytilus in the diet tends to increase θ it simultaneously decreases α and the two to some extent cancel out, so that the observed correlations of both θ and α with shell weight are in either case somewhat less than they would be were the other to remain constant. An additional result is that neither thick nor thin type shell weights show much correlation with the primary factor, abundance of Mytilus.

THE PROPORTION OF THICK AND THIN TYPE SHELLS IN THE POPULATION.

It has already been mentioned that in many localities there was a difficulty in collecting an adequate sample of the small Purpura (see p. 66). The proportion of thick type shells varied from 0 to 98%, a far greater range than could be accounted for by any error of collecting, and the percentage showed a good correlation ($-0{\cdot}42$) with abundance of Mytilus. The mean value for entirely barnacle-fed communities was 64% thick type, and that for Mytilus-fed (++++) only 28%. This character does not seem to be linked with any other, and is not likely to be understood until more is known of relative growth rates and mortalities under different conditions.

THE RELATION OF HEIGHT AT CESSATION OF GROWTH, HEIGHT AT PEAK α, AND DEGREE OF THICKENING OF THE MATURE SHELL TO SEXUAL MATURITY, AND THE RELATION OF THIS TO ABUNDANCE OF MYTILUS.

The height at which peak α occurs has a strong correlation (+0·76) with the mean thick type height, which is the mean height at which growth stops. Both have a weaker correlation with the abundance of Mytilus (+0·25 and +0·18, the latter being probably too low). Further, allowing for the lag in α already explained (p. 73), the height at which α changes proves, on the average, to be that at which growth ceases. Now if we consider the curve relating α to height for any given community, the individuals which have contributed that part of the α curve corresponding to a height greater than that at peak α are ones which have grown past the population's mean size for cessation of growth. And, although they have done this, they have responded at the size at which, were they average specimens, they should have stopped growing, by changing their spiral angle at that height. This leads to the supposition that the two characters are not directly correlated, but are mutually dependent on a third character, a likelihood which is borne out by their correlation coefficients (see above), and the most likely third character is sexual maturity. Assuming this, we can calculate approximately what the correlation coefficients should be between the various characters as shown in Figure 9. We find then a definite, but not very large correlation between sexual maturity and abundance of Mytilus, a very close correlation between height at cessation of growth and sexual maturity, and a close correlation also between the latter and height at peak α.

It was not possible to examine the sexual conditions of a large number of populations, but a single sample taken from Drake's Island, Plymouth, in July, 1935, was in complete agreement with the supposition that sexual maturity is the connecting factor governing cessation of growth. The sample was divided into three groups—thin shelled type, intermediate individuals whose shell was still growing but commencing to thicken, and non-growing, thick type shells. All animals were opened, and smears from their gonads examined. Ninety-seven thin type animals were examined, ranging up to 2·9 cm. high, and none of these showed ripe spermatozoa, or ripening or ripe ova. Eighty of the intermediate group were examined. Forty were males, and thirty-one of these contained active spermatozoa, those that did not being among the smallest specimens. Of the forty females, eleven contained maturing ova, the smallest again tending to show none. Finally, one hundred and ten thick type animals were examined, of which sixty-five were males. Sixty-three of these contained active spermatozoa, and the other two were heavily parasitised. Of the forty-five females, twenty-three contained ova in various stages of

