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STUDIES ON THE BIOLOGY OF LIMPETS

IV. THE BREEDING OF *PATELLA DEPRESSA* PENNANT ON THE NORTH CORNISH COAST

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(Text-figs. 1 and 2)

Patella depressa Pennant (= *P. intermedia* Jeffreys) has a very limited distribution in Britain. It is essentially a southern form, and is present along the south and west coasts from Bembridge, Isle of Wight, to Carmel Head, Anglesey, but has not been found in Ireland (Fischer-Piette, 1936; Crisp & Knight-Jones, 1955; Southward & Crisp, 1954; Crisp & Southward, 1958; unpublished records J. H. Orton and A. J. Southward).

On the shore *Patella depressa* has a restricted vertical range compared with the common limpet, *P. vulgata* L., and in south-west England is usually most abundant from MHWN to MTL: rarely is it found as high as MHWS or below MLWN (Fischer-Piette, 1938; Southward & Orton, 1954). It is not found in places sheltered from wave action (Evans, 1947*a*, *b*), and its preference for wave-beaten sites was amply confirmed by our quantitative observations on the Breakwater at Plymouth (Southward & Orton, 1954). However, it cannot apparently withstand severe wave action: at Shipman Head at Bryher, Isles of Scilly, and on the Eddystone Reefs, 10 miles SSW of Plymouth, it is replaced at all levels by *P. aspera*, a species which is usually restricted to low-water levels in more normal habitats.

From this brief analysis of the ecological niche occupied by *P. depressa* it is obvious that, although the species is widely distributed in the south-west, it was not easy to find places from which large samples could be taken at regular intervals. Favourable sites may be quite isolated and rough seas often prevent sampling. Furthermore, the species is difficult to distinguish by shell form, and experienced collectors are required. For these reasons sampling was concentrated at Trevone, north Cornwall, where reasonable samples can be obtained within easy walking distance, and the presence of outlying reefs gives some shelter at low water during heavy seas.

Most samples came from a level which provided the greatest numbers of large individuals, estimated as MTL to MLWN, near the seaward edge of the extensive reefs on the south-west side of Trevone Beach. There is a sewer outfall at the extreme seaward edge of these reefs, but its influence does not apparently extend to the site of limpet collection.

The samples were measured for shell length only, and then the sex and gonad stage assessed by cutting the foot from its attachment to the shell and turning it forward. The exposed gonad was graded according to the series of arbitrary stages selected for *P. vulgata* (Orton, Southward & Dodd, 1956). The larger specimens, from 31–45 mm shell length, were used for analysing the breeding sample, but smaller sizes were examined on several occasions to determine sex-proportions.

Some of the samples were sent by post from Trevone, to Liverpool and various marine laboratories where J.H.O. was working, and several days often elapsed before the sample was examined. An additional difficulty with *P. depressa*, not applicable to the other species investigated, is the smaller size of the mature animal, and hence of the gonad. There was thus a much greater possibility of confusion of stages, especially between developing and spawning stages of the same volume, which were separated in a more subjective way than the corresponding stages of *P. vulgata* (Orton *et al.*, 1956). Spawning males were recognized by the purplish tinge of the gonad, while spawning females could be distinguished only by the looseness of the eggs in the ovary.

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SEX PROPORTIONS

The proportion of sexes found in the various size-groups of *Patella depressa* was determined on five occasions. The results are shown graphically in Fig. 1 as percentages of neuters, males and females in each 5 mm shell-length group. The samples were smaller than those used for determining the sex proportions in *P. vulgata*, since it was not easy to collect the ideal sample of 100 specimens in each size-group. From the figure it can be seen that complete differentiation of the gonads in the population is reached at approximately the same length as in *P. vulgata*, about 20–25 mm. Since the maximum length found rarely exceeds 45 mm, this means that a much larger proportion of the population of *P. depressa* is sexually inactive. Moreover, after about 35 mm an increasing proportion of secondarily neuter individuals is found, since the incidence of trematode infection, which can cause complete dedifferentiation of the gonad, is higher than in the common limpet. Development of both male and female gonads occurs at a much smaller size than in either *P. vulgata* or *P. aspera*, and 10–40% differentiated individuals were found in the 6–10 mm group. In all five samples the apparent 'development' of the males

