THE BREEDING OF *BALANUS PORCATUS* (DA COSTA) IN THE IRISH SEA

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(Text-figs. 1–10)

Balanus porcatus (da Costa) is a widely distributed northern species, being found in the Arctic Ocean as far as 80° N., and in the northernmost extensions of the Atlantic and Pacific Oceans. Its southern limits are closely related to water temperatures. Whereas on the east coast of America, where the Labrador current flows southward, it extends to Long Island (lat. 40° N., see Pilsbury, 1916), on the west European coast it scarcely penetrates the English Channel (lat. 51° N.). It is found in some abundance however in the North Sea, the Skagerrak and Kattegat (Krüger, 1927), the Irish Sea, and off the west coast of Scotland and Ireland. The present survey is probably representative of its breeding habits in regions near the southern limits of its range.

In the Irish Sea it is generally found from 3 to 20 fathoms, usually in association with *Modiolus modiolus* (L.) or *Pecten maximus* (L.). This association exists probably because these molluscs provide much of the suitable substrata offshore, for the barnacle is also found on stones, pieces of coal, etc., when these happen to be dredged in the vicinity of the *Modiolus* beds. It occurs occasionally on rocks at low-water mark and at higher levels in the intertidal zone: for example a few specimens have been encountered at mid-tide level on rocks thickly draped with *Ascophyllum nodosum*, and also on the fronds of *Ascophyllum* itself at Church Island Reefs, Menai Straits.

COLLECTION OF SAMPLES

Most of the samples forming the basis of this study were obtained from a ground in Beaumaris Bay at the eastern entrance to the Menai Straits between Puffin Island and the east side of the Dutchman bank, at 3–5 fathoms. The samples were stripped off *Modiolus* shells collected in an otter trawl. Each haul swept a length of about 1 mile, and generally brought in about a hundred *Balanus porcatus*. Of these, usually about half were isolated specimens, one only occurring on each *Modiolus* shell, while the other half occurred in groups of two or more barnacles on each shell. The high proportion of isolated individuals indicated that the ground was not subject to heavy settlements of this species, but the large size of the barnacles showed that the conditions were favourable for survival and growth.

The only abundant forms whose presence was clearly deleterious to the barnacles were *Alcyonium digitatum* L. and *Cliona celata* Grant. Barnacles completely covered by *Alcyonium* were sometimes dead, or moribund, or, if alive, had very poorly developed ovaries and were therefore excluded from the survey. *Cliona* infected the shells of many older barnacles and completely filled the majority of dead shells. The only other barnacles observed in the samples were occasional individuals or small groups of *Balanus crenatus* Brug. and *Verruca stroemia* (O. F. Müller).

Samples were also kindly taken for me by the staff of the Marine Biological Station, Port Erin. These served as corroborative evidence. Most of them were taken south and west of Port Erin Bay and Chicken Rock, where *Balanus porcatus* occurs mainly on *Pecten* shells in association with *Balanus crenatus*. It is also occasionally found on *Modiolus* shells south-west of

TABLE I. DIFFERENCES BETWEEN SAMPLES OF *BALANUS PORCATUS* ON SHELLS
OF *PECTEN MAXIMUS* TAKEN SOUTH-WEST OF PORT ERIN AND ON
MODIOLUS MODIOLUS FROM BEAUMARIS BAY

	Port Erin samples	Beaumaris Bay samples
Number measured	61	271
Mean basal diameter (mm)	16·1	26·4
Percentage with basal diam. > 30 mm	0	29
Numbers examined for *Hemioniscus*	61	831
Number infected by *Hemioniscus*	4	0
Percentage infection	6·6	0

Port St Mary in association with *Balanus hameri*. The specimens from Port Erin differed from those from Beaumaris Bay in being smaller and more closely packed on the shells and, moreover, in being occasionally infected by the parasitic isopod *Hemioniscus*, presumably *H. balani* (Bate), which has been reported in several other cirripedes besides its normal host *Balanus balanoides* (L.) (Crisp, 1951; Sandison, 1954). These differences are shown in Table I. The absence of isopod parasites from *B. porcatus* dredged in Beaumaris Bay was not unexpected since the incidence of *Hemioniscus* in *Balanus balanoides* was also low on the surrounding shores.

The barnacles were removed from their substrate in the laboratory with a strong knife and were generally examined while fresh; a few samples were perforce examined after storage in 5 % formaldehyde in sea water.

On opening the barnacle, it was immediately clear whether the ovary had been discharged. Fertilized eggs formed two conspicuous masses lying in the mantle cavity on either side of the body, as illustrated by Moore (1935) for *B. balanoides*. Unfertilized eggs, on the other hand, were found within the tubules of the ovary, immediately within the calcareous basis, and had the appearance of a diffuse, fatty tissue, creamy yellow in colour. As fertilization in this species occurs in each individual only once a year, during the month

of February, the frequency of sampling was intensified in January, and throughout the ensuing period when the embryos were developing in the paired egg sacs, until their release into the sea in April and May. The period from January to May not only witnesses the most significant changes in the female gonads, but striking changes take place in the male organs, which were also studied. Sampling was continued, but less frequently, throughout the rest of the year.

THE MALE REPRODUCTIVE ORGANS

The testes, like those of other cirripedes (Darwin, 1854), consist of a mass of club-shaped diverticula lined with germinal epithelium. They communicate directly with the paired vesiculae seminales and discharge spermatozoa into them. In an early state of development the lobes of the testis are cylindrical, few in number, and devoid of sperm, hence perhaps readily overlooked; but when fully developed they are extensive and clearly visible through the cuticle. The degree of development of testis tissue in each individual examined was assigned to one of the following classes: (i) absent; (ii) poorly developed, visible only on dissection or teasing out; (iii) moderately developed, occupying a small part of the body and just visible through the cuticle; (iv) well developed, occupying a considerable part of the body and clearly visible from outside. In order to pool the information in a given sample and to represent more simply the probable state of development of the whole population on that date, these classes were scored 0, 1, 2 and 3 respectively, so that the average score taken over all individuals of the sample could be used as an index.

In these investigations only individuals of diameter exceeding 10 mm were included, smaller ones being immature; most samples consisted of from ten to twenty mature individuals.

The vesiculae seminales are paired fusiform sacs lying close to the dorsal surface visible through the cuticle as two prominent white patches, except when they are atrophied. When fully developed they become extremely bloated and turgid because of the great quantity of seminal fluid which they contain, and their elastic walls readily cause the discharge of this fluid should the ducts uniting them with the intromittent organ or penis become severed. When they are full the seminal fluid can often be seen extending to the lumen of the penis. The development of the vesiculae seminales was assessed by a method similar to that used for the testes, the classes being: (i) absent, or present as thin strands of tissue; (ii) poorly developed, sacs small, shrivelled, with a little sperm; (iii) moderately developed, sacs cylindrical, of diameter about equal to that of the gut; (iv) well developed, sacs large and bloated, exceeding the gut in diameter.