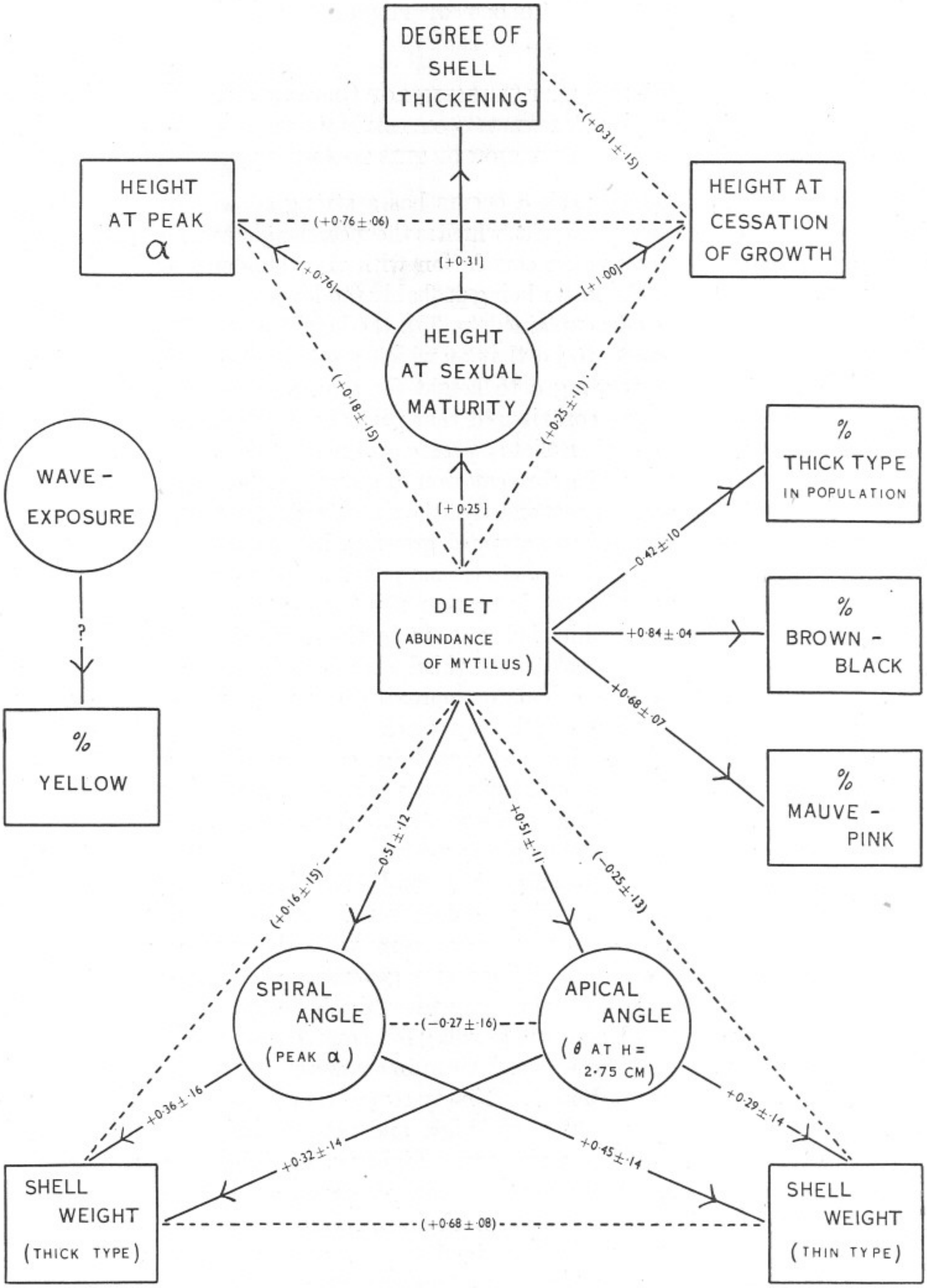

Fig. 9.—Diagram of the relationships of the various characters and factors. Thick lines indicate direct, and dotted lines secondary correlations, and arrows their directions. The observed correlation coefficients are also shown, and their standard errors. Those in square brackets are calculated from observed secondary correlations (round brackets) and are only approximate. See p. 77.

development, the rest being probably spent, though this is not certain. These results show clearly, at any rate for this locality, the coincidence of sexual maturity and cessation of growth.

The degree of thickening of the shell at maturity is a third character whose close correlation with height at cessation of growth, and small correlation with abundance of Mytilus, suggests that the correlation works through the link of sexual maturity. The amount of thickening was not directly measured, but was estimated in terms of the ratio of the weights of the thick and thin types of shell at a height of 2·75 cm. The values range from no thickening at all and a ratio of 1·0 to a ratio of 1·5, or 50% increase in weight. The thickening is greatest at the lip, and as has been shown on page 70 may reduce the size of the aperture very greatly (Fig. 5, A and B). The value of this thickening of the shell is not evident. It may be a means of disposing of excess calcium carbonate no longer needed in enlarging the size of the shell. Flattely and Walton (1922, p. 112) have suggested that in certain species of Nassa the thickening of the lip may be a protection against the attack of hermit crabs. Another possibility is that the size of the aperture in the growing animal is quite unnecessarily large, so far as the protrusion of the foot and body are concerned. The outer boundary of the shell is fixed by the necessity of producing a definite shape of shell outline, and any thickening of the growing shell would result both in the production of an unduly heavy shell and in excessive closure of the cavity which is later to contain the visceral mass of the animal. When growth ceases, neither of these objections is operative, and the unnecessarily, and possibly dangerously large aperture can be reduced as much as is required. There is no apparent reason why animals reaching sexual maturity at a greater size should tend to require a greater degree of thickening of the mouths of their shells unless this is to counteract the more than usually large apertures resulting from the tendency for θ to be higher, and α lower than the average in such communities.

THE RELATION OF SHELL COLOUR TO DIET.

Colour variation in relation to environment is well known in many Mollusca. Wesenburg-Lund (1934, p. 184) gives an account of the blackening of the shells of certain Limnæas under the influence of parasitic Cercariæ. Pelseneer (1935, p. 380) gives a number of instances of molluscs whose shell colour, and even the colour of their eggs, is dependent on their diet. Colton (1916) states that in the Mount Desert region the abundance of coloured Purpura is greater with increasing wave-exposure, although showing a slight increase also in extreme shelter. He notes that there are more white shells in the Balanus zone than in the Mytilus zone, but appears to conclude that this is a case of adaptation, probably selective, to their environment. It has even been suggested (Cooke, 1895, p. 69), that the striped specimens of Purpura found in some localities are specially adapted for escaping notice on dark rocks veined with white quartz.

