Observations on *Patella vulgata*. Part III. Habitat and Habits.

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With 2 Figures in the Text.

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Introduction.

The present contribution continues the account of studies on the common limpet, *Patella vulgata* (**1**, **2**), and forms an introduction to investigations on facts and causes of variation in shell-height, which are being continued and will be published later, and not as Part III of the series as originally intended. The cause of the variation in the shape of the shell in *P. vulgata* (**3**, **6**) has been—and continues to be—a subject of much interest to naturalists. There can be little doubt that the height of the shell varies at least roughly—but not in any simple manner—in correlation with the habitat (**5**), and that as the individual limpet rarely moves many feet away from its point of fixation (**6**, **7**, **8**, **9**) there must presumably be a close relation between certain factors in the habitat and the coexisting shape of the shell. It is therefore important in this regard to review the habits and to note and define carefully the habitats of this animal on the shore.

P. vulgata occurs on the Atlantic shores of Europe (**10**) between tide-marks. On the coasts of Devon and Cornwall the species (excluding for the present the doubtful species or variety, *athletica*) occurs mainly between a level about mean low water and one a little below the high-water spring-tide mark in the habitats and with the congeners shown in Table I, page 278.

TABLE I.

Inter-tidal Habitats of *Patella vulgata* L., and of some associated Organisms in the Plymouth District.

Splash-lines.	Height of tide in feet above or below Datum.		Patella habitats.	Littorina habitats.	Barnacle habitats.	Some Algal habitats.
	17—					
	16—15·7	M.H-W.S.	Patella rare	*Littorina neritoides* L. *rudis* rare		(A sp. of Lichen) Enteromorpha[1]
	15—					Enteromorpha[1]
	14—14·1	M.H-W.	Patella	*L. rudis*	Chthamalus rare	*Pelvetia canaliculata*
	13—				*Chthamalus stellatus*	*Fucus platycarpus*
	12—12·25	M.H-W.N.	Patella	*L. rudis*	*B. balanoides* rare	Enteromorpha Ascophyllum
			Patella	*L. obtusata*	*B. balanoides*	*F. vesiculosus*
	11—					
	10—		*athletica* form in pools	*L. littorea*		*F. serratus* Porphyra
	9—					
	8—8·15	M.T.L.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	7—		*athletica* form in pools			
	6—					
	5—4·6	M.L-W.N.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	4—				*B. perforatus*	
	3—					
	2—2·39	M.L-W.	Patella	*L. littorea*	*B. perforatus* *Verruca strœmia*	*F. serratus* Gigartina
	1—		Patella rare *athletica* form on rocks			Chondrus Himanthalia
	0—0·18	M.L-W.S.	*Helcion pellucida* rare	*L. littorea* less common	*V. strœmia*	Laminaria, spp.
	-1—					
	-2—		*H. pellucida*			Laminaria, spp.

Notes to Table I.—The levels of the organisms associated with Patella are liable to vary, especially with the local splash-line, and in localities exposed to strong wave-action and strong sunshine. The data regarding tidal levels are for Devonport (see **11**, p. 370) :—

M.H-W.S. = mean high water spring tides.
M.H-W. = mean high water.
M.H-W.N. = mean high-water neap tides.
M.T.L. = mean tide level.
M.L-W.N. = mean low-water neap tides.
M.L-W. = mean low water.
M.L-W.S. = mean low-water spring tides.

[1] Where fresh water occurs.

The Distribution of *Patella vulgata* on a Cliff-bound, Sun-baked Shore.

