

The Distribution of some Littoral Trochidæ and Littorinidæ in Cardigan Bay.

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THE physical characteristics of the Bay having been set out in the preceding paper, it will not be necessary to repeat that description here, since only special local features will be dealt with, as occasion arises. Peculiarities of distribution had been noted for the Trochidæ and Littorinidæ, and it was with a view to obtaining further information as to the operation of local littoral conditions and their effects upon the fauna that these groups were more particularly examined. These notes detail some of the peculiarities, and outline what are believed to be the controlling causes, at any rate for the central area of the Bay. It would be of great interest to know whether similar peculiarities have been, or can be, observed for other areas of coast. The region discussed lies between Gwbert-on-Sea at the mouth of the Teifi, to the south; and a point a few miles beyond Pwllheli to the north. The portion more closely examined extends from near Llanrhystyd, some eight miles south of Aberystwyth, to Mochras, a few miles south of Harlech. Some observations were also made about Portmadoc, Borth-y-Gest, and Pwllheli in the northern part of the Bay; and about New Quay, and the mouth of the Teifi to the south, the most southerly being some miles below Cemræs Head.

Much of the coast is difficult of access, and the investigation has been going on for a number of years.

The following species have been observed living within tide marks :—

TROCHIDÆ.

- (1) *Gibbula cineraria* (Linnæus).
- (2) *G. umbilicata* (Montagu).
- (3) *G. magus* (Linnæus).
- (4) *Monodonta crassa* (Montfort).
- (5) *Calliostoma zizyphinus* (Linnæus).

LITTORINIDÆ.

- (6) *Littorina littorea* (Linnæus).
- (7) *L. neritoides* (Linnæus).
- (8) *L. obtusata* (Linnæus).
- (9) *L. rudis* (Maton).

GENERAL DISTRIBUTION.

(1) *G. cineraria*.—This species is rare throughout the whole of the region examined. Two large living specimens were obtained after careful search, in the coves at Gwbert; these coves are situated seaward of the bar, and their general fauna is rich (for Cardigan Bay). Two small specimens were also found, under stones about eight miles south of Aberystwyth. Dead shells are not infrequent, so that this species may be more abundant below tide marks.

(2) *G. umbilicata* is, in certain districts, exceedingly abundant; but at Gwbert, in the coves above mentioned, I found but two. In New Quay Bay it abounds, also locally from Llanrhystyd (and probably between there and New Quay) to within some two miles of the River Ystwyth, where it gradually dies out. Further north it reappears near Towyn to the north of the Dysynni. It is abundant about Mochras, and occurs at Y-Gamlas on the *Zostera* beds beyond Pwllheli. There it is accompanied by (3) *G. magus*, the only locality for this fine species that has so far been noted in the Bay.

(4) *M. crassa* has very much the same distribution as *G. umbilicata*, but its range is more restricted, and always lies within the area occupied by that species. Both are often exceedingly abundant for considerable distances.

(5) *C. zizyphinus*.—So far only one small living specimen has been recorded, and that at Aberystwyth, where no other species of the Trochidæ exist. It probably occurs in deeper water.

(6) *Littorina littorea* has a wide distribution, but is more especially abundant and much larger in certain places.

(7) *L. neritoides* is, as elsewhere, very local. Its distribution around the Bay appears to be quite normal and to be governed by its usual requirements; a rocky foreshore, affording crevices just above high-water mark, and not exposed to the midday sun and the resulting desiccation. Given these conditions, it often will occur in very restricted areas. South of Aberystwyth, the foreshore for considerable distances is chiefly smooth rock, with a steep seaward inclination. One or two large squared masses of fallen cliff are situated just about high-water

mark, and their stratified wall-like sides afford crevices, inhabited by this species and *L. rudis*. *L. neritoides*, however, only occurs on the upper portions, and on the N. and E. faces. A few may be observed on the S.E. also, but this is exceptional. I have seen practically the same thing in similar positions on the Devon coast. On the sea walls of the promenade at Aberystwyth, this species occurs, chiefly where the rays of the summer sun will not strike about midday.

(8) *L. obtusata* occurs throughout the littoral region examined wherever *Fucus* grows, and hence is the most thoroughly persistent form.

(9) *L. rudis*.—This also is generally present, and frequently exceedingly abundant. It usually accompanies *L. littorea* in its distribution, though at a somewhat different level. These two frequently appear and disappear simultaneously, but one or other may be locally dominant.

VERTICAL DISTRIBUTION.

