A Comparison of the Biology of *Echinus esculentus* in different Habitats. Part III.

By

Hilary B. Moore, Ph.D.,

Marine Biological Laboratory, Plymouth.

With 3 Figures in the Text.

General.

In an earlier paper (Moore, 1934), an account was given of the season of spawning and the seasonal changes in the gonad volume of urchins from various depths in the Isle of Man. In order to compare these with urchins from a more southerly locality, monthly samples were taken in 1934–5 from 2 miles N. to N.N.E. of the Eddystone, in 27–28 fathoms, and in 1935–6 from 2½–3 miles S. to S.S.W. of Revelstoke Point in 17–22 fathoms. The samples consisted of about fifty urchins each time, and the gonads of these were examined by smears in the usual way, their condition being recorded as the percentage of each sex which were respectively unripe, ripe, spawning or spent. The gonad volumes were expressed as the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$ (Moore, 1934, p. 871). These results, together with temperature observations kindly supplied by Dr. H. W. Harvey, are shown in Fig. 1. Unfortunately no temperature observations are available for the actual grounds on which the samples were taken, but they may be assumed to be very similar to those at station L4 which is half-way between Rame Head and the Eddystone. At this station temperatures were available up to August 1935 only, so the observations for station E1, 10 miles SW. of the Eddystone, are also included. Although at this deeper station the temperature range at the bottom is less extreme than at L4, yet at the critical period of spawning there is little difference. An eleven years' mean temperature curve for E1 is also included from which it will be seen that the summer of 1934 was distinctly cold and the following winter rather warm, while the summer of 1935 was normal, and the following winter rather cold. Whether there is any connexion between these temperature differences and the observed differences in the gonads in the different years is doubtful.

Seasonal Gonad Changes at Plymouth.

As has already been stated, the degree of ripeness of the males is less easily defined with accuracy than that of the females. Considering the latter, therefore, it will be seen that practically no ripe females were found before the beginning of February in either year, and few before the beginning of March. Spawning commenced about the end of March in 1935 and the end of February in 1936, the time corresponding approximately with the time of lowest sea temperature. The date on which 50% of the urchins were spent, taking both sexes together, was May 3rd in 1935 and April 25th in 1936, corresponding to sea temperatures of about 9·7 and 9·2° C. The temperatures at a corresponding period in spawning in the Isle of Man were 7·0° C. in 1931 and 7·8° C. in 1932. Spawning takes place, therefore, at a higher temperature at Plymouth than in the more northerly locality, and falls at about the middle of the range of 4–16° C. given by Runnström (1927) for the normal development of *Echinus esculentus* larvæ.

The growth of the gonads at Port Erin was found to be very different on the two grounds "Breakwater" and "Breast." On the latter, at a depth of 17–20 fathoms, the gonads never filled up to a value of more than 0·4 for the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$. The gonads gradually regained size after spawning until they were at a maximum size about August, after which they remained constant until the winter and then shrank considerably, only regaining their full volume immediately before spawning. This winter shrinkage of the gonads was definitely not a second spawning, and seems more likely to have been associated with lack of food at that time. On the "Breakwater" ground, where the urchins live about low-water mark, the gonads filled up to a much greater size, with a ratio of nearly 2·0 compared with 0·4 on the Breast ground, and with no winter drop in volume. It seems probable that the greater abundance of food is here the controlling factor.

The Plymouth material appears to be of the Breast type, as might be expected from the depth from which it was taken. The gonad volume ratio was at a value of between 0·4 and 0·5 in the summer of 1934, but dropped somewhat in the winter, rising again only immediately before spawning in 1935. At their maximum the females attained a value of 0·7, being considerably bigger than the males of a corresponding test size, a phenomenon which was observed on both grounds at Port Erin also. After spawning in 1935 the gonads filled up slightly, but never reached nearly so great a size as they did the previous year, and the spawning in 1936 was extremely poor, the drop in volume of the female gonads being from 0·7 to 0·2 in 1935 and only from 0·3 to 0·2 in 1936.