In studying the distribution of *P. vulgata* on the shore, it was found that at levels above high-water neaps, exposure to direct sunlight is a very important limiting factor. This effect of sunlight is easily observed by taking a rowing-boat at about the time of high water on a neap tide along a rocky or cliff-bound shore which faces mostly, or in parts, in a southerly direction. On the parts of the cliff exposed directly to the sun's rays it is seen that the limpets are distributed along and below the line *and splash-line* of high-water neaps. Where the water at H.W. neaps runs up angular depressions in the face of the rocks, limpets may be so thick as to outline the splash of the waves (herein denoted as the splash-line*) above the general mean high-water neap level, whereas elsewhere on the dry sun-baked area above this level limpets are absent or rare. Where the cliffs jut out so as to produce shade, or in caves, or on the shaded sides of rocks, limpets will be found above the level of H.W. neaps; that is, in most places where continuous direct sunlight can be avoided. Such is the distribution of limpets on the Wembury shore at the mouth of the River Yealm, near Plymouth, as seen in a calm sea on July 11th, 1928, at high water at 12.40 p.m. (S.T.), when the height of the predicted tide (**11**, p. 3) was 12 feet 7 inches above datum (mean high-water neaps at Devonport being 12·25 feet above datum, **11**, Part I, p. 344). The distribution of limpets on the cliffs near Perranporth, on the North Cornwall coast, shows similar limitations. The cliffs to the south of Perran sands face north to north-west and are sheltered from the sun during the greater part of the day, and are also in many places damp even on a summer day. On these cliffs limpets occur abundantly in most situations above high-water neaps, but on the northern part of the sands the cliffs face westerly and in 1928 were devoid of limpets above high-water neaps except for occasional small individuals hiding under the high-level seaweeds, Pelvetia, and a species of Fucus, probably *platycarpus*, which was zoning above *Ascophyllum nodosum*. On rocky shores which do not face south and yet receive a moderate amount of direct sunlight limpets may extend above high-water neaps, but in such cases they do not usually attain a large size unless they are living in a situation which is in some way maintained in a damp condition, e.g. proximity to a seepage of water. On most north-facing rocky shores—like that of Perranporth—it would appear that limpets are seldom absent above high-water neaps unless the shore be liable to be pounded with gravel or sand, or there is some other obvious deterrent.

Thus the distribution of the limpet on the shore indicates that although this animal can exist in localities which receive a certain amount of direct insolation, there is a limit beyond which existence cannot be maintained, whether the limiting cause be absence of food or direct insolation.

In the south-west of England where the low water of spring tides occurs round about midday (and midnight) (see Fig. 1, p. 281) limpets do not occur in dry places above high-water neaps which are exposed to direct sunlight during the whole, or a large portion, of the daily period

* The splash-line is important at all tidal levels on sloping rocks or sloping beaches in apparently raising the level of a zone. I have seen Patella at least 6 feet above the general high-water spring-tide level in a cave at New Train Bay, N. Cornwall, where existence was made possible by the splash of the waves.

of duration of sunlight; but in more northern latitudes and other localities limpets may be able to exist on the southern faces of cliffs to a greater extent, especially in those situations where the *high water* of the spring tides occurs (see Fig. 2, p. 281) round about midday, e.g. south-east of England and neighbouring Continental coast, parts of northern Scotland, as at Invergordon (see Admiralty Tide-Tables, **11**, *passim*). In considering the habitats and habits of the common limpet, it is certain that the geographical orientation of the rocks comprising the habitat, the latitude of the locality, and the epoch of the day when the limpets are exposed during the spring tides, are all important factors, which if not considered might give rise to great confusion, but which when carefully noted may render concordant many apparent inconsistencies and many apparently opposed statements.

Fig. 1. Conspectus of the tidal changes in the Devon and Cornwall area, shown by a semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle. The time and duration of the exposure of the foreshore at different levels is also shown approximately.

(Data from Admiralty Tide-Tables, Part 1, 1929, from which are plotted the predicted times and heights (in feet) for high and low water for the tides at Devonport from April 7th to April 22nd).

Each small circle denotes the height and time of the tide at low or high water on the date given by the small figure adjacent to the circle. The courses of representative tides only are plotted: (after **11**, II, Table 4), e.g.:—the spring tide on April 12th (thick-line curve); the neap tide on April 18th (thin-line curve), and two intermediate tides on April 8th and 15th respectively (broken-line curves). The large circles give the seasonal maximum and minimum possible daily range of sunshine. The references to different tidal levels, M.H-W.S., etc. have the same meaning as in Table I, p. 278.