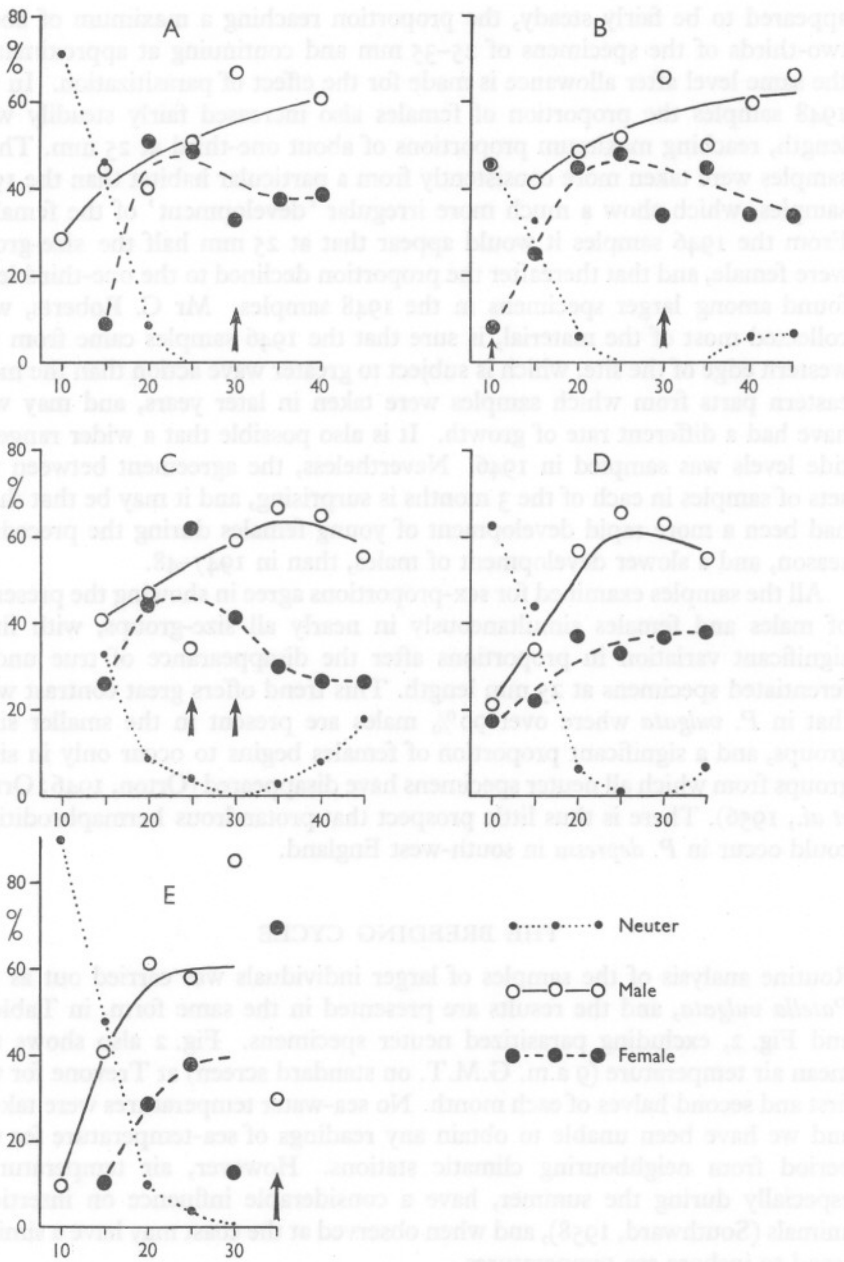

Fig. 1. Proportion of sexes (as percentage) in each 5 mm shell-length group of *P. depressa*, MTL–LWN, Trevone. A, 334 individuals, June 1946; B, 509 individuals, July 1946; C, 596 individuals, August 1946; D, 341 individuals, August 1948; E, 251 individuals, September 1948. It has been assumed that irregularities were introduced by the smallness of the samples, especially those marked with an arrow, and smooth curves have been fitted to the points by eye estimation.