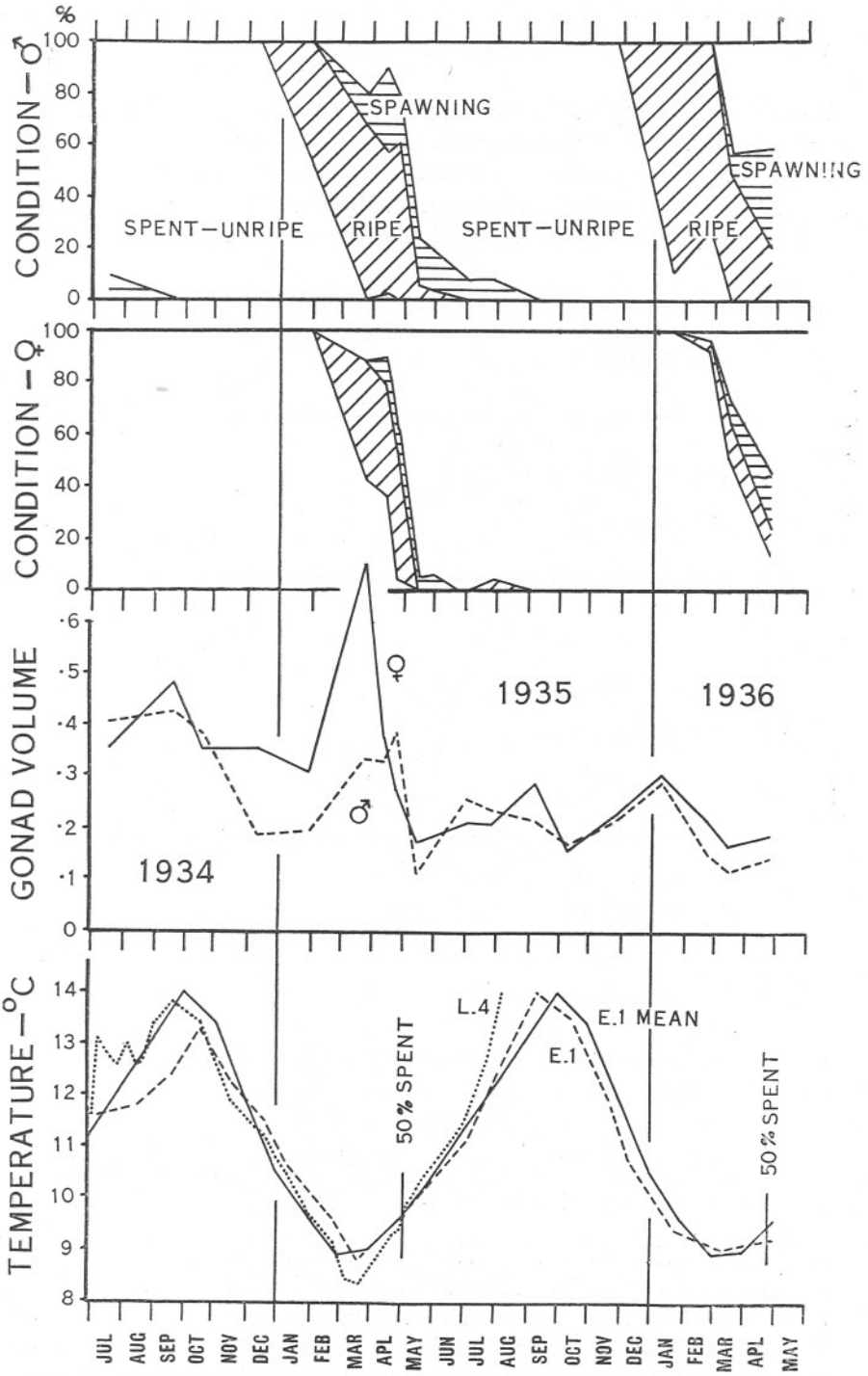

FIG. 1.—Seasonal changes in the conditions of male and female urchins from Plymouth and of their gonad volumes as indicated by the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$. Temperatures at the bottom at Stations L4 and E1 during the period under observation, and an eleven years' mean temperature curve for E1.