The distribution of the species may also be considered vertically, that is, in zones. These zones, of course, overlap considerably and are seldom all well developed, or even present in any given locality. By contrasting varying localities a general succession appears. This is not by any means arbitrary, as some of these zones may occur intermixed at times, particularly in the case of *M. crassa*, *L. littorea*, and *L. obtusata*. *L. neritoides* is constant when conditions permit, and *L. obtusata* is dependent on the presence of Furoid Algæ. *C. zizyphinus* has occurred once, but in its normal position.

Allowing for local differentiation and overlap, the succession is, more or less, as follows :—

L. neritoides.
L. rudis.
 { *M. crassa*.
 { *L. obtusata*.
 { *L. littorea*.
G. umbilicata. *G. magus*.
G. cineraria.
C. zizyphinus.

The succession of the Littorinidæ can be best followed in the Aberystwyth district, where the Trochidæ are absent.

On the sea wall of the promenade below the University the following succession can be observed :—

- (a) Barren stonework.
- (b) Zone of *L. neritoides*.

- (c) Zone of small green *Algæ* and many *L. rudis*.
- (d) „ „, few scattered Fucoids and a few *L. rudis*.
- (e) „ „, thick coating of *Fucus* and a few *L. obtusata*.
- (f) Base of wall, with pools at foot, with *Enteromorpha*, *Ulva*, etc., and *L. littorea*.

M. crassa is local in Cardigan Bay, but often extremely abundant; and in the area south of Aberystwyth exhibits a striking peculiarity in that it there breaks zone by following fresh-water influence, sometimes as far as the low-water mark of spring-tide; it is then often of remarkable size. Proceeding southwards from Aberystwyth, the mouths of the Rheidol and Ystwyth and a storm beach are passed, and a high slaty cliff with eroded rocky foreshore is reached. About halfway around this headland (Allt Wen), i.e. two miles from Aberystwyth, *G. umbilicatus* puts in an appearance, at first only sporadically, two or three small individuals here and there. As it becomes more numerous, *M. crassa* also appears, and both increase rapidly to the south of the headland, where the cliffs are composed of glacial drift. A number of springs flow down, and in one or two localities fresh water percolates through a shingle bank on the foreshore, and affects more or less the whole of the lower rocky and stony portions of the tidal region, which is there mainly composed of boulders covered to some extent by *Algæ*. Where there is fresh-water influence, *M. crassa* follows it. Streamlets often follow a kind of channel or gutter, where the boulders lie less thickly, and the shore level is somewhat lower. In these channels, *M. crassa* swarms upon the nearly bare boulders, and extends almost to low water. *G. umbilicata* is seldom to be observed within the fresh-water influence, although abundant close by. Where a section of the shore is affected by fresh water, *M. crassa* tends to become abundant throughout. It appears to feed upon minute *Algæ*, and I am indebted to Dr. Fleure for a recent attempt to determine the food of this species: all that could be made out, however, was that "the contents of the gut consisted of finely triturated vegetable matter, too fragmentary for identification." H. J. Fleure and M. M. Gettings state (Q.J.M.S., 1907), "*T. crassus* [*M. crassa*] is found to some extent with the previous species [*G. umbilicata*], but it lives, for the most part, near high-tide level, so much so that specimens may remain for a considerable time in corners washed only by high spring-tides. It crawls over the rocks chiefly at half-tide level, but is more lethargic than *T. obliquatus* [*G. umbilicata*], and less inclined to browse on the larger *Algæ*. During stormy periods, especially in winter, numbers may be found huddled in sheltered nooks,

often with a number of *Littorina littorea* as companions. As is well known, the spire of *T. obliquatus* is much lower than that of *T. crassus*, and this is probably correlated with the greater activity of the former in the shore zone, where a high spire would give too much purchase to a side blow from a wave." Recent observations lead to the same conclusions: the animals crowd the tops of the boulders in calm summer weather, and in winter tend to occupy the sides and angles of boulders and reef-pools.

It is evident that in this region *Trochus* is extending its range northward. Quite recently Mr. W. Whitehouse informed me that he had seen specimens on the Aberystwyth side of Allt Wen. This I found to be the case, as I found a colony of *G. umbilicata* and one specimen of *G. cineraria* about the spot indicated. This is well to the north of any other record, but is close to an isolated patch of boulder clay. I have examined this spot at intervals ever since 1906, and Prof. Fleure knew it well for some years before that, and no *Trochi* have ever been seen there.