appeared to be fairly steady, the proportion reaching a maximum of about two-thirds of the specimens of 25–35 mm and continuing at approximately the same level after allowance is made for the effect of parasitization. In the 1948 samples the proportion of females also increased fairly steadily with length, reaching maximum proportions of about one-third at 25 mm. These samples were taken more consistently from a particular habitat than the 1946 samples, which show a much more irregular 'development' of the females. From the 1946 samples it would appear that at 25 mm half the size-group were female, and that thereafter the proportion declined to the one-third level found among larger specimens in the 1948 samples. Mr C. Roberts, who collected most of the material, is sure that the 1946 samples came from the western edge of the site, which is subject to greater wave action than the more eastern parts from which samples were taken in later years, and may well have had a different rate of growth. It is also possible that a wider range of tide levels was sampled in 1946. Nevertheless, the agreement between the sets of samples in each of the 3 months is surprising, and it may be that there had been a more rapid development of young females during the preceding season, and a slower development of males, than in 1947–48.

All the samples examined for sex-proportions agree in showing the presence of males and females simultaneously in nearly all size-groups, with little significant variation in proportions after the disappearance of true undifferentiated specimens at 25 mm length. This trend offers great contrast with that in *P. vulgata* where over 90% males are present in the smaller size-groups, and a significant proportion of females begins to occur only in size-groups from which all neuter specimens have disappeared (Orton, 1946; Orton *et al.*, 1956). There is thus little prospect that protandrous hermaphroditism could occur in *P. depressa* in south-west England.

THE BREEDING CYCLE

Routine analysis of the samples of larger individuals was carried out as for *Patella vulgata*, and the results are presented in the same form, in Table 1 and Fig. 2, excluding parasitized neuter specimens. Fig. 2 also shows the mean air temperature (9 a.m. G.M.T. on standard screen) at Trevone for the first and second halves of each month. No sea-water temperatures were taken, and we have been unable to obtain any readings of sea-temperature for the period from neighbouring climatic stations. However, air temperatures, especially during the summer, have a considerable influence on intertidal animals (Southward, 1958), and when observed at the coast may have a similar trend to inshore sea temperatures.

From Fig. 2 it is obvious that *P. depressa* is a summer-breeding species in south-west England. In all 4 years redevelopment of the gonads began in April and May as temperatures rose, and was usually completed by June or

July. Spawning, as indicated by a rapid fall in the mean state of development of the gonad to below 1·0 and an increase in recognizable post-spawning and spent stages to 80% or more of the sample, occurred between the latter half of July and the first week in September. In each year it coincided with what we may term 'high summer'—the attainment of maximum air temperatures. During the following autumn and winter the proportion of recognizable