The difference between the two seasons may be due to the shift in the grounds from which the urchins were taken, but the two grounds are very similar in character and it seems likely that the differences were, in part at any rate, due to 1936 having been an abnormal year.

There appears to be a definite increase in the size of urchins southwards,

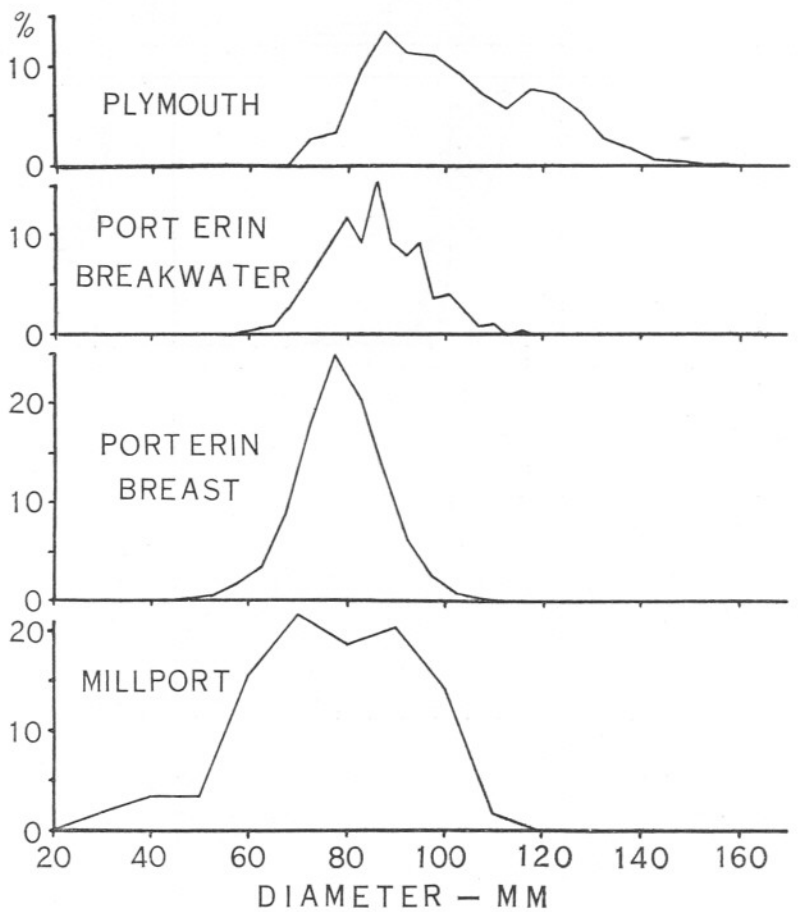

FIG. 2.—Mean size distribution curves for all samples examined from Plymouth, Port Erin (Breakwater and Breast) and Millport, showing greater size of urchins in the south (see text below).

as indicated in Fig. 2. It should be noted that in this figure the samples from Port Erin (Breast) and Plymouth are deficient in the smaller sizes, the curves having been abstracted from the records of gonad examinations for which the smaller sizes were rejected. Those for Port Erin (Breakwater) and for Millport are, however, complete. At Millport and Port Erin, specimens were never recorded over 121 mm. in breadth, corresponding

to a volume of about 800 c.c. (external), whereas urchins were frequently taken at Plymouth with a diameter of 150 mm., corresponding to a volume of about 1800 c.c., and still larger specimens have been recorded.

Deposition of Pigment.

