A Comparison of the Biology of *Echinus esculentus* in Different Habitats.

Part I.

By

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With 5 Figures in the Text.

THE material for this study of racial differences in *Echinus esculentus* was obtained from three grounds in the neighbourhood of Port Erin, Isle of Man. The three grounds differed widely in nature, and hence the means of capture, and the ease of obtaining adequate samples was different for each ground. The first locality, designated " Breakwater," is on the lee side of a ruined breakwater in the mouth of Port Erin Bay, entirely submerged at high tides, but accessible by boat at low water. The Breakwater stands on a bottom of sand and shell, in a depth of about five fathoms. It is composed of loose concrete blocks, largely overgrown with *Balanus balanoides* and *Spirorbis borealis*. It is too exposed to support a very large Fucoid vegetation, but in the lower zones there is a very heavy growth of *Laminaria cloustoni*, *L. digitata*, and *Saccorhiza polyschides* with an undergrowth of *Gigartina stellata*. The urchins were collected with a long-handled net, and thus include some individuals which were actually exposed to the air, and others from a depth down to about one fathom at low water. In this particular locality urchins are extraordinarily abundant, and large numbers are exposed at low water of spring tides.

The second ground, the " Breast," lies about a mile off Port Erin, and in a depth of 17–20 fathoms (Fig. 1). The bottom is sand and shell, with a typical fauna (**4**, p. 36, Pl. I). Urchins were obtained from it with a small otter trawl. The third ground—" Chickens "—lies about four miles west of the Chickens rock in 37 fathoms, on a bottom of rather muddy sand mingled with boulders. The urchins are obtained from this ground in traps set by the fishermen to catch " Buckies " (*Buccinum undatum*). The urchins obtained from these creels are of small size, and it has been suggested that this is due to a selective action in the catching power of the creels. But this is negatived by the fact that similar creels, similarly baited, and set on inshore grounds, in a depth of about five fathoms,

habitually take large numbers of large urchins. As only twelve creels were in use, and the supply from them was dependent on visits from fishermen, the number of urchins from this ground was limited, and the data obtained from them are in general not as full as those from the other two grounds. The present paper is concerned more particularly

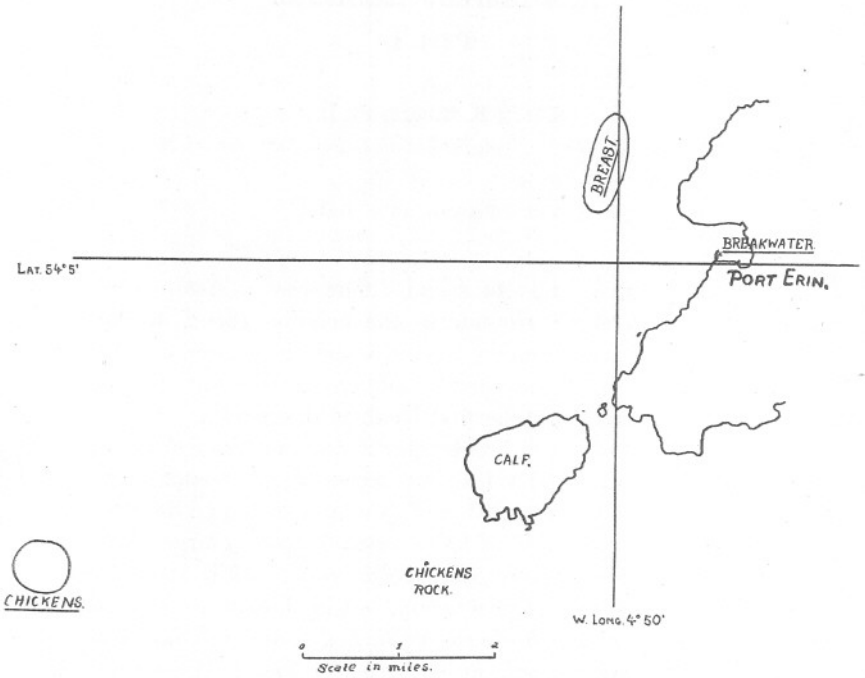

FIG. 1.—Map of the south end of the Isle of Man showing the positions of the grounds from which the three types of urchins were obtained—Breakwater (Littoral), Breast (17–20 fathoms), and Chickens (37 fathoms).

with the first two grounds, and it is proposed to discuss in another paper the special significance of the " Chickens " type of urchins.

METHODS.

Wherever possible, samples of at least fifty individuals were taken, but as this was not always possible, the numbers used are in every case indicated in the tables. In a few cases, samples taken from the same ground within a few days have been grouped in order to obtain an adequate sample. With regard to the adequacy of the sample, those from the breakwater were always from exactly the same locality, and the samples are fairly regular in their constitution. Those from the Breast and Chickens are, on the other hand, liable, from the method of their

collection, to come from slightly varying localities, and the resulting irregularity is apparently reflected in the less regular graphs obtained from these grounds.