A remarkable influence of fresh water in larger volume upon the littoral Mollusca has been noted, about the mouths of several of the smaller rivers. It is particularly noticeable for some half-mile or so on either side of the mouth of the Afon Wyre, near Llanrhystyd. The cliffs thereabouts are very low, and composed of glacial drift, with the usual result that the foreshore consists of shingle, while the lower portion of the tidal region is occupied by boulders of medium size. These extend to low-water mark, but pass into sand and shingle both to the N. and to the S.; and this boulder area is fairly well covered with Algal growth. The river debouches upon a shingle bed, and spreads out in a fan-like manner over the boulders; and, to judge by the distribution of mussels, would appear, as usual, to trend up-coast, at least during some states of the tide. To the south of the river where the boulder area commences (and, indeed, throughout the area) the zones of *L. neritoides* and the upper portion of that of *L. rudis* are absent owing to the presence of shingle. The boulders are at first considerably incrustated with *Sabellaria*, and no Mollusca are present except a few specimens of *Patella*, probably owing to the proximity of much sand and shingle. As the boulder area widens *G. umbilicata* appears, and rapidly becomes abundant. That lack of shelter and attrition are the excluding factors is borne out by the fact that, where *Gibbula* first appears, the shells of many are much worn and eroded, and in several cases actually broken. I examined certainly 1000 *Gibbulas*, and only discovered two specimens of *cineraria*.

Both were small, flattened, and occurred beneath stones. *L. obtusata* accompanies *Fucus*, and is the most persistent species throughout. *L. littorea* appears about the same time as *G. umbilicata*, but does not become abundant until fresh-water influence is an appreciable factor; it then increases in number and size. *G. umbilicata* is dominant for a considerable distance, but as the river is approached, *M. crassa* appears, here one and there one, amidst the crowds of *Gibbula*. Those first noticed are rather small, but there is a gradual increase in size and abundance until it equals *G. umbilicata* in numbers. That species then dies out as fresh water is approached, and is replaced by a rather squat, solid, smooth form of *L. rudis*, which in its turn rapidly becomes larger and more numerous, while *M. crassa*, after being a dominant species for a while, dies out in its turn. Then for a space, *L. rudis* and *L. littorea* alone occupy the ground; but both are absent from the actual flow of the stream. On the northern side of the river, mussels are abundant in the crevices of the stones for some distance along the shore, and are accompanied by *L. rudis* and *L. littorea*. Then, as the mussels disappear, *M. crassa* reappears, and in company with the Littorinas becomes very abundant. *G. umbilicata* recommences by degrees, increases in numbers, and with *M. crassa* continues until the boulder area once more gives place to shingle.

This lateral distribution or zoning may be expressed thus (the order in each instance is that of abundance):—

1.	2.	3.	4.
<i>G. umbilicata.</i>	<i>G. umbilicata.</i> <i>L. littorea.</i> <i>G. cineraria.</i>	<i>G. umbilicata.</i> <i>L. littorea.</i> <i>M. crassa.</i> <i>G. cineraria.</i>	<i>G. umbilicata.</i> <i>M. crassa.</i> <i>L. littorea.</i>

Littorina obtusata.

5.	6.	7.	8.
<i>M. crassa.</i> <i>L. littorea.</i> <i>G. umbilicata.</i> <i>L. rudis.</i>	<i>L. rudis.</i> <i>L. littorea.</i> <i>M. crassa.</i> <i>G. umbilicata.</i>	<i>L. rudis.</i> <i>L. littorea.</i> <i>M. crassa.</i>	<i>L. rudis-littorea.</i>

. . . *Littorina obtusata.*

	1.	2.	3.	4.
River.	<i>L. littorea-</i> <i>rudis.</i>	<i>L. rudis-litto-</i> <i>rea. M. crassa.</i>	<i>L. rudis-L. litto-</i> <i>rea. M. crassa.</i>	<i>M. crassa.</i> <i>G. umbilicata.</i> } <i>L. littorea-</i> <i>rudis.</i>

THE LITTORINIDÆ.

It may be mentioned that the shells of *L. obtusata* often bear a striking resemblance in both form and colour to the vesicles and conceptacles of the species of *Fucus* upon which they live; so much so, in fact, that when collecting this species, I have more than once mistaken the vesicles of the *Algæ* for the shell of the Mollusc.

The conceptacles of all the species of *Fucus* are of shades varying from white to bright yellow, and, indeed, the whole of the parts of the plant exposed to sunlight are frequently much lighter in hue than the more sheltered portions, which are usually dark brown or olive. One would expect that the lighter coloured forms of *L. obtusata* would tend to occur upon the surface, and the darker among the masses of the plant. I have made a considerable number of observations in the district with the object of testing this idea. What I have found is, that the darkest varieties are seldom found upon the surface of the Algal masses, and that the majority of varieties are found in abundance crawling on the exterior, but are often in harmony with their surroundings. It may be mentioned that many shells which appear out of harmony, are not so in reality, the change of colour being due to drying of the shell during low water. The greatest resemblance is between the light brown and yellow-shelled varieties and the vesicles of *F. vesiculosus* and between the colour of the frond and the ordinary brown and olive shells. Bright yellow *Littorinas* may be found at times upon the dark stems of the *Algæ*, and are then very conspicuous. I do not find the yellow variety to be really common in the district.