The penis is a highly extensible and muscular organ, arising medially between the most posterior cirri. It bears annular thickenings in the cuticle,

and sensory setae at the tip. Its lumen is continuous with those of the vesiculae seminales, the ducts of which unite just before entering it. In a few individuals of each sample the contracted penis was measured, using a binocular microscope provided with a calibrated micrometer eye-piece. As the penis is readily stretched, great care was taken to treat all samples similarly during measurement. The length of the penis is a function of the
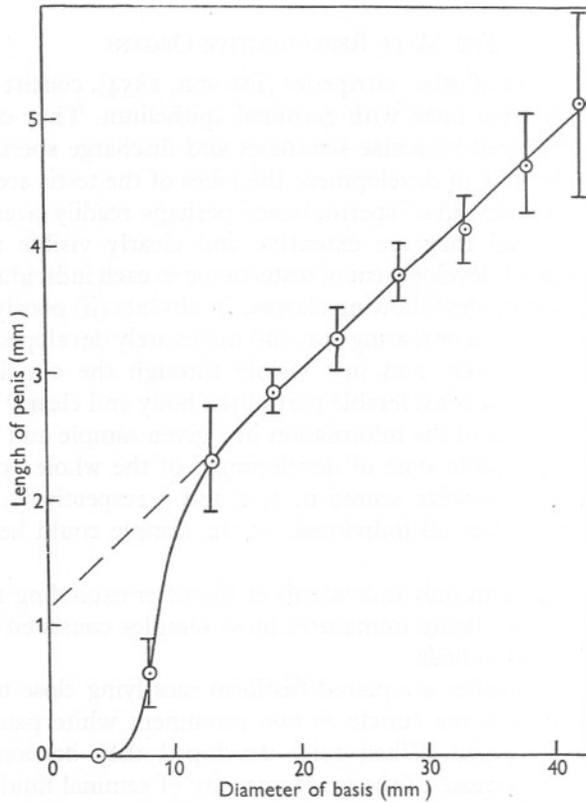

Fig. 1. Relation between the mean lengths of penis (vertical axis) and the basal diameter (horizontal axis) in *B. porcatus*. The vertical lines represent the standard error associated with each point.

size of the individual; therefore the diameter of the basis of each individual was recorded at the same time. If all the results of penis measurements throughout the year are grouped according to the size of the individual bearing the penis, the relation illustrated in Fig. 1 is obtained. The mean penis length is here plotted against the diameter of the basis, with upper and lower limits showing the standard error in the penis length associated with each point. Although there is a wide variation in length for individuals of each size-group,

it is clear that the growth of the penis is very rapid during the period in which the basal diameter increases from 6 to 10 mm. It is probably even more rapid than appears from the graph since this represents a mean of measurements on numerous individuals which will probably vary in the size-range over which the rapid growth of the penis occurs. If so, such variations would have the effect of spreading the rapid increase in mean length over a wider range of size than would be characteristic of the growth of an individual penis. The basal diameter at which the penis shows this heterogonic growth is attained towards the latter part of the first year of life, and probably takes place in the majority of individuals shortly before copulation is imminent. After the attainment of a basal diameter of 14 mm the mean growth of the penis in relation to basal diameter is approximately constant, the equation relating its length (l) to the basal diameter (d) being $l = (1 \cdot 10 + 0 \cdot 095\, d)$ mm. In plotting seasonal changes the mean penis length was therefore corrected for variations in size of the individuals in the sample by means of the above equation, each record being reduced to a standard basal diameter of $d = 20$ mm. The mean reduced length was then employed as an index of development.

Seasonal Changes in the Male Reproductive Organs

Fig. 2 illustrates the seasonal changes in the testes, vesiculae seminales, and penis, the index of each being plotted on the vertical axis against the time of year on the horizontal.

Prior to copulation in early February the male reproductive organs attain their fullest development. The vesiculae seminales occupy a large part of the body space, having steadily increased in size since the preceding summer. They reach their maximum size at the time of copulation. The penis is also enlarged at this time, measuring in some individuals as much as 10 mm, and being capable of extension to some two or three times this length. The testes, which also occupy a prominent part of the body space, reach their fullest development a little earlier, and have already begun to decline by the time copulation takes place. After fertilization a marked recession, heralded by rapid degeneration of the testes, affects all the male organs. The penis shrinks, the vesiculae seminales wither into two faint tubes lying dorsal to the gut, and the testes become transparent and devoid of sperm before gradually disappearing.

During April, however, regeneration of the testes begins and within a few weeks these organs are almost reconstituted; indeed the new growth can often be seen to have commenced before the older tissue has been resorbed. Concurrently, the vesiculae seminales are restored and become gradually refilled with sperm. The size of the penis, however, does not increase until later in the year. Thus the slight expansion of the penis in mature individuals and the rapid initial growth in first-year barnacles occur at about the same time.

The decline in the male reproductive organs does not depend upon discharge of accumulated sperm, nor upon the discharge of ova following copulation with other individuals, for it occurs on an identical scale in isolated individuals which cannot inseminate and which retain an unfertilized ovary,
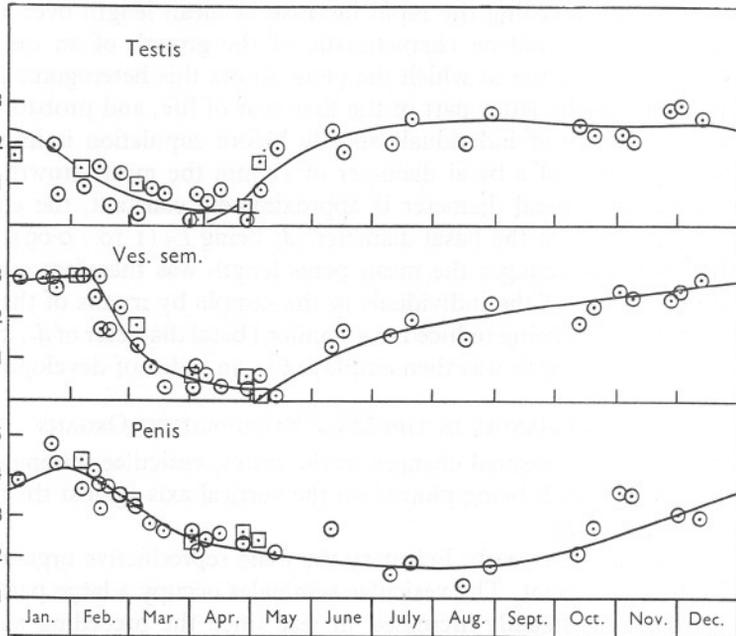

Fig. 2. Seasonal changes in development of penis (bottom curve), vesiculae seminales (middle curve) and testis (top curve). Penis length is given in mm. For the methods of assessment of these organs see pp. 475–7. ⊙, adjacent individuals; ▫, isolated individuals.

TABLE II. PARALLEL DEGENERATION OF MALE ORGANS IN ADJACENT AND ISOLATED INDIVIDUALS DURING THE PERIOD FEBRUARY TO MAY

	Testis		Vesiculae seminales		Penis	
Date	Adjacent	Isolated	Adjacent	Isolated	Adjacent	Isolated
6. ii. 52	0·95	1·4	3·0	3·0	3·65	4·4
4. iii. 52	0·3	1·1	1·3	1·8	3·25	3·4
1. iv. 52	0·1	0·1	0·3	0·6	2·6	2·4
5. v. 52	0·9	1·6	0·6	0·1	2·55	2·45

self-fertilization not taking place in this species (p. 483). Table II lists the indices of the development of the male organs for parallel sets of solitary unfertilized individuals and for normal adjacent individuals taken during this period and demonstrates that there is no appreciable difference in behaviour.