M.H-W. (=mean high water) and M.L-W. (=mean low water) occur midway between M.H-W.S. and M.H-W.N., and M.L-W.N. and M.L-W.S. respectively. These are important biological levels, but are not given in Admiralty Tide-Tables.

The heights of high or low water—with reference to the chart datum (which is only 0·18 foot above mean low-water springs)—are plotted as ordinates in feet, while times of day (G.M.T.) at which high or low water occurs are plotted as abscissæ. The cycle of tides shown in the diagram is repeated at essentially the same times and with slight modification in height throughout the year. Around the period of the equinoxes, March and September, the rise of tide during spring tides is higher and the fall lower than at other times: in winter, the morning high spring tides are higher and the succeeding low tides lower than the night tides, whilst the contrary is the case in summer. In the lunar cycle the greater spring tides occur after full moon in winter, but after new moon in summer. With reference to mean tide-level, in this district neap tides rise on the average higher than they fall, but spring tides fall lower than they rise on the average.

The time of high water on the same day varies slightly in Devon and Cornwall, being about one hour earlier in the extreme west (Land's End) than at Devonport, decreasing along the south coast to Devonport,

FIG. 1. DEVONPORT

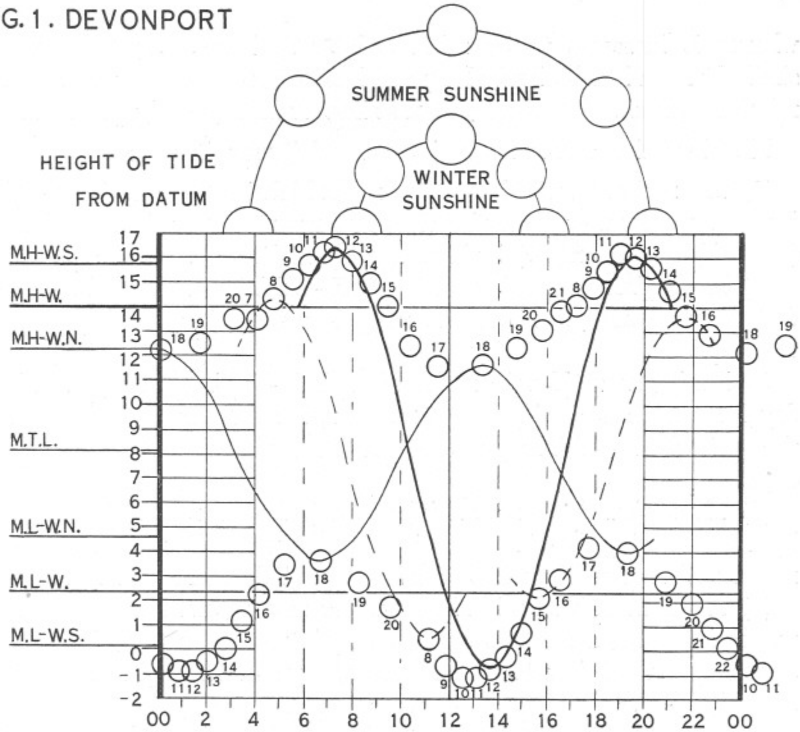
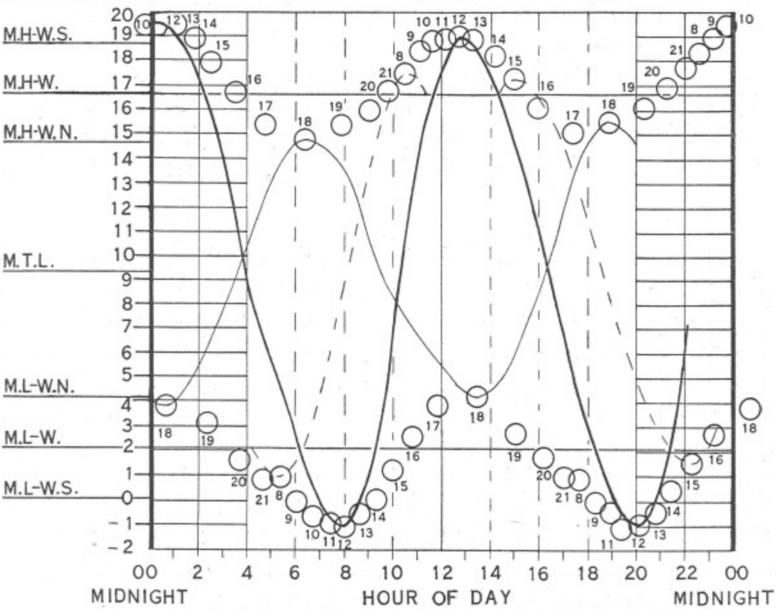


