

On the Occurrence of *Echinus esculentus* on the Foreshore in the British Isles.

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RECORDS AND SIGNIFICANCE OF OCCURRENCE ON THE FORESHORE.

ECHINUS ESCULENTUS, the larger common sea-urchin, occurs in the British Isles between tide-marks on rocky shores at about low-water spring-tide level in the localities given in Table I, page 292. It is, however, absent from apparently suitable foreshores in the Plymouth district, for reasons which are discussed in the present paper. Chadwick (1) states that "In Port Erin Bay it may be collected by hand on the beach, and on the ruined breakwater at low water of spring tides." Elmhirst (2) records that "In this district (Millport) *E. esculentus* occurs abundantly between tide-marks in spring and early summer on rocky coasts; a few may be found at almost any other season. About February or early March a shoreward migration seems to set in, so that in suitable weather conditions some hundreds may be collected at springs between April and June. Then their abundance decreases until about November, from when until January it is at a minimum."

Storrow (3) reports that these "sea-urchins were plentiful on the local rocks (at Cullercoats, Northumberland) during July of last year (1920)," and it is known that *E. esculentus* is collected at low water by the Leeds University Biology Classes at Robin Hood's Bay, Yorkshire. Miss Trewavas (4) collected 5 specimens of *E. esculentus* near low-water mark during two equinoctial spring tides at Mousehole and an adjacent island on the south Cornwall coast, and states that "It should be mentioned that both these shores are sheltered on the west by the mainland, while the island acts as a breakwater on the east. This sheltered position

may be connected with the occurrence of *E. esculentus* above low-tide mark in this locality," and further suggests that "either the climatic conditions of Cornwall or the Cornish seas, as contrasted with those of the Isle of Man, are unsuitable to the occurrence of 'zarts' (*E. esculentus*) in the tidal zone; or the general climatic conditions are suitable and, except in the case of Mousehole, local conditions are unfavourable." In this locality the fishermen report that "zarts" are often found exposed at low water, but elsewhere in Devon and Cornwall no records of the occurrence of the larger common sea-urchin on the foreshore are known, except a reference by Cocks (5) in 1849 to the finding of a young specimen of *E. sphaera* (almost certainly=*E. esculentus*) attached to stones at low-water mark in the Falmouth locality.

E. esculentus does not occur on the well-known rocky foreshores in the Plymouth district (6), and I have not seen it on rocky shores at low-water spring tides in frequent visits to Looe mainland and Island at all times of the year; in occasional visits to the Falmouth district (July); to Gribben Head (Sept.); to Widemouth Bay, Bude (April and Sept.); to Crackington Haven (Sept.); to Croyde Bay (Oct.); to Morwenstow (Marsland, Sept.). Nor did I find it at Sennen Cove (April), where the fishermen report that large "sea-eggs" (*E. esculentus*) may sometimes be obtained from a boat at low-water spring tides. At all these localities, however, *Parechinus miliaris* (= *Echinus*) were discovered hiding under stones or in crevices.

E. esculentus probably occurs on rocky foreshores in other less well-known localities, especially in Scotland and Ireland, and Dr. Marie V. Lebour informs me that she collected when a schoolgirl large sea-urchins—almost certainly *E. esculentus*—at Kyle Akin, in the Isle of Skye, Scotland. The absence of the species from apparently suitable and much-worked rocky shores in the Plymouth district, and in Devon and Cornwall generally, is noteworthy, and challenges explanation.

Offshore it is known (7) that *E. esculentus* occurs all around the British Isles down to depths of about 50 fathoms usually, but sometimes also in deeper water.

The fact that *E. esculentus* occurs off the coast all around the British Isles renders it virtually certain that the post-larval stages will be washed on to most shores from off-shore situations at some time, and would establish themselves in any localities where conditions were favourable. In the Plymouth district this species occurs in 5 to 10 fathoms close in-shore (e.g. off the Mewstone and Revelstoke Point) and has never been recorded (except as flotsam) on the adjacent rocky collecting-grounds in this locality. The existence of adult individuals so close to the shore on this part of the Devon coast makes it highly probable that the post-larvæ will be fairly frequently cast on the shore, as indeed are those of *P. miliaris*.