The following measurements were taken, though not all of them were obtained from every specimen : *Test diameter*, taken with pointed-ended calipers between the spines. *Test height*, measured in the same way. *Test volume* (TV), obtained by immersion of the whole animal in a vessel full of sea-water, and fitted with an overflow, so that the displacement could be measured. *Gonad volume* (GV), estimated by immersing the whole gonad, after removing it from the animal, in a measuring cylinder containing a known amount of water. A series of measurements of *Shell thickness*, in conjunction with certain other factors, was made on a separate series of specimens from each ground. The measurement was made under a microscope, fitted with a micrometer eyepiece, on the ground edge of the shell, the latter having been cut at mid-height, at the suture of the inter-ambulacral plates. These shell thicknesses will be discussed in more detail in a future paper.

Ripeness was estimated by examination under a microscope of a pipette sample taken from the gonad, and smeared on a slide. The criterion of ripeness varied slightly in the two sexes. Since the male products are mostly ripe by the time they are shed into the cavity of the gonad follicle, the smear would not normally show many spermatogenesis stages, even in an unripe individual, although these would be present in the follicle wall. The presence of a considerable number of ripe and active sperm in the cavity of the follicle has been taken as the criterion of the ripeness of the male, but this does not mean that many more sperm may not be in the process of ripening. In the case of ovaries if unripe ova are present in the follicle at all, these will be found in the smear, along with any ripe ova which are present. In the case of females ripeness was recorded only when more than about 95% of the ova were actually ripe. Although this difference of criterion between the two sexes will in part account for the apparent earlier ripening of the males, it does not seem to do so entirely, and it must be remembered that the males so recorded as ripe were at least capable of yielding considerable quantities of ripe sperm.

Physical Conditions on the Grounds.

A general description of the nature of the grounds has already been given. The sea temperatures for Port Erin Bay, and hence for the Breakwater specimens, are discussed later. The temperatures on the Breast are less extreme than those in the shallow waters of the Bay, and further, the intertidal specimens will, if above low water, be exposed to extremes of air temperature from which those living below low water are

protected. Not much is known of other conditions on the grounds beyond the obvious fact that there is much more light on the Breakwater ground than on either of the other two. How this factor may affect the urchins is not known. The Breakwater is very much richer in food than either of the other two grounds, and examination of the urchin gut contents shows that those from the Breakwater are feeding largely on

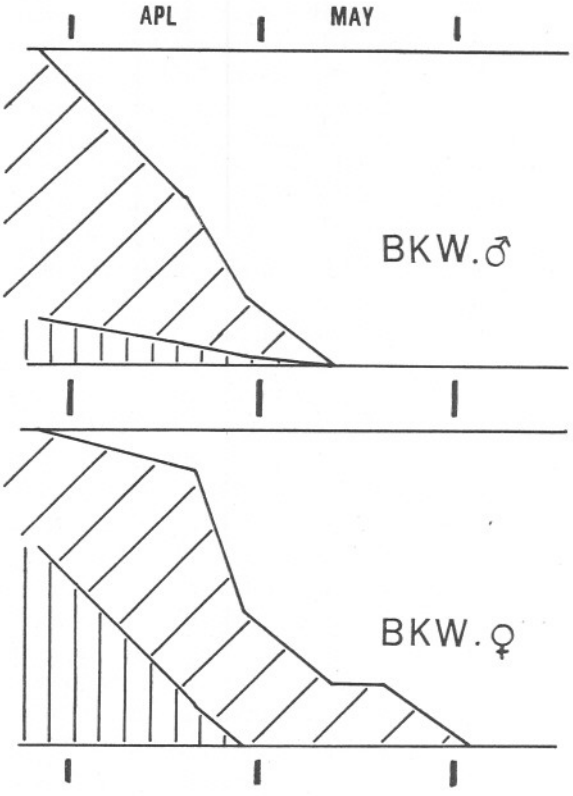

FIG. 2.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the Breakwater in 1931. For details see Fig. 3.

Balanus and algæ, both of which are very abundant in this littoral zone. Algæ appear to form a big proportion of the diet, and the specimens from the two deeper water grounds will only be able to obtain an algal diet from such weeds as may drift out to sea and settle on their grounds. The bottom on the Chickens ground is probably rather muddy, and it is known that it is bordered on the seaward side by a region of deeper water and mud bottom on which Echinus could not thrive.

Ripening of the Gonads.