FIG. 2. DOVER



NOTE.—Height of tide from datum is given in feet.

whence it increases to 35 minutes later at Exmouth; it decreases similarly from Land's End along the North Cornwall coast to about 2 minutes earlier at Ilfracombe than at Devonport. (**11**, II, pp. 32 and 54.)

The chart shows that in the Devon and Cornwall area :—

(1) The region on the shore *above* mean high-water neaps (M.H-W.N.) is uncovered by the tide during the greater part of the middle of the day (and middle of the night) during *every* day of the year.

(2) The region on the shore below M.H-W.N. is uncovered by the sea during spring tides, but covered during neap tides, in the *middle* part of the day.

(3) During neap tides the region above M.H-W.N. may remain entirely dry for one or more tides, or in summer, for one or more days, while that below M.L-W.N. may remain covered during one or more tides or days.

(4) The region above mean high water (M.H-W.) may not be covered by the sea during about 7 days and that below mean low water (M. L-W.) may remain covered by the sea during about 7 days in a semi-lunar cycle.

(5) The time of immersion in sea-water of a region above mean high water varies from about 3 hours at spring tides to a slight wetting according to the height of the tide on any day and the height of the region above M.H-W.

(6) The time of exposure of a region of the shore below mean low water (M.L-W.) varies from about 3 hours to momentary exposure according to the height of the tide (above or below datum) and the level of the region below M.L-W.

(7) During the period of the higher tides (i.e., those rising to and above M.H-W. and including the spring tides) the different levels on the foreshore are exposed in the middle of the day, approximately and on the average, as follows :—

M.H-W.	11 to $9\frac{1}{2}$	hours	ranging	between	about 5	and	20·30	hrs.
M.H-W.N.	$9\frac{1}{2}$ to $8\frac{1}{4}$	,,	,,	,,	,, 6	,,	19·30	,,
M.T.L.	ca $6\frac{3}{4}$ to $6\frac{1}{2}$	,,	,,	,,	,, 7·30	,,	18·30	,,
M.L-W.N.	ca $4\frac{3}{4}$ to 4	,,	,,	,,	,, 8·30	,,	17·15	,,
M.L-W.	$3\frac{1}{2}$ to 1	,,	,,	,,	,, 9·30	,,	16·0	,,
M.L-W.S.	2 to 0	,,	,,	,,	,, 11·30	,,	15·0	,,

Fig. 2. Semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle showing the times of exposure of the foreshore at different levels during the daytime in localities where high-water spring tides occur about midday, e.g. south-east of England and neighbouring continental coast, and northern Scotland, as at Invergordon.

(From Admiralty Tide Tables, Part I, 1929, from which are plotted the predicted times and heights of high and low water at Dover from April 8th to April 21st.)

Fig. 2 shows that in any locality where high-water spring tides occur at about midday the high-water foreshore is necessarily protected during the period of the higher tides from direct exposure to air and sunshine during the hottest part of the day. In the period of neap tides the foreshore down to M.L-W.N. is exposed during the middle of the day. The region about mean low-water springs is only exposed to air and sunshine about 6 to 9 a.m. and 6 to 9 p.m., and in general the exposure conditions to extremes of temperature and insolation are much less severe than in such a region as is shown in Fig. 1.