The Female Reproductive Organs

The gross development of the ovary of each individual in a sample was classified, scored, and pooled to give an index, following the same general procedure described above. The ovary was classed as: (i) absent, no ovary visible; (ii) poorly developed, only a thin layer of ovarian tissue in the basal membrane; (iii) moderately developed, ovary apparently filling about a third of the mantle cavity; (iv) well developed, ovary apparently filling the greater part of the mantle cavity. A small piece of ovarian tissue was taken where possible and teased out on a slide in a drop of sea water, the size of several of the largest ova present being then measured with a calibrated micrometer. eyepiece.

During the breeding season the number of individuals bearing fertilized egg-masses was recorded as a percentage of the total number examined, somewhat larger samples being employed for this purpose than were used in determining ovarian development.

Development and Fertilization of Ova

The ova are of large size compared with those of other British species (Table III), being exceeded only by those of *B. hameri*. In the ovarian tubules they are compressed to a polygonal shape, but when ripe they round off immediately upon release into sea water, where, as would be expected, they may increase somewhat in size if the water is hypotonic and decrease if it is hypertonic. When fertilized they are at first only slightly compressed into an ellipsoid by the egg-shaped membrane which is formed around them. Calculations of the relative volume prior to and after fertilization (ab^2/r^3), treating the egg as an ellipsoid, show that there is a slight reduction in volume when the ripe egg becomes fertilized and is surrounded by an egg case. This appears to be general in several species of cirripedes (Groom, 1894) and is known to occur in other animals (Glazer, 1914; Okkelberg, 1914). It seems likely that just after copulation the eggs are discharged via paired oviducal openings at the bases of the first cirri; these openings become swollen and glandular at the breeding season and may be responsible for secreting the matrix which subsequently hardens and holds together the eggs within each of the egg masses. A moult probably occurs at the time of copulation, as in some other arthropods (Jurine, 1820; Höglund, 1943; Burkenroad, 1947; Schöbl, 1880) since at this time many cast skins appear in the plankton.

Fig. 3 shows the observed changes in the state of the ovaries of mature individuals taken during 1951–52 in Beaumaris Bay. The records are arranged to show the full annual cycle of ovarian development, which may conveniently be divided into three periods. These are demarcated on the graph by the letters A, B, C and D.

The ovary which will give rise to the subsequent year's brood begins to

develop whilst the mature ovary or the fertilized eggs are still present. Its rudiments are first clearly discernible in mid-February (A) as a diffuse fatty tissue containing minute ova. During March and April the ovary grows rapidly, and by the end of May (B) this new ovary is almost full size. During

TABLE III. SIZES OF OVA AND FERTILIZED EGGS IN BARNACLES

(All figures are means of measurements on eggs from several individuals. The measurements listed in the first three columns of figures are in μ.)

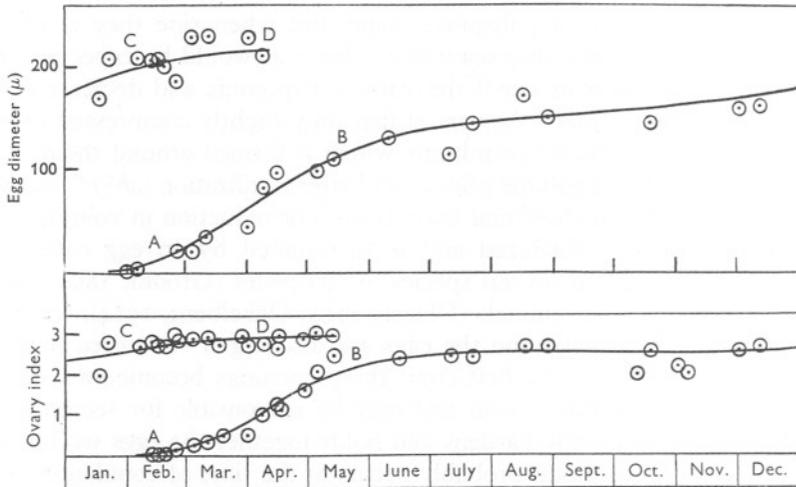| Species	Diameter of ova when fully developed ($2r$)	Length of fertilized egg ($2a$)	Breadth of fertilized egg ($2b$)	Ratio of volume: ab^2/r^3	Ratio of length to breadth of fertilized egg: b/a	Volume of fertilized egg in ml. $\times 10^{-6}$
Balanus hameri	265	385	205	0·87	0·53	8·50
B. porcatus	225	307	168	0·76	0·55	4·52
B. balanoides	210	284	154	0·73	0·54	3·53
B. crenatus	170	237	120	0·69	0·51	1·78
B. perforatus	160	221	115	0·72	0·52	1·54
B. improvisus	123	161	93	0·75	0·58	0·73
B. amphitrite var. denticulata	120	150	90	0·71	0·60	0·64
Elminius modestus	125	190	93	0·84	0·49	0·86
Chthamalus stellatus	130	191	94	0·77	0·49	0·88
Verruca stroemia	140	205	100	0·75	0·49	1·07

Fig. 3. Seasonal changes in the ovary. The upper curve illustrates the growth in size of ova, the lower curve variations in the ovarian index based on gross appearance (p. 479).

this same period the ova are swelling rapidly as indicated by measurements of the mean size of ova throughout the population. The size of the ova continues to increase, though more slowly, throughout the remainder of the year, until they are of mature size and age in early February (C) and remain so until fertilized (C–D). As there are individuals with varying stages of ovarian

development included in both the curve of the growth of the ovary and that of the growth of the eggs, the slope does not exactly represent the rate of development in a single individual; this probably takes place more rapidly than is indicated by the curves.

The eggs become fertilized and discharged into the mantle cavity immediately after copulation during February. Fig. 4 shows the progress of fertilization throughout a population during 1952 (upper rectangle), together with offshore and inshore temperature records (lower rectangle).

The vertical lines associated with each point in the upper graph give the 20 % confidence limits based on Stevens' tables. Thus the curve representing the progress of fertilization throughout the population should pass through at least four-fifths of these lines, and should be as close to the points as possible. The full curve illustrated refers to the numerous samples taken in Beaumaris Bay, and is satisfactory in not passing outside these limits. The onset of fertilization at Port Erin, represented approximately by the broken lines, occurred at about the same time, but the number of samples available was lower, and it was not possible to compare the exact dates very closely. It will be noted that the percentage fertilized rose to an average maximum of about 80 % in the Bangor samples, but almost 100 % at Port Erin. This was almost certainly a reflexion of the lower density of the population at Bangor. Despite their greater size their sparse distribution probably resulted in a proportion being too distant from their neighbours for copulation. The lower fertilization maximum is unlikely to be due to innate sterility, for the Bangor individuals showed greater growth and gonad development, and never harboured the isopod *Hemioniscus balani*, which sometimes exercises a sterilizing or debilitating effect.