The available data on the condition of the gonads throughout the year are given in Tables III, IV, and V, and are also shown in Figures 2 and 3. The 1931 spawning was watched in detail on the Breakwater only, but that of 1932 was watched on all grounds. The gonad condition during the intervening period was watched on the Breakwater and Breast, but sufficient material was not available from the Chickens. It will be seen in the first place (Figs. 2 and 3) that on all grounds the males ripen before the females. The partial explanation of this has been mentioned already. On the Breakwater the males ripen during the summer, and are nearly all ripe by the autumn ; while fully ripe females do not begin to appear until February, and during the early part of the spawning time, spent females may be found alongside unripe individuals. On the Breast the males begin to ripen later, i.e. in October, and are nearly all ripe by the end of February, when the females commence to ripen. The data from the Chickens are few, but the gonad condition on that ground seems to follow a very similar course to that on the Breast.

Gonad Volumes.

In order to allow of the comparison of the sizes of gonads in animals of different ages, the gonad volume has been expressed in Figure 4 and Tables I and II as ten times the actual gonad volume, divided by the test volume $\left(\frac{10.GV}{TV}\right)$. The test volume has been chosen as a measure of size of animal in preference to test diameter, since the relative height may vary considerably both with increasing age, and among individuals of the same age from different grounds. At first the animals were divided into several size groups, and these considered separately, but it was found that there was no difference of relative gonad size according to the size of the animal, so all sizes were eventually grouped together, thus allowing larger samples, and more accurate results. In the same way there was found to be no difference in the time of spawning, according to the size of the individual, so in considering the time of spawning, all sizes have again been grouped together.

The great difference in size attained by the gonads on the Breakwater and on the Breast is most noticeable (Fig. 4), and is specially significant when it is remembered that the gonad is the only organ of the body in which the urchin is able to lay up a reserve of food material, and that the Breakwater affords the richest feeding-ground. That the whole of the food so stored is not required for spawning is indicated by the fact that the gonad volumes on the Breakwater do not ever fall as low as the