In Fig. 1, page 281, it is shown that in the area of Devon and Cornwall (and similar tidal localities) the region above high-water neap-tide level is always exposed in the middle of the day to the air, and therefore also in certain situations also to the sun's rays. Thus, where limpets are present on the shore below and up to the level of high-water neaps, and also present in shaded places immediately above this level, while at the same time they are absent in the same locality from intermediate areas above high-water neaps which are exposed to direct sunlight, it is manifest that direct sunlight in these situations is in some manner a limiting factor in the distribution. Since, however, the limpet can exist above high-water neaps in places subject to a certain amount of direct insolation, it is also clear that this animal may be able to exist above high-water neaps at different levels on different shores, according to the duration and intensity of the incident direct insolation in different areas.

The distribution of limpets above high-water neaps indeed shows that individuals can withstand strong direct insolation for a short period, and a less strong direct insolation for a longer period, and also that resistance varies to some extent with the size of the animal (when thickness of the shell is doubtless an important factor). The absence of limpets from strongly insolated areas above high-water neaps may, however, be due either to absence of encrusting (e.g. algal) food, or to the direct effect on the animal of the sun's rays, or both of these factors. In this regard the occurrence of abundance of limpets on the high-water neap-tide line and their absence above this level in a strongly insolated area indicates that the higher level is untenable as a habitat, and that prolonged direct insolation may be as effective a limiting cause as absence of encrusting algal food. Such food is, however, apparently absent from many (shaded) situations at high water where limpets are abundant and apparently flourishing (**8**, **10**, and self), and apart from the possibility of the limpets making long feeding excursions when covered by the tide the mode of feeding in such habitats is not known. There are indeed grounds for suspecting that Patella may obtain food in other ways than in browsing on rocks. This animal will eat calcareous sand and detritus (H.-W. Looe Is.), and in aquaria I have known it eat putty and red lead, as shown by the fæces, but I have not yet detected any method of feeding whereby plankton is utilised as food. Thus the absence of encrusting algal food in any area cannot at present be regarded in itself as a certain limitation of such a habitat for the limpet.

The spat of limpets—ranging in length from 2 to 8 mm.—have been specially searched for above and below high-water neaps, but even in the latter zone tiny individuals of this size are rarely found except in very damp places, e.g. crevices or small pools. If therefore such spat settled in very dry sunny places, it is fairly certain that they would die from desiccation before succumbing to starvation. Thus, in accounting for the absence of adult limpets in strongly insolated areas of the shore above high-water neaps, it is necessary to allow some value to the fact of relative scarcity of encrusting food, though the direct effect on the animal of the actual intensity and duration of direct sunlight would appear to be the main limiting factor.

The Movements of Patella in Relation to Habitat and Climatic Conditions.

Russell (**5**, p. 856) has shown that there is no agreement among the many observers on the time that the limpet leaves its home in search of food; for example, "Lukis, Jeffreys, and Robertson state that the limpet wanders when covered by the tide; Davis and Fischer that it wanders while uncovered, and Fischer that young ones wander only when covered; Bouchard-Chanteraux that it makes excursions just after the tide goes out; Lloyd Morgan that it wanders chiefly as the tide leaves it and as the tide returns; Lloyd Morgan and Roberts are of the opinion that it does not move about when submerged." Loppens (**9**) found exposed limpets on the move between Ladram Bay and Sidmouth, but never on the beaches near Exmouth. Russell found in his experiments that limpets above 20 mm. or so in length did not wander when uncovered by the tide, but that smaller ones may wander at any time, and concluded that a habit of fixity becomes established only when the shell has attained a length of 10–15 mm., and that they wander chiefly when covered by the tide. The present writer has seen limpets of all sizes on the move away from their "homes" at high and low-tide levels at some time or other. At high water in damp situations or in situations not exposed to direct sunlight some individuals can usually be found creeping and feeding away from the home, but in dry situations at high water which are exposed to sunlight the animals are rarely seen on the move except in damp or wet weather. Small to medium-sized individuals may be seen moving on the shaded side of rocks at various tidal levels even in warm sunny weather, as may also large individuals under seaweeds near low-water mark, but limpets are very rarely seen moving when exposed to direct sunlight, while probably everyone can form a mental picture of immobile Patella at or near high-water mark in sunny warm weather.