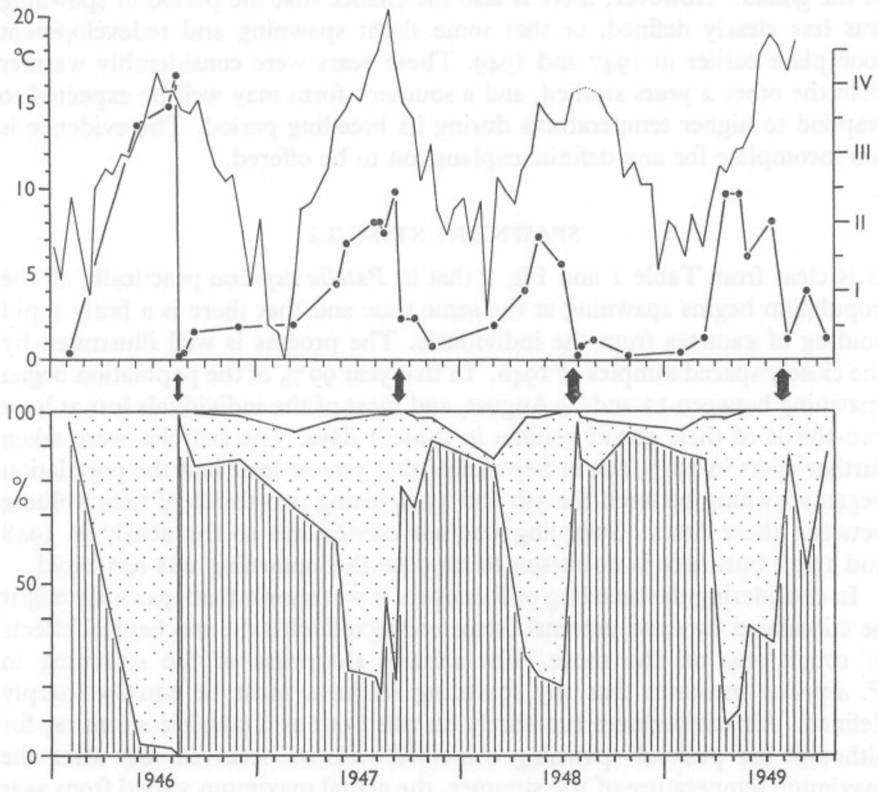

Fig. 2. The breeding cycle in *P. depressa*, MTL–LWN, Trevone. Lower graph: percentage of neuter, developing and post-spawning (including spent) stages in samples of individuals 31–45 mm shell length. Upper graph: mean state of development of the gonad (heavy line and circles), and twice-monthly mean air temperatures at Trevone (thin line). □, Neuter; ▦, developing; ▥, post-spawning & spent. Heavy arrows indicate the assumed spawning periods.

post-spawning and spent stages continued at a level of 70–80%, and although in some years (not 1948–49) some slight redevelopment of the gonad occurred soon after spawning, very few neuter stages were found until the early spring. Even then the proportion of neuter individuals remained below 15%, and there was no extensive resting condition for the population such as was found in *P. vulgata* at most British localities during the same years.

If details of the cycle are studied, we find considerable differences between the years. Some of these differences are undoubtedly due to sampling bias, especially in 1946 (see p. 656), and to the smallness of the samples in the last 2 years. The variations in the gonad index (MSD) in August 1947, May 1958, and May 1949 were probably due to inclusion of a few assessed post-spawning stages from a different habitat (e.g. pools) with a different rate of development of the gonad. However, there is also the chance that the period of spawning was less clearly defined, or that some slight spawning and redevelopment took place earlier in 1947 and 1949. These years were considerably warmer than the other 2 years studied, and a southern form may well be expected to respond to higher temperatures during its breeding period. The evidence is too incomplete for any definite explanation to be offered.

SPAWNING STIMULI

It is clear from Table 1 and Fig. 2 that in *Patella depressa* practically all the population begins spawning at the same time and that there is a fairly rapid voiding of gametes from the individuals. The process is well illustrated by the closely spaced samples of 1946. In that year 99% of the population began spawning between 12 and 14 August, and most of the individuals lost at least two-thirds of their gonad volume in those 2 days. The samples were taken further apart in 1947, but in September that year at least half the population began spawning between the 5th and 15th, losing two-thirds of their volume between those dates. Sampling was not carried out so frequently in 1948 and 1949, but there is no reason to suppose that spawning was less rapid.

In considering the breeding of *P. vulgata* it was shown that spawning might be stimulated by some external factor connected with the mechanical effects of rough seas on the shore. The relative sharpness of the spawning in *P. depressa* indicates that any spawning stimulus must be equally sharply defined. Air temperature can surely be ruled out as a possible stimulus, for although the peak of spawning coincided with or occurred just after the maximum temperature of the summer, the actual maximum varied from year to year by as much as 3°–4° C. The annual cycle of the species may well be keyed to the temperature cycle, so that the peak of gonad development occurs at the highest temperatures, which might be expected to be beneficial to a southern species at its northern limit (cf. Orton, 1920), but this is not a spawning stimulus.

Some difficulty arises when examining meteorological records (Air Ministry, 1946–49) for a possible connexion between the onset of spawning in *P. depressa* and strong winds. The site at Trevone is on a coast facing north-west and therefore sheltered to some extent from the S. and S.E. winds which are often strong in south-west England. On the other hand, the physical nature of the north Cornish coast is such that indirect swell can set up a heavy surf.

In the absence of observations on the state of sea it is not possible to be very precise as to the effects of various winds, but we might consider the sector from S.W. via N. to N.E. as being most likely to cause wave action.