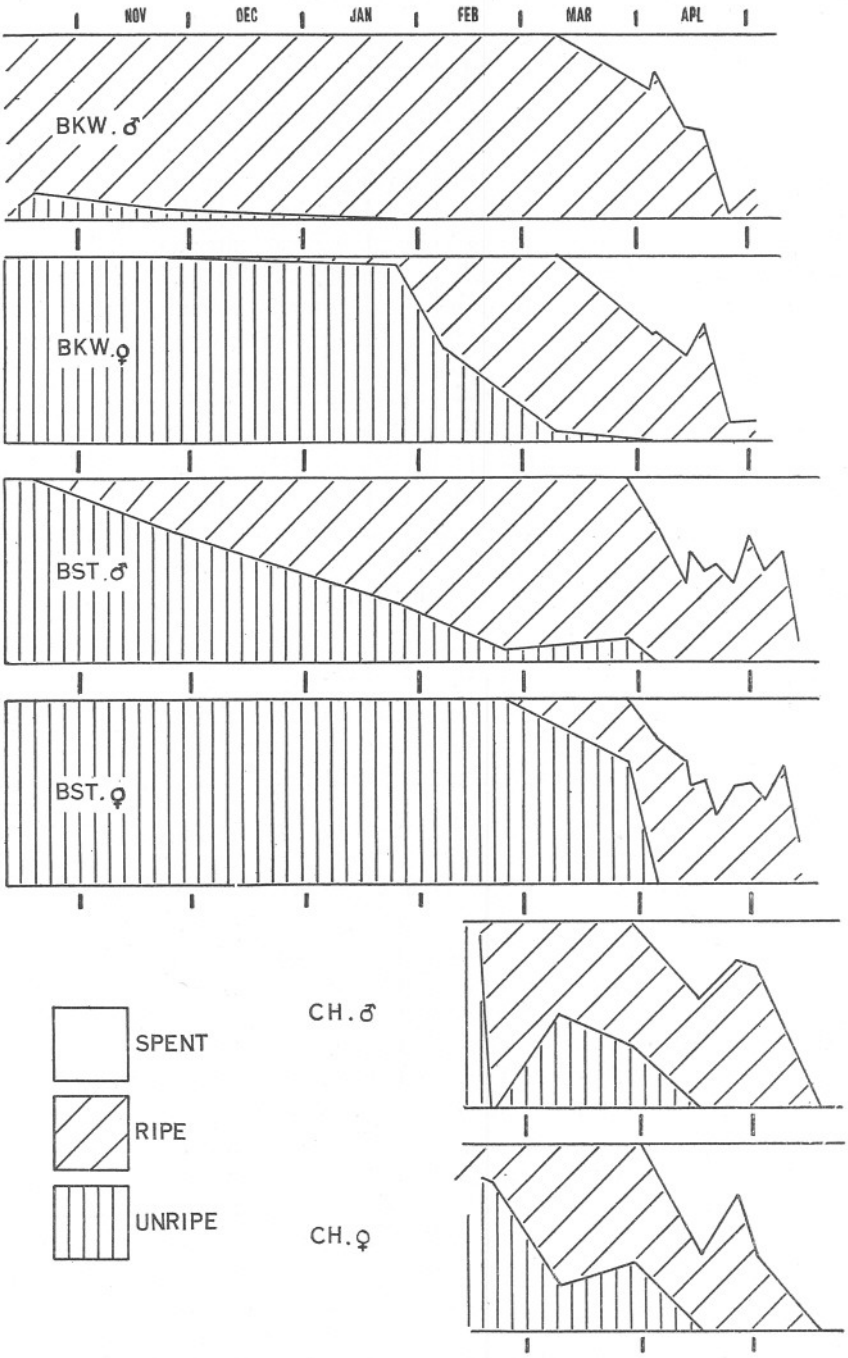

FIG. 3.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the three grounds in 1932—Breakwater (BKW), Breast (BST), and Chickens (CH).

maximum value obtained by the gonads in the Breast. This is true not only of the population as a whole, but also of individuals. The Breakwater urchins never become spent completely, while on the Breast the spent

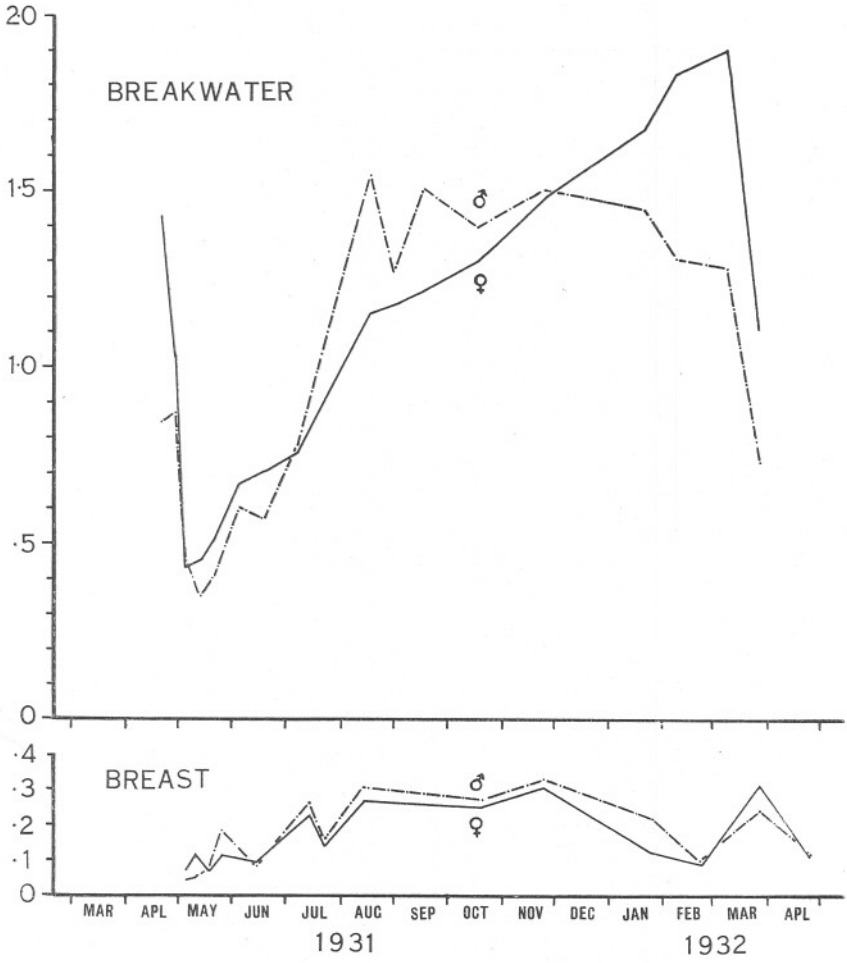

FIG. 4.—The seasonal variation in the volume of the gonads of urchins from the Breakwater and Breast grounds in 1931–32. The gonad volumes are expressed as ten times the actual gonad volume divided by the test volume of the animal.

gonad is reduced to a very small trace. At their maximum the Breast gonads attain a value of $\frac{10.GV}{TV}$ of only ca.0·4 while the values on the Breakwater rise as high as 2·0, and even higher in individuals.