It is therefore a reasonable inference that the post-larvæ and the young of *E. esculentus* cannot exist on the foreshore in this locality. In a similar way it may be deduced that the general conditions are unfavourable on other rocky shores, which are apparently suitable habitats, but are constantly devoid of this sea-urchin. The general distribution of *E. esculentus*, however, indicates that this Echinoid is essentially a demersal form. Its occurrence on the foreshore may be regarded, therefore, as due either to highly favourable local conditions, which may produce a habitat suitable for both adults and young during the greater part of the year, or the habitat may only be suitable for a temporary shoreward migration at a certain part of the year. The sporadic occurrence of *E. esculentus* on the shore on some parts of the coast (3) indicates that this species tends to migrate shorewards, as Elmhirst noticed at Millport (2), at certain seasons.

DISCUSSION ON SOME FACTORS DETERMINING FORESHORE DISTRIBUTION.

In reviewing the localities where *E. esculentus* occurs on the shore it would appear that some fundamental difference occurs in the general environmental conditions at Plymouth in comparison with those especially at Millport and Port Erin, for in the former locality occur protected rocky shores apparently suitable for but devoid of *E. esculentus*, and in the two latter *E. esculentus* thrives in the region of ordinary low-water springs.

In a comparison of the general conditions in the localities in the British Isles where this sea-urchin does and does not occur in apparently suitable habitats above low-water springs, one broad correlation of importance may be discerned, namely, connected with the time of day of low-water spring tides, but this requires to be considered in relation to other factors.

The chief factors contributing to the presence or absence of *E. esculentus* on the shore appear to be :—

1. The periods of the day when low-water spring tides occur.
2. The latitude of the locality.
3. The nature of the foreshore and its degree of exposure to wave-action.
4. The general seasonal hydrographic conditions in the locality.
5. The nature of the substratal approach to the foreshore from deeper water.

TIME OF LOW-WATER SPRING TIDES.

It has been shown in a preceding paper in this *Journal* (8, p. 277, herein) that low-water spring tides occur on the Devon and Cornish coasts at about and just after 1 a.m. and 1 p.m. (8, Fig. 1, p. 281). As a result of this local tidal phenomenon the region about low-water spring-tide level is

exposed to air and sunshine in nearly the hottest part of the day, and to air in a very cold part of the night. On the other hand, at Millport and Port Erin, low waters in the spring tides occur in the early morning and in the late afternoon or early evening at about the same times as at Dover (see 8, Fig. 2, p. 281). There is thus a marked difference in the temperature conditions on the shore at the time of low water at Plymouth as against those either at Millport or Port Erin, and these differences will be accentuated by the difference in latitude.

The variation in the time of high-water spring tides on the coasts of the British Isles is especially well shown in a figure by Jenkins (9, Fig. 21, p. 126), while the actual (predicted) times of high and low water in particular localities are given in Admiralty Tide Tables (10), Parts I and II. The standard high and low tides in any locality are those which occur immediately after the moon, at full or at the change (i.e. new), has crossed the meridian (H.W. F. and C. and L.W. F. and C.), but these are not the highest or the lowest tides. The highest and lowest tides occur one to two hours later in the day than those immediately following the full and the change of the moon (see 11, Figs. 41-43, and 8, Figs. 1 and 2). Thus at Devonport the time of H.W. F. and C. is 5.32 (10, II, p. 32), but the highest tides occur about, i.e., before and after, 7 a.m. and 7 p.m. (or 19 hours), and the lowest round about 1 hour and 13 hours (see 8, Fig. 1, p. 281).

The epochs of the day and night, before and after which high- and low-water spring tides occur in the various localities where *E. esculentus* is found on the foreshore—including Kyle Akin—are shown approximately in the following table:—

TABLE I.