In 1946, spawning at Trevone coincided with prevalent local storms, with S.W. winds up to gale force on 12 and 13 August, and there is little doubt that considerable wave action was present on the beach. In 1947 the peak of spawning was relatively late. This was a well-remembered summer in the south-west and winds of more than force 3 or 4 did not occur for some weeks before spawning. At St Eval, near Trevone, south-westerlies of force 5 were recorded on 9 September, and again on the 10th, 14th and 15th, while W.S.W. winds up to force 6 occurred on the 16th, just before the sample was

TABLE 1. DISTRIBUTION OF GONAD STAGES IN SAMPLES OF *PATELLA DEPRESSA* FROM TREVONE

		Males										Females								
	No. in	Developing					Post-spawning					Developing					Post-spawning			
Date	sample	I	II	III	IV	V	IV	III	II	I	N.*	I	II	III	IV	V	IV	III	II	I
1946																				
5 Feb.	31	—	—	—	1	—	—	3	6	8	—	—	—	—	—	—	—	—	4	9
6 June	61	—	2	15	14	4	—	1	1	—	—	—	2	10	12	—	—	—	—	—
29 July	95	—	—	7	49	5	—	1	—	—	—	—	7	6	20	—	—	—	—	1
12 Aug.	101	—	—	10	20	27	—	—	—	—	—	—	1	11	20	12	—	—	—	—
14 Aug.	107	—	—	2	—	—	—	9	59	11	—	—	—	—	—	—	—	—	13	13
22 Aug.	92	—	—	1	1	—	1	19	34	—	3	—	—	—	—	—	—	—	22	11
13 Sept.	110	—	6	7	1	—	—	9	58	3	—	—	1	3	—	—	—	—	16	8
2 Dec.	105	—	—	5	3	—	2	22	36	8	1	—	4	2	2	—	—	1	6	13
1947																				
7 Mar.	97	—	12	—	—	—	—	—	28	19	6	—	2	4	—	—	—	—	6	20
23 May	100	—	10	15	2	—	—	1	20	10	2	—	8	4	1	—	—	—	12	15
10 June	105	1	23	20	—	—	—	2	24	—	2	3	29	1	—	—	—	—	—	—
29 July	104	—	24	23	3	—	—	—	15	—	1	—	16	10	2	—	—	—	9	1
8 Aug.	108	—	25	33	2	—	—	2	11	1	1	—	13	12	2	—	—	—	4	2
19 Aug.	104	—	5	10	13	4	—	15	23	1	1	—	5	10	7	1	—	1	8	—
5 Sept.	109	—	6	24	10	—	—	12	8	—	—	—	—	10	21	7	8	—	1	2
16 Sept.	103	—	5	5	—	—	—	5	49	8	—	—	8	4	1	—	—	—	16	2
8 Oct.	98	—	15	6	—	—	—	2	27	11	2	—	4	—	—	—	—	—	18	13
8 Nov.	114	—	4	1	1	—	—	3	31	34	2	—	1	1	—	—	—	1	10	25
1948																				
1 Mar.	49	—	1	—	—	—	—	—	4	24	7	—	—	—	—	—	—	—	—	13
24 Apr.	51	8	11	3	—	—	—	—	—	10	1	11	2	—	—	—	—	—	—	5
19 May	56	2	22	8	—	—	—	—	1	—	1	2	7	1	—	—	—	—	8	4
29 June	60	13	18	—	—	—	—	—	1	9	—	12	5	—	—	—	—	—	—	2
28 July	34	1	—	—	—	—	—	—	—	26	—	—	—	—	—	—	—	—	—	7
3 Aug.	57	5	2	—	—	—	—	—	5	23	1	—	—	—	—	—	—	—	—	21
30 Aug.	57	—	5	—	—	—	—	—	23	8	2	1	2	—	—	—	—	—	8	8
29 Oct.	51	—	1	—	—	—	—	—	2	23	2	—	—	—	—	—	—	—	—	23
1949																				
31 Jan.	49	—	—	—	—	—	—	—	1	24	3	—	—	—	—	—	—	—	—	21
14 Mar.	55	—	3	2	—	—	—	—	7	21	1	—	2	—	—	—	—	—	—	19
21 Apr.	54	2	8	19	3	—	—	—	—	2	1	2	7	4	2	—	—	—	—	4
11 May	56	—	15	14	4	—	—	—	—	—	—	—	7	7	1	—	—	—	6	2
27 May	53	—	13	12	3	—	—	3	2	1	—	4	6	1	—	—	—	—	8	2
11 July	56	—	6	14	4	3	—	3	6	—	—	—	2	4	4	—	—	1	7	1
9 Aug.	54	—	6	—	—	—	—	—	25	8	—	—	1	—	—	—	—	—	5	9
10 Sept.	53	—	13	3	—	—	—	—	16	5	—	3	5	—	—	—	—	—	3	5
19 Oct.	55	1	5	—	—	—	—	—	5	24	—	—	—	1	—	—	—	—	3	16