It is interesting to note that if in place of percentages in Fig. 4 the probits (Finney, 1952) are plotted against time, there is a reasonable approximation to a linear relationship over the period during which fertilization is taking place (Fig. 4, inset). This indicates that the frequency with which fertilization occurs is normally distributed about a central point of time. At this point, when the probit is 5·0, 50 % of the population bear fertilized egg-masses. This fact offers a useful means of obtaining the central or mean date of fertilization using all the available data. This is shown to be 17 February for the Beaumaris Bay samples at which time the temperature was at its minimum. From a similar procedure the central date of liberation of nauplii is found to be 1 April. The interval of 44 days is thus an estimate of the embryonic life in this area, based on all samples taken. The curve representing the liberation of nauplii in the Port Erin samples was again close to that of the Beaumaris Bay material.
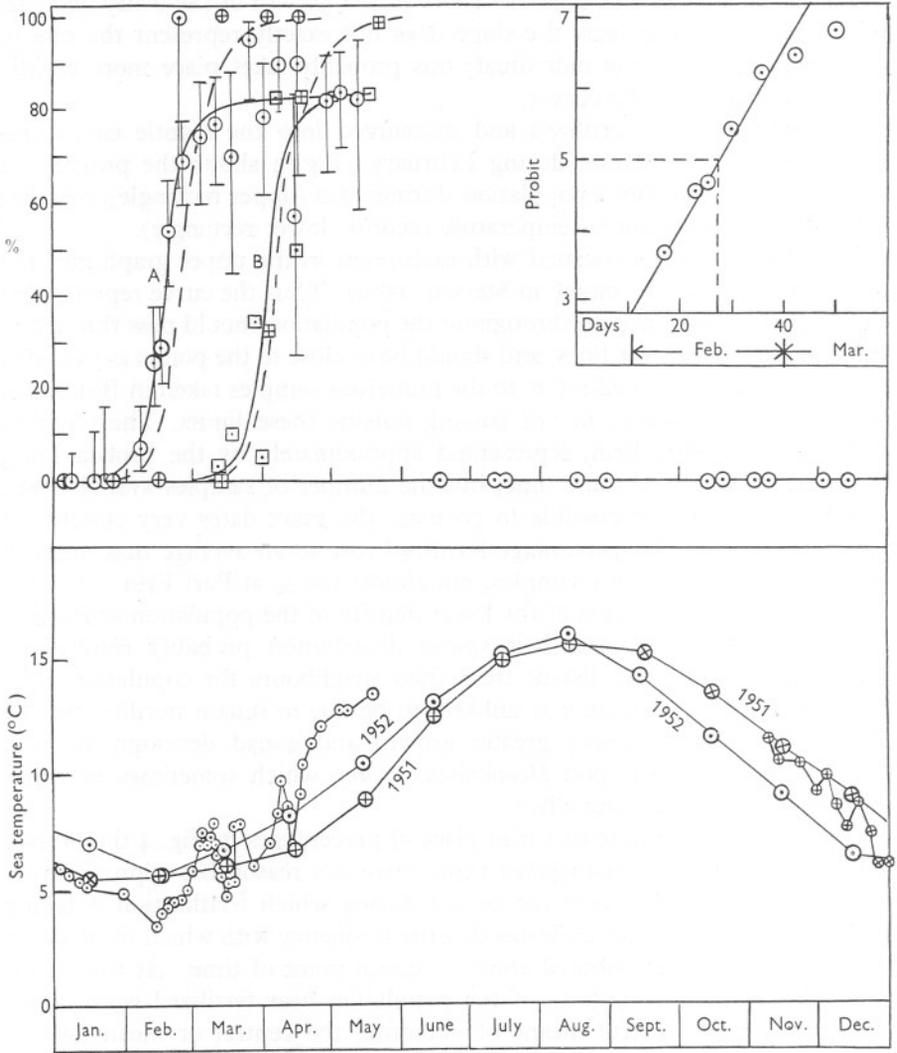
Fig. 4. Upper rectangle. Fertilization and liberation of nauplii in *Balanus porcatus* (1952).
⊙, percentage of individuals bearing or having borne fertilized egg masses in Beaumaris
Bay samples; ⊕, ditto, Port Erin samples; ⊡, percentage of individuals having liberated
their nauplii, Beaumaris samples; ⊞, ditto, Port Erin samples. To avoid confusion 20 %
confidence limits are shown only for the points giving the fertilization of the population
in Beaumaris Bay. Lower rectangle, temperature records for 1951 and 1952. ⊗, monthly
mean offshore temperatures, Beaumaris Bay, 1951; ⊙, monthly mean offshore tem-
peratures, Beaumaris Bay, 1952. ⊗, inshore temperatures, Menai Straits, 1951; ⊙, in-
shore temperatures, Menai Straits, 1952. *Inset.* Probit transformation applied to
fertilization records in Beaumaris Bay samples.

EVIDENCE FOR OBLIGATORY CROSS-FERTILIZATION

Cross-fertilization is known to be obligatory in *Balanus balanoides* (Chipperfield, unpublished thesis), in *B. crenatus* and in *Elminius modestus* (Crisp, 1950). The present samples offered suitable material to investigate *Balanus porcatus*, since the individuals were often found singly on bivalve *Modiolus* shells. Such individuals, which were termed 'isolated', sometimes constituted more than half the catch. Where two or more individuals were found on a shell these were termed 'adjacent'. This division was rigidly adhered to even if the two individuals were at the extreme ends or on opposite valves of *Modiolus* and appeared to have little opportunity of inseminating each other, or if a minute and apparently sterile individual occurred on the same shell as an otherwise

TABLE IV. DIFFERENCES IN BREEDING BEHAVIOUR BETWEEN ADJACENT AND ISOLATED INDIVIDUALS

Date of sample	Numbers with fertilized egg masses		Numbers with full size ovaries	
	Adjacent	Isolated	Adjacent	Isolated
6. ii. 52	3/42	0/12	28/42	10/12
12. ii. 52	9/35	1/16	—	—
15. ii. 52	16/55	0/26	23/55	19/26
19. ii. 52	19/35	3/32	—	—
25. ii. 52	5/5	0/1	—	—
4. iii. 52	23/31	5/38	5/31	16/38
11. iii. 52	22/30	4/30	5/30	16/30
18. iii. 52	6/12	1/22	3/12	15/22
26. iii. 52	12/20	0/1	1/20	1/1
1. iv. 52	14/19	1/18	3/19	14/18
8. iv. 52	3/41	1/38	8/41	21/38
15. iv. 52	1/7	0/17	1/7	10/17
16. iv. 52	—	—	1/10	8/12
29. iv. 52	—	—	1/22	5/15
5. v. 52	—	—	11/32	3/4
13. v. 52	—	—	6/11	3/6
Total	133/332	16/251	96/332	141/239

isolated specimen. In both such cases the barnacles would be termed 'adjacent', since it was considered preferable to adhere to a definite criterion, rather than to attempt to make a judgement on the likelihood of cross-fertilization being possible, with a risk of introducing personal bias.

Table IV gives a series of parallel counts over the breeding period on samples which contained 'adjacent' and 'isolated' individuals. It will be seen that only a small fraction of the 'isolated' samples ever contained fertilized egg-masses, yet the adjacent samples showed a maximum of about 80 % bearing them. Similarly, the fraction containing full-size ovaries fell to a minimum in the 'adjacent' samples, whereas the proportion of isolated individuals with large ovaries was maintained without significant change, since none had discharged egg-masses. These differences over the whole

set of samples are overwhelmingly significant. It is likely that before being dredged, a small number classed as isolated, might well have been in close proximity to individuals of the same species on other shells or objects nearby, whilst some of those classed as adjacent admittedly may have had little chance of insemination. The observed difference in behaviour of the two sets of samples is therefore slightly less than would be expected had an absolute division been possible into two classes, the one with and the other without mutual access for copulation. It is therefore clear that fertilization is at least greatly facilitated by individuals lying close together, and it is probable that this species also is an obligatory cross-fertilizing hermaphrodite. There is no indication that fertilization is merely delayed in isolated individuals, as would be expected if facultative self-fertilization were possible, and as apparently occurs in *Chthamalus stellatus* (unpublished data).