In the present work four colour types were distinguished. The first was white, sometimes masked by algal coloration (see p. 68). The second was brown which shades into black when more intense. This is the colour which shows the strongest tendency to longitudinal banding, although it may often be diffuse over the entire shell surface. The third colour type was mauve, grading through in very rare cases into pure pink. Although generally associated with brown, this colour is quite distinct from it. It is always diffuse, and I have never seen a specimen banded longitudinally with mauve on white. It may however be overlaid with bands of brown or black. When mauve is overlaid with diffuse brown or black, this may mask the mauve and result in some of the figures for this colour in Table I being too low.

The fourth colour type distinguished, yellow, sometimes shading into orange, and often extremely vivid, is quite distinct in its distribution from the other two. It is usually diffuse, although some specimens banded with yellow on white occur, and it may be found mixed with either of the other colours. The relation of yellow shells to environmental factors is very doubtful. It is definitely not correlated with abundance of Mytilus, but there seems to be some connexion, possibly secondary, with wave-exposure. All the populations of Purpura with a high percentage of yellow shells occur at wave-exposures lying between 20 and 60, yellow being practically absent in extreme shelter and extreme exposure (Fig. 10). The presence of yellow has also been found to be independent of the proportions of the two barnacles *Balanus balanoides* and *Chthamalus stellatus* in the diet, since on an almost pure Chthamalus diet the percentage of yellow has been found varying between 3% at Land's End and 32% at Tresco in the Scilly Is., while on a pure Balanus diet it varies from 0% at Port Erin, in the Isle of Man, to 96% at Redcliffe, Dorset.

The other two colour types, brown (Fig. 11) and mauve, are unquestionably dependent on the abundance of Mytilus in the diet. They show a close correlation, +0·84 and +0·68, with abundance of Mytilus, and none with wave-exposure except for the secondary one already explained (p. 73).

In order to test experimentally this dependence of colour on diet, a number of Purpura were kept on a controlled diet in tidal tanks in the laboratory. With yellow shells no conclusive results were obtained. White shells, from a Balanus-fed community, failed to show any pigmentation of their newly formed shell after a period of six months on a diet of Mytilus, but this may have been due to the too short duration of the experiment. It appears to require a long period of feeding on Mytilus before sufficient pigment is accumulated in the animal to appear in the new shell. This must be borne in mind in examining populations of Purpura on newly formed Mytilus beds. Coloured shells from a Mytilus-fed community were kept on diets of Chthamalus, Balanus and Mytilus respectively. Those fed on Mytilus showed no change in pigmentation in either the brown or the mauve types. In all the specimens fed on Chthamalus or Balanus, and in which there was sufficient growth of new shell, the amount of pigmentation in the new growth became less and less. The speed of this reduction varied considerably. In some, such as that shown in Figure 5, G, the change from black to white was immediate and almost complete, but in most it took place more gradually. Such specimens when finally replaced on a Mytilus diet eventually regained their original degree of pigmentation, as seen in the subsequent shell growth of the same specimen (Fig. 5, H and I). In this particular example, the pigmentation was regained very much more slowly than it was lost.

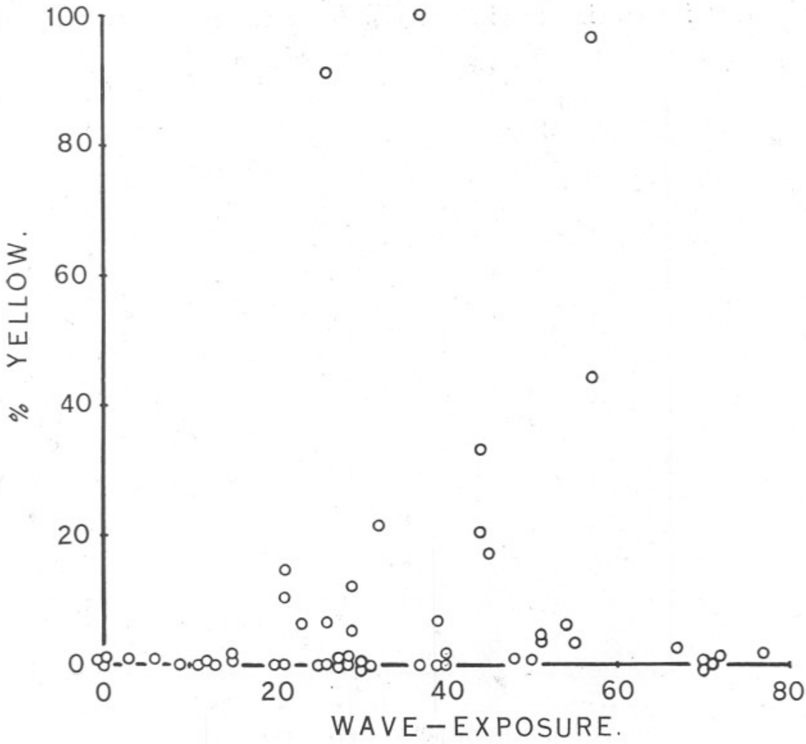

Fig. 10.—The relation of the abundance of yellow shells in the population to wave exposure.