In colour also the Plymouth urchins resemble most closely the Breast urchins, the violet colouration of the test which was so frequent on the Breakwater, but rare on the Breast, having never been noted at Plymouth. Violet colouration of the spines is, however, frequently seen. The violet pigment is probably derived from some food, possibly algal, which is obtained more readily in the alga-covered littoral and sub-littoral zone than in deeper water. Griffiths (1900) has described a violet pigment with lipochrome properties from the integument of *Echinus esculentus*, while MacMunn (1885, 1889) has given the name Echinochrome to a reddish pigment occurring in the elaeocytes in the perivisceral fluid of *Strongylocentrotus lividus*, *Echinocardium cordatum* and *Echinus esculentus*. Later workers have studied a similar pigment found in the test, and McLendon (1912) and Cannan (1927) have described the same or a similar pigment from Arbacia at Woods Hole.

Dr. K. G. Stern (personal communication) when working on *Echinus esculentus* at Plymouth, found that this red pigment, which he calls Echinorubin, and which was similar to, although apparently not identical with that of McLendon and Cannan, was present in the elaeocytes of the body fluid and also in the test, but was present in far the greatest quantities in the walls of the intestine. The pigment appears to be absorbed into the intestine with the food, transferred to the elaeocytes in the body fluid, and finally excreted into the outer surface of the shell where it is deposited. I am indebted to Dr. Stern for permission to publish these notes on the amounts of pigment found by him in the intestines. The extraction with solvents of a large number of the latter, sent to him at intervals throughout the year, proved that the red pigment which was so abundant in the intestines in the summer and autumn, was absent from them in the winter and spring, its place being apparently taken by a brown oily substance. Table I shows the yields of echinorubin obtained by him from the intestines of the Plymouth urchins, but it must be realized that these are only notes on the yields obtained in the preparation of the crystalline substance, and not in any way quantitative analyses.

The tests of urchins from both grounds at Port Erin and also those from Millport showed the deposition of the red pigment, and of the violet one when present, in the period between about April and December (Moore, 1935). As, however, shell growth was confined to the period between November to January and the end of March, there being no further growth

during the summer months, and since pigment laid down in the surface of the plates will remain at the surface until overlayed by a layer of non-pigmented shell at the next period of shell growth, there can be no evidence of the precise time at which the pigment is deposited beyond the fact that this occurs between the limits of about April and December. Since the pigment is now shown to be the same as that which is present in large quantities in the intestine during summer and autumn, it seems probable that the annual summer rings of pigment in the test represent periods of

TABLE I.

Date.	No. of urchins.	Yield of crude echinorubin crystals.	Notes.
1934.			
Sept.–	ca. 50	ca. 80 mg.	together yielding 50 mg. of recrystallized
Oct. 20	ca. 50	ca. 40 mg.	echinorubin.
Dec. 14	45	30 mg.	
1935.			
Jan. 11	ca. 50	35 mg.	
Feb. 2	ca. 50	trace only	extract yielded a brown oily substance.
April 18	?	trace only	
May 15	65	some	
May 23	18	none	

feeding on some particular diet, or quite possibly the main periods in which the urchin is feeding at all. On the other hand, the females from the Breakwater at Port Erin continued to show gonad growth right up to the time of commencement of spawning, and on all grounds where there is a drop in gonad volume in winter there is a corresponding rise just before spawning, presumably correlated with an increased supply of food at that time. It is noteworthy, however, that on the Breakwater ground, where algal food is abundant throughout the entire year, and where there is no winter drop in gonad volume, the pigment rings were sufficiently clear to be counted in only 46% of the urchins as compared with 79% on the Chickens ground farther offshore. And with regard to the source of the pigment, Awerinzew (1911) has shown a close correlation between algal and urchin pigments in the case of *Strongylocentrotus draebachiensis*. This species varies in colour from yellowish green to deep reddish purple, and it was found that urchins of the former colour occurred almost invariably on a substratum of sandy gravel while the reddish purple ones were found on the red calcareous alga Lithothamnion. Finally the reddish purple urchins soon began to lose their colour when taken into the aquarium. So it is very probable that here also the urchin is obtaining its pigment from the food that it eats.