This study of the breeding cycle was therefore confined to adjacent individuals, except where otherwise stated.

DEVELOPMENT OF EMBRYOS AND RELEASE OF NAUPLII

The fertilized eggs develop rapidly and uniformly into embryos, which remain separately enclosed in egg-cases retained in the mantle cavity of the adult up to the time of their liberation as stage 1 nauplii.

The egg-cases are transparent, and details of development may be discerned simply by teasing one of the paired masses of eggs on a slide and examining under low power. After fixation in 5% formaldehyde in sea water the eggs retain their typical appearance, but most other fixatives render them opaque or cause cytolysis. Apart from small variations during the earliest stages, the development of all the eggs present in a given individual is uniform.

The development of the embryos was referred to a scheme of clearly distinguishable stages as outlined in Table V. Groom's (1894) description of the development of the eggs of *Balanus perforatus* has been found to be applicable to this and to other species of barnacle; reference is therefore included in the table to the appropriate illustrations in Groom's paper.

Unfortunately it has not been found possible to promote development *in vitro*; hence the rate of development has been ascertained only indirectly by means of population studies. In a population where the onset of fertilization is gradual, a range of several stages of embryonic development is to be found in different individuals at any one time. If enough samples of *equal* size are examined at *regular* intervals, throughout the whole period during which egg-masses are present, the percentage of the total number of individuals which are in a given stage will clearly be proportional to the time which this stage occupies in the whole developmental period. If sampling is irregular suitable adjustments for the variation in numbers of individuals in the samples and for the different periods of time between taking samples

are necessary. The proportionate time occupied by a given stage in the full term of development will then be given by the relation

$$t_n/T = \sum_i (S_n/S)_i \, \Delta t_i / \sum_n \sum_i (S_n/S)_i \, \Delta t_i,$$

where t_n is the time interval between stage n and $n+1$, $(S_n/S)_i$ is the fraction of the total number in the ith sample lying between stages n and $n+1$, and Δt_i is half the time interval between the $(i-1)$th and the $(i+1)$th sample.

TABLE V. THE DEVELOPMENTAL STAGES OF EMBRYOS IN THEIR EGG-CASES

| | | | Corresponding stage from Groom (1894) | | |
| | | | Figures illustrating stage in | | |
Stage	Description of development of embryo	Stage	*Lepas anatifera*	*Balanus perforatus*	*Chthamalus stellatus*
1	Unsegmented egg in oval or pyriform case	A	Pl. 14, figs. 1–7	Pl. 16, fig. 49	Pl. 18, figs. 83–86
2	Two simple blastomeres		Figs. 8–11	Fig. 50	Figs. 87–88
3	Upper blastomere divided, yolk not completely covered. 3 to 32 blastomeres	B	Figs. 12–19	Fig. 51; Pl. 17, fig. 64	Figs. 89–93
4	Yolk all undivided, completely or nearly completely covered by blastoderm cells		Pl. 15, figs. 20–23	Figs. 65–71	Fig. 94
5	Yolk cell divided in two by an oblique furrow, and completely covered by blastoderm cells		Figs. 24, 25	Fig. 72	Figs. 95, 96; Pl. 19, fig. 97
6	Yolk cell divided into 3 to 5 cells enclosed in blastoderm	C	Figs. 26, 27	Fig. 72 a, b	—
7	Six or more yolk cells. Posterior thiceningk of mesoblast present		Fig. 28	Figs. 73–75	—
8	Embryo divided by two or more constrictions between rudimentary swellings giving rise to the appendages	D, E	Figs. 29–35	Fig. 76	—
9	Appendages clearly visible as short bifid swellings, setae absent or not evident	F	Figs. 36–37	Fig. 77; Pl. 18, fig. 80	—
10	Appendages with distinct setae. No eye visible	G	Figs. 38–40	Fig. 81	—
11	Median eye red or poorly pigmented, mass of yolk cells present		Fig. 41	Fig. 82	—
12	Eyes darkly pigmented, black or reddish brown; endoderm forms a clearly defined gut. Not hatching within a few minutes of placing in sea water	H	—	—	—
13	As 12, but more strongly pigmented. Hatching within a few minutes of placing in sea water. In formalized material a few often found freed from egg-cases		Fig. 42	—	—

Since T, the total time of development, is known, the absolute intervals t_n between the various stages can be computed. In this way a developmental time-table can be compiled (Table VI). It will be seen that the earliest developmental stages are quickly over, but that at the end of development apparently fully developed embryos (Stage 13) are retained for some time before being liberated. This results in a wide variety of embryonic stages being present simultaneously in the early part of development, and giving place to

an appearance of greater uniformity towards the end. The degree of over-lapping of embryonic stages is, however, limited, since each fertile individual produces one, but not more than one, annual brood.

During embryonic development the egg-masses change slowly in texture and appearance. When first discharged they appear bright creamy yellow and of the consistency of weak jelly, but gradually the egg-cases harden and the egg-masses become firmer. As the embryos develop more pigment, the colour of the egg-masses changes from yellow to ochre, then to fawn, and finally to dark brown. Each paired egg-mass is surrounded by an enveloping membrane in addition to the separate cases around each embryo. Immediately after fertilization spermatozoa may sometimes be seen between the fertilized eggs, but not within the substance of this enveloping membrane. Shortly

TABLE VI. DURATION OF EMBRYONIC STAGES IN *BALANUS PORCATUS*

Stage	Time of passing (days)	Duration (days)	Percentage of total time	Cumulative percentage
1	1·1	1·1	2·5	2·5
2	1·9	0·8	1·7	4·2
3	3·2	1·3	2·9	7·1
4	4·2	1·0	2·2	9·3
5	6·2	2·0	4·6	13·9
6	8·1	1·9	4·2	18·1
7	11·1	3·0	6·9	25·0
8	14·3	3·2	7·3	32·3
9	19·5	5·2	11·8	44·1
10	21·8	2·3	5·2	49·3
11	24·0	2·2	4·9	54·2
12	31·3	7·3	16·7	70·9
13	44·0	12·8	29·0	100

before liberation which, like copulation, appears to be accompanied by a moult of the adult barnacle, the egg-masses soften and break down, so that the egg-cases lie almost loose in the mantle cavity. Hatching occurs after liberation into the sea. The hatching movements of the embryos are inhibited in water of low oxygen tension. Possibly the oxygen tension in the mantle cavity of the adult is lowered by respiration, so that hatching is prevented until the eggs are individually expelled from the mantle cavity, and exposed to a greatly increased oxygen tension in the surrounding water.

Liberation of first-stage nauplii begins towards the end of March and continues through the early part of April. They moult almost at once, giving rise to second-stage nauplii. These are normally the earliest stage found in the plankton and may be distinguished from the second-stage nauplii of *B. balanoides* by their slightly larger size and longer forked process. The remaining stages are also larger than those of *B. balanoides*, with which they might otherwise readily be confused. There is no evidence that nauplii retained in the mantle cavity developed further as suggested by Barnes (1953a); in one instance abortive egg-masses were found still remaining towards the end of April, but, unlike those reported by Barnes (1953b), these

did not appear to be viable. Barnes (private communication) now considers that the larvae are invariably planktotrophic (Crisp & Knight-Jones, 1953).

The larvae have been found only in very small numbers in the plankton from Beaumaris Bay, but are much more common in samples taken in April and early May south of the Isle of Man, where the beds of *B. porcatus* are probably more extensive.