A verification of the first part of the experiment was obtained under natural conditions by transplanting a number of strongly coloured, Mytilus-fed Purpura from north Cornwall to Drake's Island, Plymouth, where they had only Balanus to eat. In all those which survived, and showed a sufficient amount of new shell growth, there was a greater or lesser degree of paling of the original colour.

The effect of a change of diet, indicated by a transverse band of changed pigmentation cutting at right angles across the normal markings, is sometimes found in wild specimens. The change may be from coloured to white, as in the specimen shown in Figure 5, F, or *vice versa*. If we accept the presence of brown or mauve pigment in any part of the shell as evidence of a Mytilus diet at the time when that part of the shell was being produced, we find an interesting record in the shell of Purpura from localities where Mytilus is sparse and mostly confined to crevices. In such places we very often find that the large Purpura have white shells except for a small pigmented area at the apex. This suggests that when young they were feeding on Mytilus, and therefore living in the sheltered crevices, and that when they were older they came out on to the open

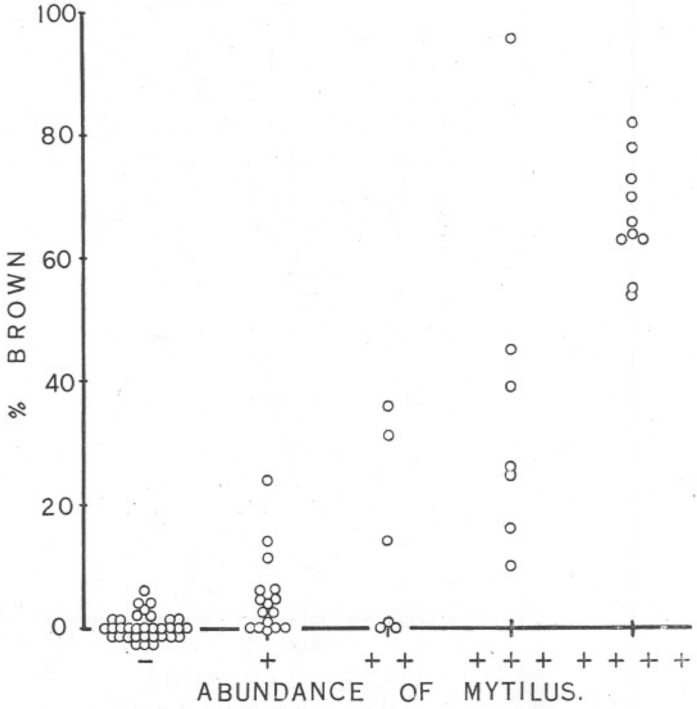

FIG. 11.—The relation of the abundance of brown-black shells in the population to the abundance of Mytilus in their diet.

rocks to feed on Balanus. This would be in agreement with our own observations on the habits of young Purpura, as well as with those of Colton (1916).

In Mytilus-fed communities, clusters of Purpura egg capsules are frequently found which are brownish or mauve instead of the yellow normally produced by Balanus-fed animals. The yolk in these capsules is strongly pigmented, and the young Purpura which hatch out from them are also strongly coloured. The pigment, however, affects only the first formed shell, and unless the young Purpura immediately commences to feed on Mytilus, the subsequently formed shell becomes white. There seems to be little doubt that these are the progeny of coloured parents, and that we have here a limited case of somatic inheritance.

The spiral pigment bands found on many Purpura shells are constant in position throughout the life of the animal, and vary only by intensification or dilution of their pigment. In the specimen shown in Figure 5, G, H and I, where the banding has been eliminated by a change in the diet of the animal, the pigment bands reappeared in the same position as before when the animal was replaced on a pigment-producing diet. That the banding is produced by localisation of the pigment in certain areas of the mantle edge can be seen on dissection of a banded specimen. The fact that some parts of the mantle edge may be loaded with pigment, while other parts are completely free from it, together with the fact that the width of the pigmented bands may vary so greatly in different individuals, suggests that in extreme cases the pigment-susceptible areas of the mantle edge may be narrowed to extinction, resulting in an animal which, though fed on a pigment-producing diet, would be unable to lay any of it down in its shell. This might account for the presence of a certain number of white-shelled individuals in a community apparently entirely fed on Mytilus.

VARIATION IN SHELLS LIVING BELOW LOW-WATER MARK.