CORRELATION OF THE MEAN TIME OF LOW-WATER SPRING TIDES AND THE OCCURRENCE OF *E. ESCULENTUS* ON THE FORESHORE.

No.	Locality.	H.W. F. & C.	Approx.		Lat. N.	Occurrence of <i>E. esculentus</i> on the foreshore.
			mean time of day of H.W. springs.	mean time of day of L.W. springs.		
1.	Plymouth District and N. Cornish Coast (Devonport)	5.32	7.0	19.0	1.15 13.15	50 22 Absent.
2.	Mousehole (Penzance)	4.35	6.0	18.0	0.15 12.15	50 07 Occasional at L.W. equin. springs.
3.	Robin Hood's Bay (and Cullercoats) (Whitby)	3.45	5.15	17.15	11.30 23.30	54 29 Present ca. L.W. equin. springs.
4.	Isle of Man (S.) (Port St. Mary)	11.10	0.40	12.40	7.0 19.0	54 04 Present L.W. ord. springs.
5.	Millport, Scotland	11.50	1.20	13.20	6.30* 18.30	55 45 Ditto.
6.	Kyle Akin, Isle of Skye	6.16	7.45	19.45	2.0 14.0	57 16 Ditto.†

* The interval between H.W. and L.W. springs varies from 5½ to 5¼ hours at the Standard port, Greenock.

† Dr. Lebour's record from memory, see p. 290.

A review of Table I shows that where *E. esculentus* is easily obtained at low water on ordinary spring tides, localities 4 and 5, the time of low water falls in the early morning and late afternoon. If, however, Kyle Akin proves to be a locality where the sea-urchins are also normally easily obtained, it is seen that the time of low water in this locality is, on the contrary, in the hottest part of the day, and approaching the coldest part of the night. In locality 3, where *E. esculentus* occurs low in the zone, the time of low water is very nearly midday and midnight, while in locality 2, where sea-urchins only occur at dead low-water springs, and not in abundance, the time of low-water springs is just after midday and midnight. At Plymouth, and in North Cornwall, where *E. esculentus* is absent, low-water falls about 1.15 in the night time and 1.15 in the early afternoon.

There is thus a broad correlation at the lower latitudes between the occurrence of low-water spring tides in the morning and evening and the presence of *E. esculentus* on the shore at the level of low-water ordinary spring tides; and the absence of the sea-urchin—or its occurrence at a very low level on the foreshore—when low-water spring tides fall about midday and midnight. It would appear that at the lower latitudes at Mousehole and Robin Hood's Bay tidal and climatic conditions are just sufficiently favourable to permit the existence of *E. esculentus* at extreme low-water mark, but that at the higher latitude at Kyle Akin conditions may be sufficiently favourable to permit the existence of *E. esculentus* when low tides occur at the hottest part of the day.

NATURE AND EXPOSURE OF THE FORESHORE.

It is a fundamental fact that life on a rocky foreshore is inversely proportional in amount to the degree of exposure of the foreshore to wave-action. Very few freely moving animals can live above low-water mark on a wave-swept beach unless protection can be found under stones or in crevices. Thus even *P. miliaris* is absent or rare on heavily swept beaches where crevices and stones are rare, and it may be assumed that *E. esculentus* would require greater protection on the shore than its smaller ally. To avoid exposure to air and sunshine, the smaller sea-urchin, *P. miliaris*, hides at the time of low water under stones and in remote crevices, but the larger size of *E. esculentus* would only permit this habit on foreshores where large rocks occur, or where gulleys are common. *P. miliaris* has also the habit of covering itself with shells, stones or bits of seaweed, and such a habit undoubtedly gives additional protection from desiccation and extremes of temperature during the time of low water. *E. esculentus* does not adopt this habit in 5 to 10 fathoms of water, and it would be interesting to know whether such a habit is acquired anywhere on the foreshore.