SETTLEMENT AND GROWTH

Not only have the larval stages been sparse in the Bangor area, but the settlement of the past two years has been correspondingly scanty compared with the heavy settlements of intertidal barnacles commonly observed. The proximity of the species to its geographical limits may explain its inability to produce heavy annual settlements as was also found in *B. balanoides* at Plymouth (Harris, 1946). Owing to the small numbers of spat found, it has not been possible to date settlement with great precision, but young spat have not been observed prior to the first week in May, and the main settlement appears to take place in the latter half of this month. By July considerable growth has occurred, and by August it is not easy to distinguish the settlement of the current year from the smaller individuals of the previous season. This difficulty results from the considerable individual variation in rates of growth, a feature which appears to be common in cirripedes, and is probably largely due to environmental differences.

Fig. 5 shows in histogram form the size-distribution of three samples of *B. porcatus*, the first taken in mid-April, a month before settlement; the second at the end of July, about $2\frac{1}{2}$ months after settlement; and the third in December. The absence of well marked peaks indicating year-groups is due partly to variation in growth rate and partly to the small spatfalls of 1951 and 1952, which were scarcely sufficient to maintain the population at its present level and constituted only a small fraction of the total.

There can often be noted on the parietes of the shell of an old individual a series of slight concentric irregularities or ridges (Fig. 6), at which the angle of the shell changes slightly but abruptly. These discontinuities are not directly associated with moults, for animals kept in shallow dishes in the laboratory moult at frequent intervals; whereas no more than four such shell discontinuities are discernible on most large individuals. The histograms shown in Fig. 7 illustrate that the discontinuities measured from the apex of the barnacle form a regular series of frequency peaks. Slight changes in the thickness of the basis can also be observed, usually, but not always, agreeing in number with the discontinuities of the shell. It seems probable that both the parietal ridges and the basal growth bands are due to annual changes in the rate of growth. By equating the number of growth bands to the probable age, the individuals from which the histograms shown in Fig. 5 were derived were grouped, and the results of this grouping are shown as divisions within
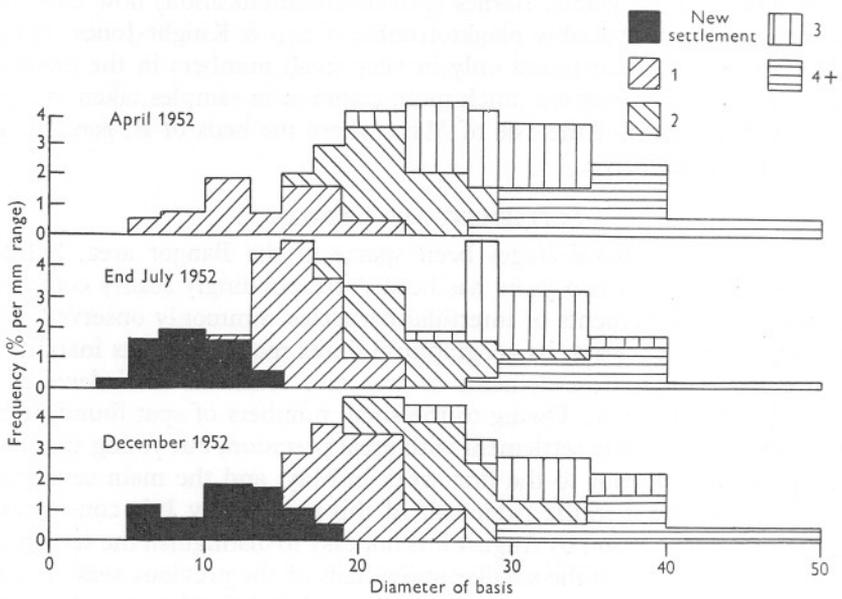
Fig. 5. Histograms of size frequency in *B. porcatus*. The size is measured as mean basal diameter in millimetres. The histogram is divided internally to show year groups, 1 being those in their first year of growth in April 1952, 4+ being those in their fourth or later years.
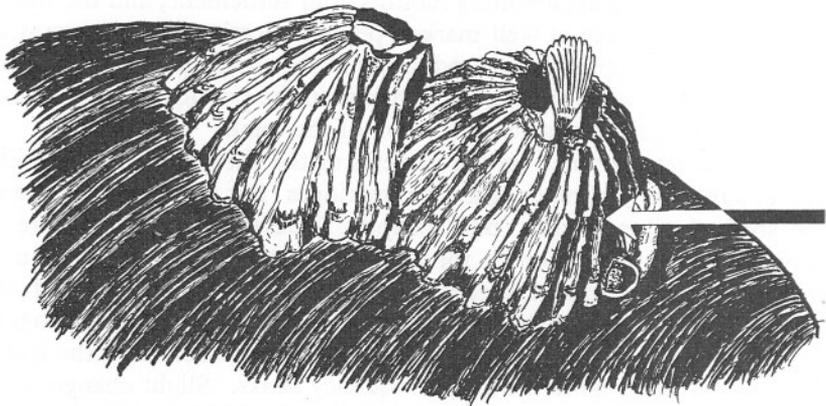

Fig. 6. Two individuals of *B. porcatus* in their third year of growth. The arrow shows in the right hand individual the position of the rather prominent parietal growth ridges corresponding to the first year; the other growth ridges are present but are only just discernible in the original.

Fig. 7. Histograms relating to *B. porcatus* selected because they showed growth bands on the parietes. The frequency of occurrence of bands is plotted against the distance measured vertically (in mm) from band to apex. The horizontal scale therefore represents the probable height of the barnacle when the growth ring was formed, if increase in height is due solely to basal growth.
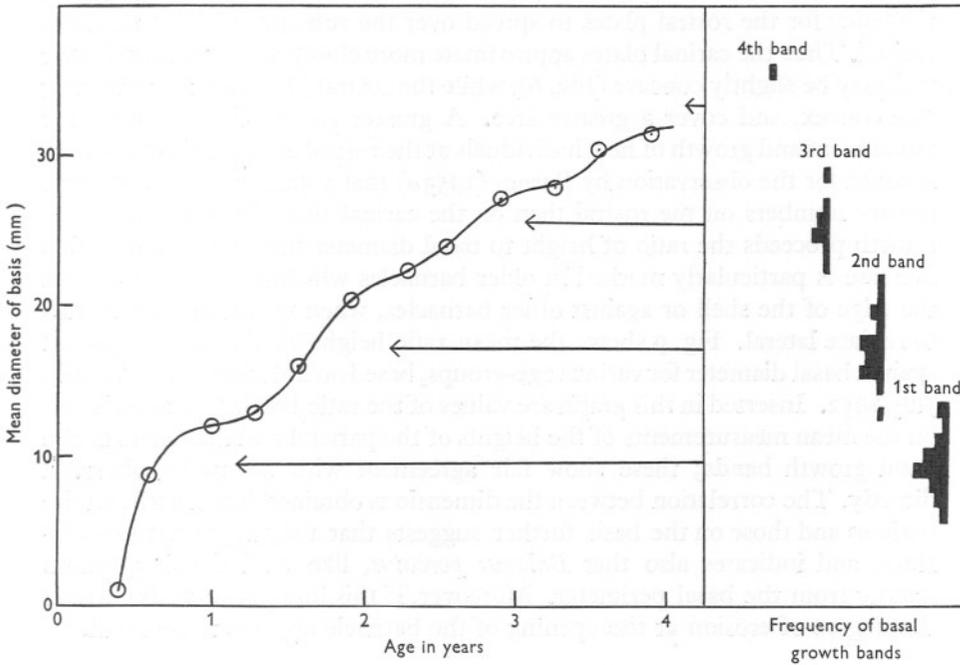