Deutler (1926) has demonstrated the presence of similar pigment bands

in the plates of the urchin *Colobocentrotus atratus*. From these bands, he states, the age can be determined; and he shows that they are seen clearly in those echinoderms which feed at any rate to some extent on algæ, and which migrate into the littoral zone. He quotes a number of such urchins which live in the littoral zone, and some of which migrate in and out of it annually, and he suggests that the zonation of the pigment in their plates is due to a seasonal feeding rhythm which makes them deposit pigment in the summer at the time when they are feeding most.

If a large seasonal migration into and out of the algal region of the shore took place in *Echinus esculentus* this would necessitate such changes of diet as might well produce the observed seasonal differences in pigment, and some such migration has been suggested both at Millport (Elmhirst, 1922) and at Port Erin (Stott, 1931). The former, however, states that the migration is only from the actual intertidal zone down to a depth of one to two fathoms (where algæ are still very abundant), and so far as Port Erin is concerned I have never been able to satisfy myself that such a migration occurs at all. Certainly there is no such migration of the deep-water Chickens urchins which live at a depth of 35 fathoms and yet show clearly distinguished pigment zones. It must, therefore, be assumed that some seasonal rhythm of feeding occurs in both the littoral and the deeper-water urchins, and that the main difference between the two lies firstly in the greater food supply available in the littoral zone, resulting in larger gonads and absence of a winter drop in gonad volume, and secondly in a difference in the nature of the food as reflected in the greater frequency of occurrence of the violet pigment in the tests of the littoral urchins.

Outline of Seasonal Changes.

Reid (1935) has recently brought together what is known of the relation of *E. esculentus* to its external environment, and in Fig. 3 an attempt is made to summarize the existing knowledge of its internal changes, e.g. growth, spawning, etc., and the seasons at which they occur. Since the information available is incomplete, and of necessity drawn from different localities, the results must be taken as a generalization only, from which any individual locality may diverge considerably.

At the beginning of the year the shell starts to grow, and continues to do so up to some time between April and June, the exact time varying with locality and year. At the same time, on the offshore grounds, feeding appears to have slowed down, and the gonad which is the main reserve of food material has been shrinking since October–November. It is replenished, however, in February and March, and about March, when the sea temperature is at its minimum, spawning commences with concurrent shrinking of the gonad. Spawning continues until about May, by which

time the gonad is beginning to fill up again, and this it continues to do until about August. In the case of the females only from the Breakwater, gonad growth continued right up to the commencement of spawning the following year. Stott (1931) has shown that in the period between December and the end of March, the percentage of glycogen in the gonad