Thus the factors controlling the feeding movements of the limpet when uncovered by sea-water appear to be mainly those which contribute to the risk or absence of risk of desiccation, and there can be no doubt that the main feeding excursions are made in all habitats when the animals are covered by water. By rowing alongside rocks covered with limpets, especially when the tide is rising at about the time of high-water neaps, it is easy in calm weather to see that the animals begin to move away from their scars very soon after immersion, just as Wells found for Acmæa and Lottia (**13**).

It is now a well-established fact that a majority of the medium to large-sized individuals return to a definite position in space after undertaking feeding excursions (see Russell, **5** ; Pieron, **7** ; Loppens, **9**, and Orton **8**, and **2**) ; but this general statement requires qualification. I agree with Loppens (**9**) that sometimes individuals do not return to the same place, and that evidence of this can sometimes be found in the lines of growth on the shell. Loppens states : " En effet, si la place ne convient plus, soit que la nourriture y manque, soit que la roche s'est trop effritée, ou pour n'importe laquelle raison, le mollusque cherche une autre résidence et ne revient plus à la première. On remarque cependant que beaucoup d'individus résident longtemps à la même place si elle est convenable. Patella peut, en effet, circuler dans un rayon de 2 mètres pour chercher la nourriture et retrouver aisément sa place sur les rochers." It is probable that Patella changes its " home " more often on a smooth and wet surface than on an uneven surface, while at the same time it is undoubtedly true that the bulk of the individuals retain the same scar for long periods in most habitats where the surface of attachment is uneven. On Padstow Dock vertical walls, which have a somewhat rough though uniformly plane surface, I found one limpet six feet above high-water neaps, carrying empty barnacle shells, which had undoubtedly grown below high-water neaps. On such a uniform surface it is probable that a limpet shell will fit fairly well at many places, and the necessity for homing is not so imperative as on more uneven surfaces. Lloyd Morgan's experiments (**12**) also show that a change of site is possible under natural conditions.

In some high-water situations adult individuals occur where younger ones could apparently not exist ; for in such situations small individuals (less than 25 mm.) can only be found in crevices or under weeds (*Pelvetia canaliculata* and *Fucus platycarpus*) where some protection from direct solar rays and drought is obtained. In these habitats, therefore, the older individuals must have moved into their final positions after attaining a medium size. In a broad consideration of the movements of Patella, it is manifest that the bulk of the larger individuals retain a definite position or home for long periods, and that the changing of the site is unusual for medium to large individuals in most habitats, but may occur more frequently in others, e.g., on smooth and wet surfaces.

The foregoing studies have therefore shown that the period of exposure of the foreshore to direct solar rays, and other conditions conducive to desiccation, as well as relative dampness of a locality, are all very important factors in determining the viable habitats and habits of the common limpet.

Remarks on the form *Patella athletica* F. and H., or *P. vulgata*, var. *depressa* Jeffreys.

The experienced conchologists Forbes and Hanley (**10**) arrived at the conclusion, apparently however with some doubt, that the form *athletica* is sufficiently distinct from other varieties of limpets to be entitled to specific distinction. A little later Jeffreys (**3**), also an experienced conchologist, reduced the status of this form to that of a variety of the common limpet, *Patella vulgata* L., as var. 4, *depressa*. In referring to this form, Jeffreys states : " I once considered myself an adept at picking out the variety *depressa* (or ' China limpet,' as it has been called), by merely seeing the outside ; but I have since failed, and a recent examination and comparison of a great many living individuals of each form has quite convinced me that they are not separate species." In most accounts of the habitat it is stated that the form *athletica* occurs at low water ; for example, Clark, quoted in Forbes and Hanley, states : " They inhabit different levels, the *vulgata* being always in the higher zone." This latter statement is not quite accurate, the form *athletica* occurs in permanent pools (**1**, p. 860) at all levels up to high-water neaps, but also out of pools at low-water mark in some localities on the Devon and Cornwall coast and elsewhere. It has also been shown that the proportion of females with green gonads in this form was greater (in one sample) than in adjacent typical *vulgata*, nevertheless brown and green gonads occur among the females in both types (*loc. cit.*). The range of variation in all the characters of *P. vulgata* is, however, very great ; Jeffreys records that Spence Bate found the lingual ribbon broader and shorter, and the teeth perhaps somewhat larger in *athletica* (≡*depressa*) than in the common type, but the main differences so far found between these forms occur (1) in the habitat, and (2) the nature of the internal calcareous lining of the shell. With regard to habitat the form *athletica* is continuously or almost continuously immersed in water in contrast with *vulgata*, which experiences in most situations relatively long periods of exposure to the air. The lining of the shell in the former is white and entirely porcellanous, with often an orange coloration in the spatula or apical region, whi'e *vulgata* has a greyish brown nacreous lining with a chalky-white or vitreous greyish white spatula, which may attain a great thickness (e.g., 10·1 mm.) in some high-water habitats.