On the Breakwater the males attain their maximum gonad volume

in August, and then remain more or less constant until spawning sets in. The females, on the other hand, increase rather more slowly, but their gonads continue to grow in volume right up to the time when spawning commences, and by then they are considerably larger than those of the males. On the Breast both sexes seem to run a more or less similar course, reaching their maximum about August, but the variation between successive samples somewhat masks the finer details of the process. The drop in the gonad volumes in both sexes on this ground in Jan.–Feb. may be due to inequalities of sampling, but may, on the other hand, have a real significance. But since the data are insufficient to decide either way, the point need not be discussed here, although it would be most interesting if it could be investigated further.

Stott (**3**) has described the changes in the percentage of glycogen, total carbohydrate, and total fats in the gonads of urchins from the Breakwater, during maturation and over the period of spawning. In the first place he finds no significant difference in the percentages of any of these between the two sexes, and as the various percentages vary during the year, they do so more or less similarly in both sexes. The percentage of total fats does not seem to alter much throughout the year, but the percentage of total glycogen in the gonad rises very sharply after spawning (his first post-spawning measurement is in June), and then drops steadily until spawning again occurs. There is a suggestion that this glycogen is being converted into some other form of carbohydrate, at any rate immediately prior to spawning. Now he shows that the percentage of glycogen in both ova and sperm is considerably less than it is in the whole gonad from which they were obtained. This fact, together with the sudden rise in the percentage of glycogen in the gonad when the ripe genital products have been shed, suggests that the food reserves are stored in the form of glycogen in the nutritive bodies in the gonad, and are transformed into other substances as they are absorbed into the ripening genital products. Further, his data with regard to the similarity of carbohydrate and fat percentages in the two sexes, in conjunction with the evidence of different behaviour in the rate of increase of size of gonad in the male and female (Fig. 4), suggests that there must be a marked difference in the feeding behaviour between the male and female, since the former produces fresh gonad very rapidly, and then remains little changed throughout the late summer, autumn, and winter, while the female is continuously increasing throughout this period. Finally the full female has a gonad about twenty per cent bigger than that of a full male.

Time of Spawning.

The only reliable data for 1931 are for the Breakwater, and these are shown in Figure 2. The results for all grounds for 1931 are shown

in Figure 3 and all are tabulated in Tables III, IV, and V. The 1932 spawning, at any rate on the Breakwater, took place between two and four weeks later than it did the preceding year, that is to say it took place in April–May in 1931 and in March–April in 1932. On the Breast and Chickens, spawning took place about a fortnight later in 1932 than on the Breakwater, and on all grounds the spawning period covered about two months. Whereas, however, the spawning of both sexes is more or less complete on both the deep water grounds, on the Breakwater relict sperm and ova are retained in considerable quantities in the gonads, and artificial fertilisations were readily made with them throughout the summer, and even as late as Christmas.

The Relation of Spawning to Temperature.

The later spawning of the Breakwater urchins in 1931 as compared with 1932 is associated with lower temperatures in the water of the bay in the year of later spawning (Fig. 5). The year's minimum temperature occurred in both 1931 and 1932 in the second week of March, and in both years spawning commenced within a few weeks of this date. In 1931 spawning commenced about the end of March, when the temperature in the bay was about 6·5° C., and in 1932 it commenced about the first week of March at a temperature of about 7·2° C. But, since the exact date of the commencement of spawning is difficult to determine accurately, it is preferable to compare the dates at which 50% of the community are spent. This took place in 1931 at a temperature of 7·0° C. and in 1932 at 7·8° C. No temperatures were recorded on the Breast in either of these years, but in 1933 the Breast temperatures at the spawning season were about 0·5° below the corresponding temperatures in Port Erin Bay. This would correspond with a lapse of about a fortnight before the Breast attained the temperature at which spawning set in on the Breakwater. Although this is only a rough approximation, it is in agreement with the lag of about a fortnight between the times of spawning on the Breakwater and Breast. In 1931 (Fig. 2) the urchins of both sexes ripened considerably later on the Breakwater than they did in 1932, and this also is perhaps associated with the lower temperatures in the winter of the former year.

Orton (**2**) records that urchins taken in from five to ten fathoms at Plymouth, spawned from April to June, when the temperature ranged from about 9·0° to 13·0° C. At Millport, in the Clyde, the spawning period given by Elmhirst (**1**) is from February to August, with a maximum in May. This corresponds with a temperature range there of about 7° to 13° C. with a maximum spawning at about 9·8° C. Our figures of 7° to 8° are therefore slightly lower than those for Millport, and

FIG. 5.—The relation of spawning (percentage of spent individuals—broken line) to temperature (whole line) on the Breakwater in 1931 and 1932. The position of 50% spawning is indicated by a vertical dotted line in each case.

definitely lower than those for Plymouth. Also the spawning time seems to be about a month earlier here than it is at either Plymouth or Millport. But in all three localities the commencement seems to follow fairly soon after the temperature first starts to rise, although the interval would seem to be least at Port Erin.