Although normally living between tide marks, and probably in many cases deterred from colonising the sub-littoral zone by the heavy growth of algæ there, Purpura sometimes occurs several fathoms below low-water mark. There is very little information available on this subject, and I myself have never met with a locality where it happens, but Purpura are sometimes taken by fishermen in their inshore crab-pots, and a locality is known at Rhoscolyn where *P. lapillus* var. *imbricata* (Fig. 5, E) may be dredged from a submerged reef which is said to be covered with barnacles (*Balanus crenatus ?*). This var. *imbricata* is widely distributed, being recorded from places as far apart as Brittany, the Murmansk coast and America. In its most marked form it is a delicate shell which could not possibly survive undamaged if it were subjected to much wave action, and I have never found any but slightly imbricate shells between tide marks, and these among the younger specimens. On grounds such as Rhoscolyn the variety seems to be fairly common, although even there it is found living among large numbers of the typical form. It is possible that the imbrication is a phenomenon comparable with the "ledging" described in Patella (Moore, 1934) when kept permanently submerged. The Patella shell at first flattens, but later returns to its original shape, and it is possible that a rhythmical succession of such expansions and withdrawals, induced by the abnormal submerged conditions, might result in the formation of the lamellæ on the shell of var. *imbricata*. It is interesting to note that an allied species, *Thais* [=*Nucella*] *lamellosa* Gmel. from the American coasts, is normally imbricate in a very similar way, and Dall says (1916, p. 562) that it " . . . appears to frequent banks of rock and coarse gravel which are rarely uncovered by the tide, and yet are favourite haunts of barnacles, and of oysters, Anomias and other rough bivalves upon which the young Nucella feed."

Another character which seems to be associated with sub-littoral life is the excessive size of many of the Purpura. In the British Museum there are specimens up to sixty-three millimetres in height, whereas forty-five millimetres is a large size for the shore, and Mr. Tomlin has told me that many, if not most of these very large shells, which were taken at Minehead and Swanage, were obtained from crab-pots in depths of down to ten fathoms. Every shell of over fifty millimetres in length which I have been able to examine has been of the thin type, a fact which suggests that the giant size is due to the absence in these sub-littoral conditions of the factor which normally inhibits growth at maturity, and induces thickening of the shell edge. No soft parts were available for examination, but a parallel is suggested to the giant individuals produced as a result of parasitic castration in *Peringia* [=*Hydrobia*] *ulvæ* (Rothschild, 1936).

SUMMARY.

By examination of samples of *Purpura lapillus* from the whole of their European range, it appears that the species can exhibit quite as wide variation within a relatively small region such as that studied in the Dorset-Devon-Cornwall area, as it can over its whole geographic range. Population samples were taken from seventy-six localities, mostly in the south-west of England, and covering a wide range of environmental conditions, and the variations in these shells were studied in relation to two primary environmental factors, degree of exposure to wave-action and diet. Various authors have ascribed a strong influence on shell-shape and colour to the former, but the present examination shows that the only

character on which wave-exposure has any apparent effect is the abundance of yellow coloration in the shells. All other characters studied were found to be correlated either directly or indirectly with the nature of the diet, which varies from one of mussels (*Mytilus edulis*) to one of barnacles (*Balanus balanoides* or *Chthamalus stellatus*). Increase in Mytilus in the diet tends to produce a fatter shell with a more open spiral, and hence a wider aperture. Both these influence the weight of the shell, but as they act in opposite directions they tend to cancel out, and as a result there is little traceable relation between diet and shell weight.

Increase of Mytilus in the diet also decreased the proportion of mature (" thick " type) shells in the population, at the same time increasing the height at which sexual maturity sets in. Closely dependent on the onset of sexual maturity are the cessation of shell-growth with the concurrent thickening of the lip of the shell, as well as the degree of such thickening which takes place, and also the size at which the change in the spiral angle α occurs. Finally the two colour types brown-black and mauve-pink, whose pigments are derived directly from the Mytilus, are closely correlated in their abundance with the proportion of Mytilus in the diet, and may in fact be taken as an indicator of it. Two characteristics seem to be frequent in shells from a sub-littoral habitat, the variety *imbricata*, and a tendency to gigantism.

I wish to acknowledge my indebtedness to all those who have given assistance during this work and especially to Mr. G. M. Spooner for statistical treatment of the results : to the trustees of the British Museum for access to the Cooke collection, to Mr. R. Winckworth for access to his collection and for the loan of the shells illustrated in Fig. 6, C, D and E, to Dr. A. Gibson for very great assistance in collecting the north Cornish samples, to the staff of the Plymouth Laboratory, and to all the following who have kindly obtained samples for me : Mr. J. R. Bruce, Mr. R. Elmhirst, Dr. E. Fischer-Piette, Mr. W. Fowler, Mr. J. H. Fraser, Dr. F. P. Koumans, Mr. W. J. Rees, Mrs. R. S. Sturdy and Dr. E. Wordley.

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TABLE I

OBSERVED CHARACTERISTICS OF THE POPULATIONS OF *Purpura lapillus* EXAMINED, AND OF THE LOCALITIES. All heights in cm.; weights in gm. Figures in brackets are approximate only.

For map of localities see Fig. 4. N.D.=North Devon. S.D.=South Devon. N.C.=North Cornwall. S.C.=South Cornwall.