Fig. 8. Growth rate of *B. porcatus* in Beaumaris Bay. The horizontal axis gives the estimated age, the vertical axis the mean basal diameter from the histograms illustrated in Fig. 5. On the right-hand side are shown histograms of the basal growth marks of a few individuals in which they were clearly distinguishable; these correspond approximately to annual rings.

the histogram. From the mean size of each of these age-groups, a curve showing the mean growth rate of the population has been derived (Fig. 8). To check the validity of the method the mean sizes of the growth bands in the bases of a number of well-formed individuals were measured, and histograms based on measurements of the 1st, 2nd, 3rd and 4th bands are inserted on the right-hand side of the graph. The mean diameter of each growth band agrees reasonably well with the mean population size of each year-group. Neither the parietal ridges nor the basal growth bands seemed generally to be sufficiently reliable guides to age to enable estimates to be extended beyond the fourth year of growth. The largest individuals in the population, of between 40 and 50 mm basal diameter and 20–30 mm height, were probably some 5 or 6 years old.

Individual shape varies considerably according to the substratum on which the barnacle grows. In general, growth on the convex part of a *Modiolus* shell tends to give a tall individual, particularly if the edge of the barnacle reaches the edge of the molluscan shell and cannot grow further. Conversely, *Balanus porcatus* growing on a concave surface, as for example on the inside of a dead *Modiolus* shell, is often flatter than usual. There is also a marked tendency for the rostral plates to spread over the substratum more than the carinal. Thus the carinal plates approximate more closely to the perpendicular and may be slightly concave (Fig. 6), while the rostral plates are more sloping and convex, and cover a greater area. A greater area is thus available for attachment and growth of new individuals at the rostral end, which may partly account for the observation by Barnes (1953a) that young barnacles occur in greater numbers on the rostral than on the carinal side of the aperture. As growth proceeds the ratio of height to basal diameter increases slightly; this increase is particularly marked in older barnacles which have grown against the edge of the shell or against other barnacles, when upward growth tends to replace lateral. Fig. 9 shows the mean ratio height/basal diameter plotted against basal diameter for various age-groups, based on individuals collected in July 1952. Inserted in this graph are values of the ratio height/diameter based on the mean measurements of the heights of the parietal and diameters of the basal growth bands; these show fair agreement with the ratios observed directly. The correlation between the dimensions obtained from marks on the parietes and those on the basis further suggests that they represent growth-rings, and indicates also that *Balanus porcatus*, like *B. balanoides*, grows mainly from the basal perimeter. Moreover, if this interpretation is correct, the degree of erosion at the opening of the barnacle appears to be small.

DEVELOPMENT OF GONADS IN RELATION TO AGE

Fig. 10 illustrates the relation between size and gonad development, scored as described above (pp. 475–9). The data on which this graph is based are necessarily restricted to those seasons when the gonad is normally well developed in
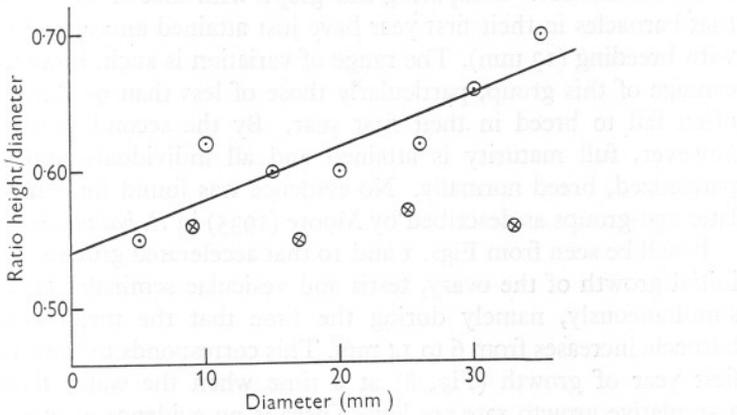
Fig. 9. Ratio of height to basal diameter in *B. porcatus*. ⊙, mean ratios based on measurements of groups of individuals of a given size range; ⊗, ratios based on mean values for 1st, 2nd, 3rd and 4th parietal and basal growth marks respectively.

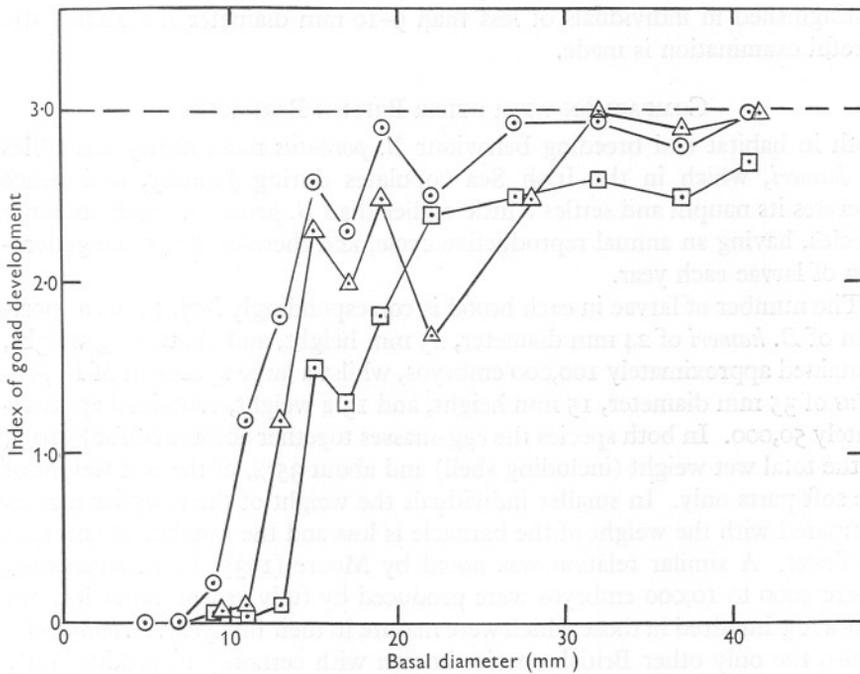Fig. 10. Growth of gonads in relation to mean basal diameter (mm). ⊙, Index of development of ovary (p. 479). △, Index of development of vesiculae seminales (p. 475). ▫, Index of development of testis (p. 475).

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mature barnacles. Comparing this graph with that of Fig. 8, it will be seen that barnacles in their first year have just attained an average size consistent with breeding (13 mm). The range of variation is such, however, that a percentage of this group, particularly those of less than 9–10 mm in diameter, often fail to breed in their first year. By the second year and thereafter however, full maturity is attained and all individuals, unless isolated or parasitized, breed normally. No evidence was found for senility among the later age-groups as described by Moore (1935) in *B. balanoides*.

It will be seen from Figs. 1 and 10 that accelerated growth of the penis and initial growth of the ovary, testis and vesiculae seminales take place almost simultaneously, namely during the time that the mean diameter of the barnacle increases from 6 to 14 mm. This corresponds to the latter part of the first year of growth (Fig. 8) at a time when the water temperature and assimilative growth rate are low. There is no evidence at present to suggest that any one of the reproductive organs precede in development or initiate the growth of the others. The slightly earlier recorded appearance of the penis and ovary may be due only to the greater facility with which these structures can be observed in a rudimentary state, for the testes also can often be distinguished in individuals of less than 9–10 mm diameter if a sufficiently careful examination is made.