General Character of the Urchins from the Three Grounds.

The Breakwater urchins show a greater range of colours than those from deeper water. The Breakwater ones range from violet to rusty red, the colour being present throughout a fairly thick layer in the surface of the test. The Breast and Chickens practically never show a violet colouration except in the spines, the test colour varying between pale brown and reddish.

Shape is not a good criterion since it varies greatly with age ; a young specimen of 1 cm. diameter having a value of $\frac{\text{height}}{\text{diameter}}$ of 0·52 while one of 7 cm. diameter will be considerably taller with a value of about 0·7. But this varies on the different grounds. A small sample taken in about $3\frac{1}{2}$ fathoms at the Niarbyl, north of Port Erin, had a normal H/D value at 1 cm. diameter, but at 4 cm. it was 0·8. Specimens of the same size from the Breakwater were not nearly so tall. In fact these were the tallest specimens found here. There seems, further, to be a tendency for the largest specimens to flatten somewhat. The largest specimen taken by us on the Breakwater had a diameter of 12·1 cm., and an H/D of 0·63.

In shell thickness there is a regular difference between the Breakwater and the Chickens urchins at all sizes, the shell thickness for a Chickens urchin of 4 cm. diameter being 0·71 mm., while that of a Breakwater urchin of the same size is 0·96 mm. The Breast urchins are of a curious type, the young ones having a shell thickness typical of what a young Breakwater one would have were such ever found (see below), while the adults from the Breast have the typical thickness of the rarely found adult Chickens urchin. It is not intended to discuss in the present paper more than the fact that such a well defined difference does exist between the urchins from the three types of ground. Its significance will be dealt with in another paper.

Finally, the three grounds differ markedly in the size of the urchins which are found on them. On the Breakwater no very small specimens are taken, the smallest which I have seen being 2·5 cm. diameter, and even this was in 1933 when exceptionally small specimens were being taken there. Normally, urchins are hardly ever seen there with

a diameter of less than about 7 cm. The same may be said of the littoral specimens obtained at the Niarbyl and in the Calf Sound, at the former of which localities urchins are abundant between tide marks on a low spring tide, but in the Sound a few only are taken. On all these grounds it is normally only large specimens which are taken. Specimens up to 10 cm. in diameter are common on the Breakwater. The largest I have seen at Port Erin measured 12·1 cm. in diameter, and came from the Breakwater, but even larger ones have been recorded there.

On the Breast, on the other hand, all the smaller sizes are very abundant, and 8 cm. diameter is about the maximum size usually attained ; a few are taken up to 9 cm., but I have not seen any as large as 10 cm.

On the Chickens ground similarly, all the smaller sizes are abundant, but here the maximum size is even smaller, few over 4 cm. diameter being taken, and none over eight. In this case it is probably a case of the migration of the larger individuals off the ground, but the discussion of this probability is postponed until more data are available.

SUMMARY OF RESULTS FOR THE BREAKWATER AND BREAST.

There are two types of ground at Port Erin, differing widely in the general environmental conditions, and each with a characteristic type of urchin on it. The difference is sufficiently well marked for the local fishermen, who collect the urchins for sale to summer visitors, to distinguish them as different types. The littoral urchins from the Breakwater are larger and thicker shelled than those from the Breast. Their gonads reach a greater maximum size, and, in fact, never fall as low even as the maximum volume for the Breast urchin gonads. This difference is probably correlated with the much greater food supply on the Breakwater, since the gonad is the one organ of the body in which the animal can store reserve food material. Spawning commences in March or April and lasts for about two months, but is slightly earlier on the Breakwater than on the Breast. Ripening also takes place considerably earlier in both sexes on the littoral ground. Spawning seems to set in at a temperature of about 7° C., and the colder winter of 1931, compared with 1932, was associated with a later ripening and spawning in the former year. Similarly it is suggested that the slightly later spawning on the Breast than on the Breakwater is correlated with the slightly later rise in the temperature of the water on the deeper water ground in the spring.

I wish to express my indebtedness to Prof. J. H. Orton who is responsible for the inception of this work on Echinus, as well as for the

examination of a number of the earlier samples : I am also indebted to Miss E. C. Herdman for obtaining some of the trawled material for me, and to Mr. J. R. Bruce for examining certain samples in my absence.

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3. 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.

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TABLE I.

Seasonal Variation in the Gonad Volume on the Breakwater.