Locality.	Reference number.	Wave-exposure factor.	Abundance of Mytilus.	Presence of Chthamalus.	Presence of *B. balanoides*.	Number of specimens.	Maximum height.	Mean height of thick type.	Percentage thick type in population.	Percentage of brown-black.	Percentage of mauve-pink.	Percentage of yellow.	Thick-type weight (height=2·75 cm.)	Thick-type weight (height=2·3 cm.).	Thin-type weight (height=2·3 cm.).	Thick-type weight / Thin-type weight.	Apical angle θ (height=2·75 cm.).	Spiral angle α. Peak value.	Height at peak value of α.
Crackington Haven (N.C.) .	10	15	++	+	+	350	3·2	2·25	70·5	0·3	0	1·2	4·0	2·5	2·2	1·14	38·1	81·2	(2·4)
Millook Haven (N.C.) . .	11	37	+	+	+	42	2·5	2·03	81·0	14·2	0	0	—	—	—	—	—	—	—
Wanson Mouth (N.C.) . .	16	55	+	+	+	171	2·9	1·99	89·7	5·3	0	3·2	4·3	2·8	—	—	39·0	81·6	2·2
Salthouse (N.C.) . . .	17	54	++++	+	+	244	3·3	2·74	92·6	62·7	15·2	5·7	4·1	2·4	2·1	1·14	40·8	—	—
Duckpool (N.C.) . . .	18	45	++++	+	+	111	3·0	2·94	3·6	66·0	39·3	17·0	—	—	1·5	—	40·3	(80·3)	—
Church Reef, Wembury (S.D.)	19	29	++	+	+	133	3·0	2·42	48·2	0·6	4·5	12·0	3·4	2·4	2·0	1·20	36·4	81·4	2·3
Biddlehead, Salcombe (S.D.) .	20	6	—	+	+	327	3·6	2·87	81·8	0	0·3	0·6	4·7	3·2	2·4	1·33	40·8	81·8	2·9
Rum Bay (S.D.) . . .	21	32	+	+	+	200	3·4	2·72	65·5	0·5	0	21·2	3·2	2·2	1·8	1·22	34·1	81·4	2·5
Pier Cellers, Cawsand (S.C.) .	23	44	+	+	+	242	3·3	2·64	59·2	24·2	0	20·2	4·5	3·2	2·8	1·14	37·7	81·8	2·7
Polperro, Loc. D. (S.C.) .	29	3	—	+	+	156	2·9	2·29	71·8	0	0	0·6	3·9	2·5	2·4	1·04	(37·0)	81·7	2·1
Polperro, Loc. E. (S.C.) . .	30	30	—	+	+	55	2·4	1·99	89·2	0	0	0	—	—	—	—	—	—	—
Limmicks, Looe (S.C.) . .	34	29	+++	+	+	189	3·2	2·66	65·7	10·0	3·0	5·0	4·2	3·1	2·4	1·29	37·8	81·7	2·5
Hannafore Point (S.C.) . .	35	48	++	+	+	300	3·2	2·45	58·4	31·1	0	0·7	2·7	1·8	1·6	1·12	32·5	81·0	2·3
Treyarnon Beach (N.C.). .	39	51	++++	+	+	164	3·6	2·66	65·8	55·4	34·3	4·8	4·1	—	2·3	—	42·8	81·1	2·6
Mawgan Porth (N.C.) . .	40	50	++++	+	+	188	3·5	2·81	8·9	70·2	37·4	0·5	3·7	—	1·7	—	41·0	80·2	2·7
Bedruthan Steps (N.C.) . .	41	51	++++	+	+	241	3·1	2·46	6·9	72·6	28·6	3·2	2·8	—	1·6	—	41·4	(80·1)	—
Charlestown (S.C.) . .	45	28	+	+	+	279	3·0	2·48	70·9	11·3	0	1·4	4·2	2·7	2·3	1·17	39·6	82·9	2·1
Plymouth Breakwater (outside) (S.D.)	61	21	+	+	+	347	2·9	2·43	65·4	4·1	0	10·2	4·1	2·4	2·2	1·09	38·3	81·6	2·3
Plymouth Breakwater (inside) (S.D.)	62	—	+	+	+	307	3·1	2·34	72·9	1·9	0·3	14·1	4·1	2·5	2·1	1·19	35·5	82·2	2·3
Misery Point, Yealm (S.D.) .	63	0	—	+	+	662	3·2	2·55	60·5	0·3	0	1·4	3·5	2·3	2·1	1·09	37·1	81·6	2·1