COMPARISON WITH OTHER BRITISH BARNACLES

Both in habitat and breeding behaviour *B. porcatus* most nearly resembles *B. hameri*, which in the Irish Sea copulates during January, and hence liberates its nauplii and settles a little earlier than *B. porcatus*. Both are large species, having an annual reproductive cycle, and therefore only one generation of larvae each year.

The number of larvae in each brood is correspondingly large; thus a specimen of *B. hameri* of 24 mm diameter, 25 mm height, and about 20 g weight, contained approximately 100,000 embryos, whilst a large specimen of *B. porcatus* of 35 mm diameter, 15 mm height, and 13 g weight, contained approximately 50,000. In both species the egg-masses together accounted for 8–10 % of the total wet weight (including shell) and about 35 % of the wet weight of the soft parts only. In smaller individuals the weight of the naupliar masses compared with the weight of the barnacle is less and the number of embryos far fewer. A similar relation was noted by Moore (1935) in *B. balanoides*, where 5000 to 10,000 embryos were produced by fully grown barnacles, but only a few hundred in those which were mature in their first year. *B. balanoides* is also the only other British species known with certainty to produce only a single annual brood.

B. porcatus, *B. hameri* and *B. balanoides* are all boreal-arctic forms reaching their southern limits in British waters. All three species therefore accord with the principle, enunciated by Appellöf (1912) and Orton (1919), that

animals living in the warmest parts of their geographical range breed in the coldest months of the year. Thus the approximate periods during which embryos are found in the mantle cavity in British waters are: *B. balanoides*, November–March (Moore, 1935); *B. hameri*, early January–early March (unpublished data); *B. porcatus*, February–March.

Orton (1919) quotes, in support of this general principle, *Antennularia ramosa* and *Bougainvillia ramosa* as being winter breeders in the Mediterranean, and early-summer breeders at Plymouth, pointing out that well-defined temperature limits control the period of breeding of such species and account for their latitudinal variations in the times of breeding. It seems unlikely, however, that boreal-arctic barnacles breed during the warmer months even in high latitudes. In *Balanus balanoides*, in particular, it is known that at higher latitudes the onset of breeding occurs earlier, but only sufficiently so to compensate for more prolonged development during the colder winter. The embryos are therefore still retained throughout the coldest months, although copulation occurs slightly earlier in the autumn and liberation slightly later in the spring.

It seems probable that in these species the annual cycle is so adjusted that over a wide range of latitude their larvae are liberated in the spring, when abundant phytoplankton is available, and when conditions are favourable for rapid and prolonged growth after settlement. The rapid ovarian development which occurs during early summer in all these species, but which does not lead immediately to reproduction, may be primarily an adaptation to arctic conditions when the growing season is short. Reproduction is postponed until winter, so that the planktonic stages will not be thrown on their own resources until the spring, when the adults too begin to assimilate reserves for the following winter's breeding cycle. This behaviour is in marked contrast to that of warm temperate barnacles such as *Elminius modestus*, *Chthamalus stellatus* and *Balanus improvisus*, which produce several broods during the summer months, but lie dormant and without obvious food reserves during the winter.

The marked recession of the testes and vesiculae seminales and the slight decrease in length of the penis, that occur in *B. porcatus* immediately after fertilization, occur also in *B. hameri* and are very pronounced in *B. balanoides*, where the male organs regenerate rapidly only a few months prior to copulation (Chipperfield, unpublished). Both in *B. balanoides* and *B. porcatus* it has been shown that this recession is seasonal and occurs whether or not copulation and discharge of eggs by the ovary have taken place. It is therefore improbable that the growth of the male gonad is controlled by any hormonal influence from the ovary, as might have been thought possible from the time relations of the development of these organs.

The onset of copulation corresponds to the coldest part of the year (Fig. 4), but it is not known how far it is directly controlled by temperature. In deep

turbid water temperature is probably the only reliable indicator of season; salinity, light and biological factors varying widely from year to year. A simple relation between the onset of breeding and the immediate temperature seems, however, rather unlikely, for there is a considerable variation in the minimum temperature reached, not only year by year but also at different depths, and this would make it very difficult to explain the regularity and uniformity in breeding shown in different seasons. A direct stimulus due to change of temperature is also improbable in this species since breeding commences when the temperature changes are minimal. It is considered more likely that the gradual fall in temperature throughout autumn and winter sets in motion metabolic changes causing gradual ripening of the gonads. If these changes were suitably geared to the falling temperature gradient, copulation could follow as a result of the maturation of individuals at the appropriate season without an immediate external stimulus. The normality of the distribution of fertilization times (p. 481) is probably a reflexion of a normal distribution in the development of the gonads, and therefore supports this view. Were an external stimulus responsible, one would expect a sudden onset of fertilization in which all the ripe individuals would take part, followed by a gradual tailing off as those developing later became mature.

The growth rates and longevities of *B. porcatus* and *B. hameri* are similar; their attainment of maximum size is very gradual, but mortality is much lighter than in the smaller species of barnacles. The thick shells of *B. porcatus* do not rapidly decay, yet relatively few dead ones are found among the early year-classes. This is probably related to the quieter conditions obtaining off-shore. It is somewhat surprising, in view of the remarkable similarity in the ecology of these two large species, that their general shapes are entirely different, and that the shell of *B. porcatus* is extremely thick and the compartments well knit together, whereas that of *B. hameri* is rather fragile.

SUMMARY

Balanus porcatus is a cross-fertilizing hermaphrodite which breeds once a year, producing some 50,000 embryos in each brood.

In the Irish Sea copulation and discharge of eggs into the mantle cavity takes place in February and liberation of nauplii in March. During copulation

spermatozoa are injected into the mantle cavity and ova are discharged simultaneously. The spermatozoa become enclosed with each mass of eggs in an enveloping membrane which softens only when the embryos are fully developed and ready to hatch. Hatching occurs after liberation into sea water and is probably induced by the higher external oxygen tension. After a larval development lasting 6–8 weeks in the plankton, the cyprids settle in May and June.

In mature individuals the testes develop and the vesiculae seminales gradually fill during summer and autumn. The penis, though present throughout the year, becomes somewhat enlarged in mid-winter just before copulation. Prior to copulation the testes begin to degenerate, and just after copulation the vesiculae seminales shrivel and the penis becomes somewhat shortened.

The ovaries re-develop during spring and summer, the bulk of ovarian tissue being assimilated by autumn. The ova, however, increase in size steadily throughout the year, attaining maximum size and ripeness by mid-winter.

The rate of growth has been measured by noting the numbers of growth marks on the parietal plates and bases of the shell. The parietal marks are more distinct and are due to the angle of growth of the shell varying slightly during each season. Individuals commonly live for 3 or 4 years reaching a basal diameter of 30–40 mm: some probably survive for as long as 5 or 6 years. Some mature in their first year. Both male and female gonads appear when a basal diameter of about 10 mm has been attained, and the penis simultaneously undergoes rapid heterogonic growth.

It is suggested that the winter breeding of this species, of the closely similar *B. hameri*, and of *B. balanoides*, is an adaptation enabling the nauplii to be liberated as early as possible in the spring. They thus have the maximum available time to establish themselves during the short summer of higher latitudes. The main period of assimilation of the adult also falls during spring and summer, a long period with full gonads intervening before the postponed onset of breeding.

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