There can be no doubt, therefore, that the large size of *E. esculentus* is an important factor in rendering this species unsuitable for life above low-water mark on any foreshore, and particularly on those where very high or very low temperatures prevail at low water, and where protection is obtained with difficulty from exposure to air, sunshine, and direct wave-action. Most of the localities given in Table I, page 292, are protected in some measure from exposure to heavy seas. Robin Hood's Bay, Cullercoats, and some places on the north Cornish coast, are relatively exposed, but on the exposed coast at Robin Hood's Bay it would appear that the existence of gulleys at about low-water level afford a sufficient measure of protection from wave-action. It is again of interest to note, however, that sheltered localities in the Plymouth district yield no populations of *E. esculentus*.

HYDROGRAPHIC AND OTHER FACTORS.

If the shoreward movement of *E. esculentus* is a spawning migration, as suggested by Elmhirst (2), it is probable that the animals are seeking a region of higher temperatures, such as exists on the shore in spring and summer (12). In this event the need for migration may vary in different localities. It is possible, for instance, that sufficiently high temperatures for spawning may occur during a great part of the year below low water in the South of England (as, in fact, is the case), whereas in higher latitudes the required degree of temperature may not occur off-shore until summertime, but may easily occur over a greater range of—or earlier in—the year in an inshore habitat.

E. esculentus spawns naturally at Plymouth during the period April–June (ripe individuals regularly give successful fertilisations in March in the Plymouth Easter Class), and April–June is the period Elmhirst gives (*loc. cit.*) for the inshore spawning migration at Millport. The sea-temperature off Plymouth rises in this period from about 9.0° to about 13° C. (12, Table I), and at Millport, in shallow water, from about 45° to 52° F. (7.22 to 11.11° C.) (13). Thus, if a temperature of 10° to 11° C. be required for spawning, it is clear that *E. esculentus* would need to migrate shorewards at Millport in order to obtain the required temperature in spring or early summer. On the exposed foreshore the Echini would be subject to sea and air-temperatures, which in the daytime in spring and early summer would be higher on the average than those of the sea off-shore (12, p. 249, with bibliography).

These considerations tend to confirm the observation by Elmhirst that the appearance of numbers of *E. esculentus* on the foreshore at Millport is a result of a spawning migration, on the assumption that the optimum temperature for spawning is a specific character. As a consequence it would appear that in low latitudes (with higher mean sea-temperatures)

there is less reason than in higher ones for *E. esculentus* to migrate to the foreshore for the purpose of spawning.

The general distribution of *E. esculentus* indicates that at moderate depths (15–30 fathoms) this animal does not frequent fine sandy grounds (14). Thus the occurrence of a belt of sandy ground between a rocky foreshore and rough ground off-shore might act as a deterrent to migrating *E. esculentus*, for this large short-spined Echinoid would no doubt be subject to the danger of rolling by wave-action when passing over sandy ground in shallow water.

CONCLUSIONS.

It would appear that the presence of *E. esculentus* on a foreshore is dependent upon the following combination of factors:—

1. The necessity for finding a spawning-ground where temperature (or correlated factors) is greater (or have higher value) than in the deeper off-shore water at a certain season of the year, which is usually the hydrographic spring.
2. A suitable rocky ground protected from excessive wave-action.
3. A foreshore habitat where exposure at low spring tides does not occur in the hottest part of the day at relatively low latitudes (e.g. 50–51°), and
4. An approach to the shore from off-shore without an intervening belt of fine sand.

There can be little doubt that the incidence of the mean time of day at which high- and low-water spring tides occur has an important bearing on the constitution, distribution, and abundance of the fauna and flora in any particular locality. Therefore the absence of *E. esculentus* from the protected foreshores in the neighbourhood of Plymouth would appear to be due primarily to the absence of any necessity for a spawning migration shorewards at this latitude; and secondarily to the fact that low-water spring tides occur in this locality round about the hottest part of the day and near the coldest part of the night, thus rendering the region at low-water unsuitable for this large Echinoid.

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