TABLE I—*contd.*

Locality.	Reference number.	Wave-exposure factor.	Abundance of Mytilus.	Presence of Chthamalus.	Presence of *B. balanoides*.	Number of specimens.	Maximum height.	Mean height of thick type.	Percentage thick type in population.	Percentage of brown-black.	Percentage of mauve-pink.	Percentage of yellow.	Thick-type weight (height=2·75 cm.)	Thick-type weight (height=2·3 cm.).	Thin-type weight (height=2·3 cm.).	Thick-type weight / Thin-type weight.	Apical angle θ (height=2·75 cm.).	Spiral angle α. Peak value.	Height at peak value of α.
Drake's Is., N. side (S.D.)	67	0	++	+	+	808	3·7	2·95	54·7	—	—	—	4·5	3·0	2·4	1·25	—	—	—
St. Servan, Loc. A. (France)	70a	—	·	·	·	211	2·6	2·16	60·2	23·7	5·2	0	—	2·0	1·7	1·18	—	81·3	2·2
St. Servan, Loc. B (France)	70b	—	++++*	·	·	199	2·7	2·15	88·5	3·0	1·0	1·0	—	1·9	—	—	—	81·5	2·3
St. Servan, Loc. C (France)	70c	—	+++*	·	·	90	2·8	2·27	86·7	5·6	5·6	2·2	—	1·9	—	—	—	80·9	2·3
Gara Point (S.D.)	72	15	—	+	+	178	2·7	2·20	58·5	0	0	1·7	—	2·4	2·2	1·09	—	81·1	2·2
Start Point (S.D.)	78	70	—	+	+	52	3·2	2·69	48·1	5·8	0	0	—	—	—	—	—	—	—
Lannacombe Beach (S.D.)	79	21	—	+	+	373	3·5	2·77	89·1	0	0	0	4·0	2·5	2·4	1·04	37·5	81·2	2·6
Black Cove (S.D.)	80	11	+++	+	+	30	2·5	2·28	36·7	16·1	12·9	0	—	—	—	—	—	—	—
Mudstone Sands (S.D.)	82	13	—	+	+	516	3·4	2·81	79·7	0·2	0	0	3·0	2·9	2·5	1·16	37·6	81·2	2·7
Saltern Cove (S.D.)	84	28	+	+	+	647	3·1	2·32	74·9	6·2	0	0	3·5	2·5	2·2	1·14	35·5	81·5	2·1
Trevose Head (N.C.)	88	77	+++	+	(+)	130	3·2	(1·99)	11·5	39·2	44·6	1·5	—	—	—	—	—	—	—
Penrhyn Bay (Wales)	94	—	+	—	+	899	3·7	2·48	57·8	0	0	0	3·4	2·2	1·9	1·16	32·4	—	—
Rhosneigr (Anglesey)	95	—	—	—	+	734	3·4	2·87	44·4	0·5	0	18·8	3·5	2·2	1·9	1·16	32·8	81·9	2·3
Aberdeen	97	—	—	—	+	266	3·1	2·47	85·3	0	0	0	4·5	2·9	—	—	33·8	—	—
Langstone Rock, Dawlish (S.D.)	99	23	+++	+	(—)	148	3·7	2·80	23·7	44·9	47·6	6·1	—	—	2·4	—	40·1	80·6	2·7
St. Ives (N.C.)	100	(16)	+++	+	+	348	3·5	2·77	59·8	95·7	1·4	0	3·4	2·3	1·8	1·28	36·9	80·8	2·8
Pendeen Watch (N.C.)	101	70	—	+	(—)	635	2·8	2·10	98·5	0·5	0	0	—	3·0	—	—	—	82·1	2·2
Cape Cornwall (N.C.)	102	72	+	+	+	409	2·9	2·19	68·4	2·7	0	1·2	3·7	2·7	2·4	1·12	—	—	—
Land's End (N.C.)	103	67	+++	+	+	115	2·6	2·16	46·9	25·5	8·2	2·7	—	2·6	—	—	—	80·8	2·2
Porthcurno (S.C.)	104	9	—	+	—	822	2·6	1·89	88·6	0	0	0	—	2·6	—	—	—	—	—
Ushant (France)	105	—	+	·	·	176	3·1	2·53	48·8	1·7	0	0	4·3	2·8	2·2	1·27	37·2	82·3	2·7
Treryn Dinas (S.C.)	106	40	—	+	+	248	2·8	2·33	82·7	0·4	0	1·6	3·8	2·5	2·1	1·19	37·2	82·2	2·5
Hayle Bay (N.C.)	108	26	++++	(+)	+	577	3·5	2·63	1·2	54·0	40·1	6·6	—	—	1·4	—	39·3	—	—
Portquin (N.C.)	109	0	+	(+)	+	557	3·3	2·38	59·4	1·4	0	0·7	4·1	2·6	2·3	1·13	37·2	—	—
Trebarwith Sands (N.C.)	110	12	++++	+	+	619	3·5	2·70	4·0	78·0	63·9	0·5	3·7	—	1·7	—	43·2	80·2	2·7
Shipload Bay (N.D.)	111	30	—	+	+	687	3·0	2·18	83·8	1·7	0·1	0	4·5	2·8	2·4	1·17	40·3	81·5	2·1
Hartland Point (N.D.)	112	71	—	+	+	411	2·3	1·90	79·3	3·2	6·1	0	—	2·6	—	—	—	81·9	2·0