The Littorinidæ persist in the areas devoid of Trochidæ; and, as has already been stated, *L. obtusata* appears to be less affected by the adverse conditions than the other species; this is in all probability largely due to the protection afforded it by the food plant, and its shell-characters. *L. rudis* and *L. litorea*, are neither so large, so numerous, nor so evenly distributed as in the areas where Trochidæ are abundant. Several varieties of *L. rudis* occur in Cardigan Bay, and of these *tenebrosa*, Montagu, has so far only been found under stones some three miles south of Aberystwyth on a portion of the shore influenced by fresh water. This influence was sufficiently strong to attract a number of eels which were also hiding under the stones. Tryon describes the variety as "thin, whorls rounded, with elevated spire, brownish or yellowish, usually tessellated with white." In the Aberystwyth specimens the ribbings of the shell are not very strong, and the colour olive-green to greyish. The chequered appearance is due to the presence of a series of short white streaks dis-

posed in a spiral sequence ; these white marks, alternating in each turn of the spiral produce a chequered appearance. The usual forms, *similis* and *lævis* of Jeffreys, were both present in the same locality. The variety *patula*, Thorpe, is sometimes abundant on steep rocks at the foot of cliffs, somewhat influenced by fresh-water springs, and may be yellow, olive-green, pale greenish white, black and white in bands, or pinkish ; *compressa*, Jeffreys, occurs a little to the south of Aberystwyth.

The complete sequence of species of *Littorina* may be interrupted, and a barren area may occur between the cliff rocks and the lower tidal reefs, owing to a belt of shingle. The result of this truncation of zone is that the upper portion of the *rudis* zone may be absent except here and there where conditions allow ; while below the break, *rudis* and *littorea* may be found together in quantity, giving the impression that the latter is above its usual horizon.

Dr. Fleure considers that *L. rudis* spawns largely in the shelter afforded by the interior of dead *Balanus*, and I have found many of the young of both *rudis* and *littoralis* so small as to be just recognizable clustered within the angles of empty *Balanus*. The absence of *Balanus* from the *rudis* zone may also have a limiting effect, locally, on the distribution of the species. A curious and interesting form of Molluscan association is common on some parts of the cockle beds of the Dyfi estuary, and usually on the more muddy areas. Scattered over from one to several acres in such places, are clusters, or groups, composed primarily of one or more mussels, attached to either various dead shells which lie upon the surface, or to one or more living cockles of varying sizes. The latter occupy their usual positions in the sand, thus anchoring the mussels. Upon the cockles grow trailing tufts of various green *Algæ*, and clinging to the mass are generally several individuals of *L. littorea* and *L. rudis*, more often the former. Within the mass, amongst the byssal threads of the mussels, one or more specimens of *Macoma balthica* are frequently to be found. There are often a dozen individuals, belonging to five species of Mollusca, involved in these clusters.

FACTORS GOVERNING DISTRIBUTION.

The facts concerning distribution, association, etc., are matters of observation, record, and comparison ; the causes of distribution are problems of a much more difficult nature, and require careful consideration following wide investigation. With regard to the distribution of the Trochidæ in Cardigan Bay, it is not yet possible to state that the problem has been completely elucidated. It would appear, however,

that there is a correlation between such distribution and shore drainage. The barren area receives most of its shore drainage from lime-free slates and grits, while the "Trochus" areas receive water from boulder clay in the southern, and the same, and igneous rocks, in the northern portions of the Bay. The streamlets followed by *M. crassa* drain from boulder clay. An attempt was made to obtain additional data by a comparison of the *Algæ* from various portions of the Aberystwyth district. Certain differences were discovered (see list of *Algæ*), but none of them appear to have any direct connection with the Mollusca under consideration; and the evidence afforded is thus more cumulative than decisive. The boulder clays of different districts appear to have different lime contents. The water of the New Quay district is "hard," fruit trees grow well there and the drifts probably contain lime, whereas the boulder clay from the region drained by the Ystwyth has been analysed by Dr. T. C. James, and found to be quite devoid of lime. The northerly drift along the coast has been mentioned already; and it is noteworthy that drainage from the areas containing lime would tend to influence the coast some distance northward on that account. The limeless drainage of the Ystwyth, moreover, coincides with an area of slate and shale rocks; and this is the most barren as regards Trochidæ. The reappearance of the Trochidæ to the north again coincides with the reappearance of boulder clay, and river drainage from districts containing volcanic rock, etc.

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