Date.	♂ 10 GV* / TV	Number of specimens.	♀ 10 GV / TV	Number of specimens
1931				
April 21	(0·84)	27	(1·43)	10
April 29	(0·87)	33	(1·03)	19
May 5	0·45	19	0·43	6
May 13	0·35	13	0·46	32
May 21	0·41	4	0·51	10
June 4	0·61	18	0·67	29
June 19	0·57	18	0·71	34
July 7	0·78	16	0·76	43
August 18	1·54	5	1·16	23
September 1	1·27	3	1·18	9
September 17	1·51	2	1·22	7
October 18	1·39	26	1·30	30
November 25	1·50	18	1·48	18
1932				
January 26	1·44	31	1·67	19
February 8	1·31	29	1·83	18
March 9	1·28	27	1·90	21
March 28	0·73	12	1·11	13

TABLE II.

Seasonal Variation in Gonad Volume on the Breast.

Date.	♂ 10 GV* / TV	Number of specimens.	♀ 10 GV / TV	Number of specimens.
1931				
April 28	(·362)	19	(·218)	17
May 5	·046	16	·072	9
May 11	·062	15	·117	10
May 18	·079	14	·073	6
May 26	·186	18	·118	28
June 16	·089	33	·099	44
July 16	·264	8	·226	12
July 22	·158	51	·143	35
August 15	·310	37	·270	45
October 20	·272	22	·263	16
November 25	·332	22	·312	36
1932				
January 26	·224	23	·125	25
February 23	·112	17	·095	7
March 28	·242	23	·316	27
April 26	·121	29	·118	20

* The gonad volume is expressed as ten times the gonad volume divided by the test volume (external).

TABLE III.

Seasonal Variation in Gonad Condition on the Breakwater.

Date.	Percentages. ♂ Unripe.	♂ Ripe.	♂ Spent.	♀ Unripe.	♀ Ripe.	♀ Spent	Numbers examined. ♂	♀	Percentage of total spent.
1931									
March 27	15·7	84·3	–	62·8	37·2	–	51	51	0
April 21	7·7	46·2	46·2	12·5	75·1	12·5	26	8	38·2
April 29	3·1	18·7	78·3	–	42·1	57·9	32	19	70·6
May 5	–	5·3	94·7	–	–	100	19	6	96·0
May 13	–	–	100	–	20	80	9	10	100
May 21	–	–	100	–	20	80	8	5	
June 4	–	–	100	–	–	100	18	29	
June 19	–	–	100	–	–	100	17	33	
July 7	–	–	100	–	–	100	16	43	
October 16	8·4	91·6	–	100	–	–	12	16	
October 20	14·3	85·7	–	100	–	–	14	12	
November 25	5·6	94·4	–	100	–	–	18	18	
1932									
January 26	–	100	–	94·7	5·3	–	30	19	
February 8	–	100	–	50	50	–	28	24	
March 9	–	100	–	4·8	95·2	–	29	21	0
April 4	–	70	30	–	57	43	30	28	36·2
April 5	–	79	21	–	58	42	28	24	30·8
April 13	–	50	50	–	46	54	8	13	52·3
April 18	–	38	62	–	63	37	26	24	50·0
April 25	–	4	97	–	10	90	33	30	93·6
May 2	–	16	84	–	11	79	18	19	81·1

TABLE IV.

Seasonal Variation in Gonad Condition on the Breast.

Date.	Percentages. ♂ Unripe.	♂ Ripe.	♂ Spent.	♀ Unripe.	♀ Ripe.	♀ Spent.	Numbers examined. ♂	♀
1931								
April 28	–	–	100	–	–	100	17	19
May 5	–	–	100	–	–	100	43	39
May 10	–	–	100	–	–	100	15	10
May 26	–	–	100	–	–	100	18	27
June 16	–	–	100	–	–	100	28	32
October 20	100	–	–	100	–	–	22	16
November 27	71·5	28·5	–	100	–	–	7	18
1932								
January 26	33·3	66·6	–	100	–	–	21	26
February 24	7·2	92·8	–	100	–	–	14	7
March 28	13·6	86·4	–	66·6	33·3	–	22	27
April 5	–	73	27	–	79	21	33	28
April 13	–	43	57	–	67	33	30	20
April 14	–	60	40	–	54	46	26	25
April 18	–	50	50	–	57	43	16	21
April 21	–	54	46	–	38	62	24	26
April 26	–	42	58	–	54	46	24	33
April 30	–	69	31	–	55	45	29	27
May 4	–	50	50	–	46	54	24	24
May 9	–	60	40	–	64	36	15	31
May 13	–	8	92	–	23	77	25	26

TABLE V.

Seasonal Variation in Gonad Condition on the Chickens.

