

Observations on *Patella vulgata*.
Part I. Sex-Phenomena, Breeding and Shell-Growth.

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INTRODUCTION AND SEX-PROPORTIONS AT DIFFERENT SIZES

THE observations given in the following pages provide an introduction to the study of sex in the common limpet, *Patella vulgata*. A preliminary notice of the work appeared in *Nature* (Vol. 104, p. 373, 1919-1920).

In determining the minimum age at which *Patella* becomes sexually mature, it was found that amongst the smaller and younger individuals there is a great preponderance of males. The proportion of the sexes in samples of various size-groups, ranging from 10 to 70 mm. in length, was therefore investigated to obtain information of sex-proportions at different ages; for in a given habitat progressive size-groups may be expected to give on the average a rough indication of progressive age-groups. Large samples (1000 in a sample was considered necessary) were examined from the same or a similar habitat with the results shown in Table I, p. 854 and Fig. 1, p. 852. Altogether more than 5000 individuals were examined in October and November, 1919. In order to ascertain sex in a maximum number of *Patella* it is necessary to examine samples during the breeding season, and preferably before spawning begins. The breeding season of *Patella vulgata* in the Plymouth district may extend from about August through the winter to about March (see p. 857). After preliminary studies the investigation of sex-proportions was carried out at about the beginning of November, but it was afterwards found that the number of undeveloped gonads among the smaller individuals might probably have been reduced

by postponing the examination until one or two months later in the breeding season. Sex was recognised by microscopic examination of the freshly teased gonad wherever doubt occurred on the naked eye appearance (see page 859). The greatest difficulty occurred in the smallest individuals, with tiny shells ranging from 8 to 15 mm. in length, in which the sex-elements at the period of examination were undeveloped in a high

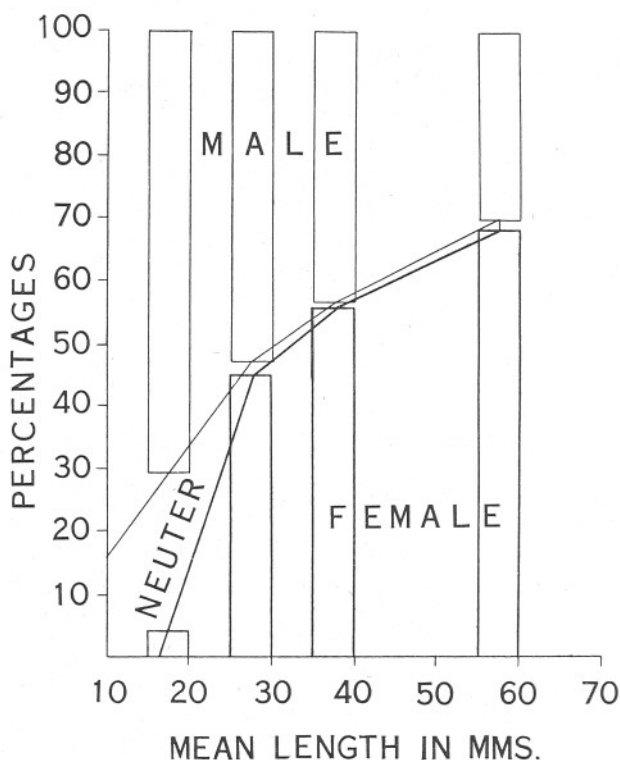


FIG. 1.—Analysis of 5350 individuals of *Patella vulgata* (Plymouth) for length of shell and sex, showing the occurrence of a high proportion of males among small individuals (about one year old), and a high proportion of females amongst larger individuals (mainly three or more years old).

proportion. An analysis of the sexual condition at mm. length-groups from 8 to 25 mm. in a sample of 1102 individuals collected at random is given in Table II, p. 855, and Fig. 2, p. 856. In this sample sex was confirmed in a large proportion of cases by microscopic examination. In a sample of small individuals (Sample 2, Table I, p. 854), examined a fortnight later than that shown in Fig. 2, the percentage of indeterminate gonads was reduced from 30.5 to 20.4 in a sample of 1233 individuals. These results establish the fact that maleness predominates to a significant

degree among young limpets. At lengths ranging from 15 to 21 mm. the percentage of males was found to vary from 65 to 86 %, and a percentage at these sizes greater than 90 could no doubt be easily obtained. In a review of all the samples, as is shown diagrammatically in Fig. 1, it is clear also that the sex-proportion changes in older individuals to show a predominance of females (68.5%), therefore, as a population of limpets increases in age there is a complete change in the proportions of the sexes. Gemmill (*Anat. Anz.*, 1896, p. 394) found 68.4% females in a sample of *Patella* of unknown but presumably large size, and recently Pelseneer (*Mém. Acad. Roy. de Belgiq.*, IX, 1928) has found 70.66% female among 4622 large sexually mature individuals. In the six samples examined (see Table I) the progressive length-groups may be taken as an approximate measure of progressive age-groups, since all samples were taken from about half-tide level and at about the same time of the year in the same year. Observations on rate of growth of *Patella* in the Plymouth district are given in this Journal, Vol. XV, 3, p. 863, on the basis of which the estimations of the range of age in samples 1 to 6 in Table I have been made.