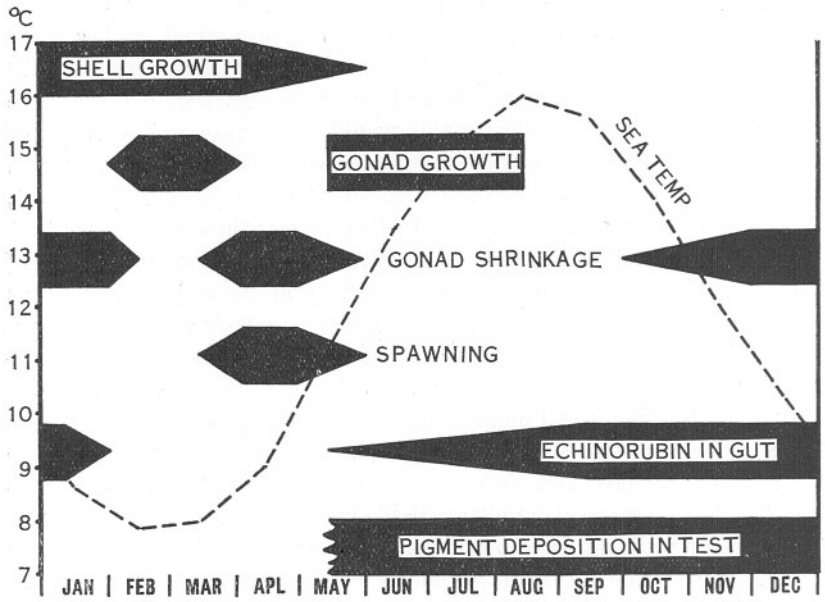

FIG. 3.—Generalized diagram of the seasons of shell growth, gonad growth, etc., in *Echinus esculentus*, with a sea temperature curve (for Plymouth).

is dropping, possibly being transformed into some other form of carbohydrate. The time of pigment deposition in the shell is not clearly defined but almost certainly follows closely the time when there is abundant pigment in the walls of the intestine, that is from about May to January, and this probably corresponds with the main feeding period. In August–September the sea temperature is at its maximum, and it is about this time that shrinkage of the gonads of the offshore urchins commences.

SUMMARY.

1. Gonad examinations were made on monthly samples of *Echinus esculentus* from Plymouth in 1934, 1935, and 1936.

2. Spawning is from February–March to May, 50% spawning occurring at a temperature of 9·2–9·7° C. compared with 7·0–7·8° C. in the Isle of Man. There was a winter drop in gonad volume one year, but not the other.

3. The nature, distribution and source of the pigments in the shell are discussed, and it is shown that pigment is found in quantity in the intestine only in the summer and autumn.

4. The known facts with regard to the seasons of growth, spawning, etc., are brought together into a generalized diagram.

REFERENCES.

AWERINZEW, S. 1911. Ueber die Pigmente von *Strongylocentrotus drœbachiensis*. Arch. de Zool. Exp. et Gén., 5e Sér., T. VIII, No. 1, pp. i–viii.

CANNAN, R. K. 1927. Echinochrome. Biochem. Journ., Vol. XXI, No. 1, pp. 184–189.

DEUTLER, F. 1926. Über das Wachstum des Seeigelskeletts. Zool. Jahrb. Abt. f. Anat. u. Ontog. der Tiere., Bd. 48, Heft 2, pp. 119–200.

ELMHIRST, R. 1922. Habits of *Echinus esculentus*. Nature, Vol. CX, p. 667.

GRIFFITHS, A. B. 1900. Sur la Matière colorante d'*Echinus esculentus*. C. R. Acad. Sci. Paris, T. CXXXI, pp. 421–422.

MACMUNN, C. A. 1885. On the Chromatology of the Blood of some Invertebrates. Quart. Journ. Mic. Sci., Vol. XXV, pp. 469–490.

—— 1889. Contributions to Animal Chromatology, *ibid.*, Vol. XXX, pp. 51–96.

MCLENDON, J. F. 1912. Echinochrome, a red Substance in Sea Urchins. Journ. Biol. Chem., Vol. XI, pp. 435–441.

MOORE, H. B. 1934. A Comparison of the Biology of *Echinus esculentus* in different Habitats. Part I. Journ. Mar. Biol. Assoc., N.S., Vol. XIX, No. 2, pp. 869–885.

—— 1935. Idem. Part II. *Ibid.*, Vol. XX, No. 1, pp. 109–128.

REID, D. M. 1935. The Range of the Sea-urchin *Echinus esculentus*. Journ. Animal Ecol., Vol. IV, pp. 7–16.

RUNNSTRÖM, S. 1927. Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. Bergens Mus. Äarbok, Naturvid. rekke, Nr. 2, pp. 1–67.

STOTT, F. C. 1931. The Spawning of *Echinus esculentus* and some Changes in Gonad Composition. Journ. Exp. Biol., Vol. VIII, No. 2, pp. 133–150.