Hartland Quay (N.D.)	113	39	—	+	+	766	2·4	1·88	91·0	0·8	0·8	0	—	2·6	—	—	—	—	—
Red Rocks Cove (Berwick)	115	—	++	·	·	596	3·0	2·43	65·8	0	0	0	3·8	2·2	2·0	1·10	37·6	—	—
The Greenaway (N.C.)	116	21	++	(+)	(+)	72	3·5	2·96	34·8	35·8	18·6	14·3	—	—	3·0	—	—	—	—
Harlyn Bay (N.C.)	117	28	++++	(−)	+	442	3·6	2·90	30·8	63·7	13·0	1·1	3·6	—	2·0	—	41·6	80·4	2·8
Blackpool (S.D.)	123	26	—	+	+	373	3·8	2·62	96·1	1·3	0	0	—	—	—	—	41·8	81·4	2·8
Mathew's Point (S.D.)	124	31	++	+	+	445	3·5	2·13	47·8	13·7	3·6	0	—	2·8	2·8	1·00	43·5	—	—
Tresco (Scilly Is.)	127	—	—	+	—	117	2·8	2·43	14·5	0	0	31·7	—	—	1·7	—	—	80·5	2·1
Carsaig, west (Argyll)	129	—	—	—	+	234	2·9	2·46	78·2	0	0	0	4·5	2·8	2·6	1·08	40·0	80·7	2·3
Carsaig, east (Argyll)	130	—	—	(−)	+	412	3·2	2·68	81·3	0	0	0	4·1	—	—	—	34·4	—	—
Domburg (Holland)	132	—	(++++)	·	·	52	3·1	—	0	50·0	0	10·4	—	—	—	—	—	—	—
Balta Sound, Unst. (Shetland Is.)	135	0	—	·	+	161	3·7	2·92	54·0	4·3	0	0	4·4	—	—	—	35·9	81·7	2·8
Fistral Bay (N.C.)	138	28	++++	+	+	372	3·6	2·80	45·4	82·1	(1·6)†	0·5	4·2	2·5	2·3	1·09	43·0	—	—
Stoke Beach (S.D.)	139	20	+	+	+	805	2·7	2·18	68·3	0	0	0	—	2·6	2·4	1·08	—	81·6	2·2
Lyme Regis (Dorset)	141	37	—	+	+	20	2·6	2·28	35·0	0	0	100·0	—	—	—	—	—	—	—
Port Erin (Isle of Man)	143	—	—	—	+	691	3·7	2·79	28·7	0·1	0·1	7·8	3·7	2·7	1·8	1·50	—	—	—
Saunton Down (N.D.)	144	57	+++	+	+	363	3·6	2·66	35·0	25·6	3·0	44·1	4·0	2·2	1·6	1·37	38·2	81·0	2·7
Lee Bay (N.D.)	145	40	—	+	+	336	3·2	2·38	93·5	4·5	0·3	0	3·9	2·7	2·2	1·23	34·9	81·4	2·2
Redcliff (Dorset)	154 160	57	+	(−)	+	726	3·6	2·82	46·0	6·2	0	96·4	3·7	2·3	2·0	1·15	34·7	—	—
Aberystwyth (Wales)	155	—	—	—	+	515	3·7	2·88	91·7	0	0	0	4·3	2·6	2·3	1·13	37·1	81·5	3·2
Hook of Holland	156	—	(++++)	·	·	95	3·1	2·72	15·8	44·2	5·3	0	3·3	—	1·5	—	—	80·3	2·5
Porth Mellin (S.C.)	157	25	—	+	(+)	13	3·5	2·10	38·4	0	0	0	—	—	—	—	—	—	—
Whitenothe (Dorset)	158	44	—	(−)	+	106	3·0	2·47	17·9	0	0	33·0	—	—	1·9	—	—	—	—
Nothe (Dorset)	158a 162	26	—	(−)	+	239	3·3	2·87	28·9	0	0	91·2	3·6	—	1·8	—	36·0	—	—
Bincleaves (Dorset)	161	(0)	—	—	(+)	59	3·7	3·00	42·4	0	0	3·4	—	—	—	—	—	—	—
Kames Bay, Cumbrae (Bute)	M.1	—	(+)	(+)	+	456	3·2	2·43	11·6	0	0	0	—	2·2	2·0	1·10	34·2	80·9	2·0
Farland Point, Cumbrae (Bute)	M.2	—	+	(+)	+	328	3·6	2·62	39·5	0	0	0	2·9	1·8	1·7	1·06	34·7	—	—
Whiting Bay, Arran (Bute)	M.5	—	—	(+)	+	167	3·4	2·84	31·1	0	0	0	3·2	—	1·8	—	33·9	81·3	2·9
Largy Beg, Arran (Bute)	M.6	—	—	(+)	+	254	3·4	2·76	26·7	0	0	0	3·5	—	1·9	—	36·3	—	—
Fairlie Pier (Ayr)	M.7	—	(+)	—	+	216	4·2	2·92	35·7	5·0	0	0	—	—	—	—	36·3	81·3	2·7

* Mytilus colonies only recently established.

† Mauve much masked by brown, giving too low a figure.