The correlation between habitat and the quality of the lining of the shell suggests that the shell-differences observed may be physiological, that is, due to the nature of the environment, and therefore not genetic, i.e., specific. Thus it is possible that young limpets developing entirely in pools, or under water, may deposit porcellanous nacreous material on the inside of the shell, while others *of the same brood* developing on rocks exposed to air and light may deposit greyish brown nacreous material and a chalky or vitreous thickening at the apex of the shell. Until this problem is solved, or until some other distinct differential specific character is found in *athletica*, it would seem that there is insufficient ground for regarding the form *athletica* other than a variety of *P. vulgata* L.

At a recent meeting of the Challenger Society with Representatives of British Marine Laboratories, G. C. Robson, who has paid much attention to *P. athletica* F. and H., suggested that this form in its relation to types of *P. vulgata* would provide excellent material for a study in evolution. It is hoped that the foregoing observations may form a nucleus in the development of such a study.

SUMMARY.

The inter-tidal habitats of the common limpet, *Patella vulgata* L., have been investigated in relation to constant lunar tidal levels and tidal zones. The habitats of some common shore organisms which occur at approximately definite tidal levels or zones—and can therefore be used with discretion for zoning the habitats of Patella—are shown in a chart.

A study of the distribution of the common limpet on the shores of Devon and Cornwall has shown that limpets are absent or rare on those parts of the foreshore above high-water neaps which are subjected to prolonged periods of direct insolation. In the same locality limpets may be totally absent from the high-water region on cliff-faces or rocks facing southerly, but present on adjacent ones facing northerly or north-westerly. Strongly insolated habitats appear to be unviable as a result of the direct effect of the insolation on the animal, but the apparent deficiency of food in such habitats is probably also a limiting factor of importance.

The importance of the *splash-line* of any tidal level is emphasised. It is shown that in Devon and Cornwall the occurrence of *low-water* spring tides at about midday (and midnight) results in exposing to strong sunshine (and correlated factors) those regions of the shore above high-water

neaps which face in a southerly direction. In other localities where *high-water* spring tides occur about midday, equivalent regions of the foreshore are not so strongly nor so persistently insolated as in the former.

Viable habitats may therefore occur in different regions on the shore in different localities or at different latitudes according to the local orientation of the substratum and local tidal phenomena.

The tendency of the common limpet to wander when uncovered by the tide was found to be greatly influenced by those factors in the environment which do or do not incur risk of the animal being dried up. Wandering may occur at any level of the exposed shore in damp or shaded environments, but rarely at any level in the absence of protection from stıong sunshine, hence many apparently conflicting statements on this subject may be reconciled. It is considered that the main feeding excursions or operations occur in all habitats when the animal is covered by the tide. It is shown that the habits and viable habitats of the common limpet are determined in a significant manner by factors representing the period of exposure of the foreshore to direct solar rays, other conditions conducive to desiccation, and the relative dampness to the environment. The characters of the doubtful species, *P. athletica* F. and H., are discussed briefly. It is noticed that this form differs from *vulgata* mainly in habitat and the quality of the lining of the shell, and it is suggested that the shell-quality may be a particular physiological product resulting from the special environment, and not to a genetic—and specific—factor.

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