Date.	Percentages. ♂ Unripe.	♂ Ripe.	♂ Spent.	♀ Unripe.	♀ Ripe.	♀ Spent.	Numbers examined. ♂	Numbers examined. ♀
1931								
May 6	–	–	100	–	66·6	33·3	2	3
May 21	–	42·8	57·2	–	20	80	14	10
May 28	–	60	40	–	–	100	5	10
June 13	–	5	95	–	–	100	20	33
June 25	–	–	100	–	–	100	1	2
1932								
February 17	92·8	7·2	–	82·4	17·6	–	14	17
February 20	–	100	–	80	20	–	3	10
March 9	50	50	–	25	75	–	6	4
March 29	33·3	66·6	–	37·4	62·6	–	12	11
April 16	–	58·7	41·3	–	41·6	58·4	17	12
April 26	–	78·7	21·3	–	73·5	26·5	14	15
May 1	–	75	25	–	40	60	4	5
May 18	–	–	100	–	–	100	12	3

TABLE VI.

Sea Temperatures in Port Erin Bay.

Taken at 9 a.m., being the average temperatures for the weeks ending on the dates given.

1931.		1932.	
February 7	7·3° C.	February 6	8·9° C.
14	7·5	13	8·0
21	6·5	20	7·5
28	7·1	27	7·8
March 7	6·1	March 5	7·3
14	5·5	12	7·1
21	5·9	19	7·5
28	6·5	26	7·8
April 4	5·9	April 2	8·2
11	6·7	9	8·0
18	7·3	16	7·8
25	6·9	23	8·0
		30	8·3
May 2	7·5		
9	7·8	May 7	8·4
16	8·3	14	8·8
23	8·6	21	9·2
30	9·3	28	9·8

ECHINUS ESCULENTUS.

SUMMARY OF GONAD CONDITIONS.

1931.	*BREAKWATER.*	*BREAST.*
	April. Varying from half-full to full. Mostly ripe. Only about 10% unripe. A few spent.	Both sexes either spending or spent. Volumes at a minimum by the end of the month.
	May. None unripe, but rather a mixed sample as to the percentage of spents. Towards the end of the month the gonad volumes are beginning to pick up a little.	Practically all spents, but some relict ova and sperm are to be found.
	June. Mostly spent, and the volume definitely picking up in both sexes. Relict sperm and ova present in some quantities.	Very much as above.
	July. All spent. The gonad volume is rising. Plenty of ripe sperm are still obtainable. The ovaries contain very small ova, and also, in many cases, considerable numbers of relict ova.	The gonads are picking up a little in volume. No spermatocytes could be found, but oocytes were beginning to differentiate, and there were developing ova up to 80μ in diam. in a few cases.
	Aug. The gonad volumes are still increasing. The males still mostly contain some active sperm, though not usually in large quantities. The females often have some relict ova. Large quantities of small ova up to ca. 5μ and smaller numbers up to 50μ. A very few up to 95μ. No sperm morulæ recognised. Female gonads about half full. Males at about their maximum size.	Gonads of both sexes have about reached their maximum size. Ova are up to 80–90μ together with a few relicts. There were a few relict sperm, but no sperm morulæ were seen.
	Sept. Very much as above. Still no sperm morulæ seen. The gonads of the males show no change in volume, but the females are still increasing.	No data.
	Oct. Sperm morulæ abundant, and sperm in some individuals. Males are much the same, but some spermatocytes are to be seen. Females contain all sizes of ova up to 110μ and their volume is still increasing.	Little change in the gonads. There are ova up to 100μ.
	Nov. The males contain large numbers of ripe sperm and also of sperm morulæ. The females have ova up to 145μ and some nearly ripe.	Little change. Ova up to 115μ. Males with abundant sperm morulæ. Some with ripe sperm.
	Dec. No data.	No data.
1932.		
	Jan. The males are nearly all full of ripe sperm, but stages of spermatogenesis are probably also present. The male gonad volumes are dropping slightly. One or two females were ripe, and a number contained up to 50% of ripe ova. The female gonad volumes were still rising.	A fair proportion of the males were ripe, many with stages of spermatogenesis. showing. Some of the females contained large ova, but none were ripe. Gonad volumes were dropping in both sexes.
	Feb. Males all ripe and full, and their volume dropping slightly. Female gonad volume still rising. About 50% of the females were ripe, and the rest mostly contained some ripe ova.	The gonad volumes of both sexes had dropped considerably further. Most of the males were ripe. No females were ripe, though there were ova up to 150μ and a few ripe ova.
	March. All the males, and nearly all the females were ripe, and spawning was commencing. The male gonad volume dropped slowly in the beginning of the month while the female was coming to its maximum. Later both dropped sharply.	The gonad volumes rapidly picked up again. Most of the males were ripe, and some few females. The rest of the latter were approaching ripeness.
	April. Most of both sexes have spawned by the end of the month.	Spawning in progress throughout the month, and the gonad volume dropping correspondingly. Still a small proportion of unripe specimens in both sexes.
	May.	Spawning practically completed by the end of the month.