* N. = Neuter

collected. During the presumed spawning period in 1948, from 29 June to 28 July, winds of at least force 5 or 6 were recorded on 6 days from directions between W.S.W. and N.N.E. In 1949 spawning occurred between 11 July and 9 August; W.S.W. winds of force 6 occurred on 2 days (1 and 2 August) during this period.

From this evidence it seems that there might be a relationship between wave action on the shore and the onset of spawning in *P. depressa*, but that further observations would be needed to show the relation closely. The stimulus required by *P. depressa* must be less intense than that needed by *P. vulgata*, since it spawns during summer storms of force 6 or so, while the latter species is exposed to equinoctial gales of force 8 to 9.

DISCUSSION

Reference has already been made to one major difference in the breeding cycle of *Patella depressa* compared with that of the common limpet: the absence of a resting stage when the majority of adult specimens have very reduced gonads of indeterminate sex. In *P. vulgata* this resting stage marks the nadir of breeding activity in spring and early summer. At certain Scottish localities sampled for *P. vulgata*, and especially at St Andrews (Orton *et al.*, 1956, table 5), the resting period was shorter, and the developing and post-spawning stages longer than at the more southern localities. It was suggested that there was a generally slower progression of the breeding cycle in the north, probably related to the lower temperatures experienced by the animals. This argument might be applied to the cycle in *P. depressa* at Trevone, where the species is not far from its extreme northern limit of distribution; a longer resting period, and quicker progression of the breeding cycle, may be found further south. It must be pointed out, however, that while the period of development is most prolonged in *P. vulgata* at St Andrews, it is the post-spawning and spent stages that are the longer in *P. depressa* at Trevone. In the latter case it is clear that the gonads cannot start redevelopment until the temperatures rise in the spring, and thus the period of development cannot be increased any further.

The most obvious differences between *P. depressa* and *P. vulgata* are in the period of spawning and the seasonal trend of the whole breeding cycle. At Trevone, during the 4 years studied, the gonads of *P. vulgata* did not begin to redevelop until July (sometimes as late as August), and the peak spawning took place in late October or November. The corresponding events in the cycle of *P. depressa* occurred some 4 months earlier and under very different climatic conditions. There is thus no overlap in the spawning periods of these species, and the chances of hybridization in nature are very remote.

The differences in breeding behaviour reinforce the already established differences in morphology, habitat and distribution, and serve to emphasize the real nature of the species concerned. We can no longer regard with any satisfaction the concept that *P. vulgata* and *P. depressa*, as well as other species of *Patella*, are ecological or distributional variants of one super-species (cf. Fischer-Piette, 1935, 1938).

SUMMARY

The breeding of *Patella depressa* was studied at Trevone, North Cornwall, for 4 years. Gonads were examined and assessed by methods described in a previous report on *P. vulgata*.

In contrast to the common limpet, *P. depressa* is a summer breeder in Cornwall. Gonad development begins in the spring and is complete by June or July. Spawning coincides with maximum air temperatures in July, August or early September. The autumn and winter period is passed with gonads in recognizable post-spawning and spent stages, and only a small proportion of completely resting neuter gonads is found in the early spring.

Mass spawning takes place, and gametes are voided rapidly. No definite spawning stimulus can be shown, but, as with *P. vulgata*, there may be some relation between onset of spawning and the occurrence of wave action on the shore.

The differences in breeding behaviour of *P. depressa* and *P. vulgata* reinforce the other differences between them and throw some doubt on the concept of super-species in *Patella*.

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