DISCUSSION ON SEX-CHANGE IN *PATELLA VULGATA*.

The occurrence of significantly high percentages of males in large samples of young *Patella vulgata* (i.e. 64 to 81%), and of significantly high proportions of females amongst older individuals (i.e. 68%), affords strong presumptive evidence of a change of sex within the species. It is possible that a differential rate of growth of shell may occur among immature males and females, or that during the course of life females survive in greater proportion than males. The occurrence, however, of so high a proportion of males as 76.5% in a sample composed of 1233 young individuals collected at random (Sample 2, Table I, p. 854) with only 3.1% females and 20.4% of indeterminate sex, along with the fact that at slightly greater sizes examined from the same locality a week later the sexes were more nearly equal in proportion and indeterminate gonads were few, indicates a general similarity of growth-rate at least amongst the smaller individuals (i.e. up to lengths of about 25 mm.). Further, if all the indeterminate gonads among the smaller samples became female, the proportion would still be too small to yield the high percentage of females found at a slightly greater age (as deduced from size). There are, moreover, good grounds for concluding that if samples of young limpets were examined for sex at a later period in the breeding season, e.g. December or January, the proportion of males would approach 90%, and the indeterminate gonads be reduced to a minimum. Although, therefore, the evidence available is not sufficiently good to prove protandry, there

TABLE I.

SEX-PROPORTIONS AT DIFFERENT SIZES IN *PATELLA VULGATA*.

No. of sample Locality Date in 1919 Length in mm. Age in years†				1	2	3	1-3	4	5	6	1-4	4-5	5-6
				G.W.W.*	Looe Is.	Hoe	Total	G.W.W.	G.W.W.	Looe Is.	—	—	—
				Oct. 31	Nov. 12	Oct. 31		Nov. 19	Nov. 6	Nov. 12	—	—	—
				10 to 25	10 to 25	10 to 25	10 to 25	20 to 35	30 to 45	45 to 70	10 to 35	20 to 45	30 to 70
				0.5 to 1.5	0.5 to 1.5	0.5 to 1.5	0.5 to 1.5	1 to 2	1 to 3	2 to <3	1.5	2.0	3.5
Male	.	No.	.	702	944	55	1701	710	255	301	2411	965	556
"	.	%	.	63.7	76.5	81.0	70.8	52.8	43.2	29.8	64.3	49.8	34.7
Indeterminate	.	No.	.	336	251	9	596	12	3	18	608	15	21
"	.	%	.	30.5	20.4	13.2	24.8	0.9	0.5	1.8	16.2	0.8	1.3
Female	.	No.	.	64	38	4	106	621	334	693	727	955	1027
"	.	%	.	5.8	3.1	5.9	4.4	46.4	56.5	68.5	19.4	49.3	64.2
Totals	.	.	.	1102‡	1233	68	2403	1343	592	1012	3746	1935	1604

* G.W.W.=Great Western Railway Wharf, Millbay Docks, Plymouth; the samples from this locality were collected mainly from a level 3 to 9 ft. above low-water spring tide level.

† The approximate range of age for samples 1 to 6 is given, and the estimated mean age in the last three columns (for observation on rate of growth see *J.M.B.A.*, XV, 3, p. 863).

‡ This sample, with the exception of 5 broken shells, is analysed for length and sex in Table II, p. 855.

TABLE II.

LENGTH-SEX ANALYSIS (IN MM. GROUPS) OF A RANDOM COLLECTION OF 1097 *PATELLA VULGATA* (LESS THAN ONE INCH IN LENGTH) AT THE GREAT WESTERN RAILWAY WHARF, PLYMOUTH, OCTOBER 31, 1919.

Lengths in mm. groups.			8.1 to 9	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26.1 to 27	Totals		
Males	.	No.	.	.	0	0	1	3	11	30	64	80	75	90	78	83	77	43	36	13	9	2	1	696
„	.	%	.	.								65.6	73.5	86.5	86.5	84.0	83.5	80.0						63.7
Females	.	No.	.	.	————— nil —————					3	0	2	6	9	12	11	10	5	5	1	0	64		
„	.	%	.	.								2.5	0.0	1.9	6.7	9.1	13.0	20.0						5.8
Sex indeterminate	No.	.	.	.	0	0	3	6	9	20	40	33	27	12	6	7	3	0	1	————— nil —————			167	
upon examination	%	.	.	.																				15.2
Sex undertermined	No.	.	.	.	2	6	22	22	43	49	20	6	————— nil —————										170	
not examined	%	.	.	.																				15.4
Totals			.	.	2	6	26	31	63	99	124	122	102	104	90	99	92	54	47	18	14	3	1	1097*

* Excluding 5 broken shells this is the same sample as Sample I, Table I p. 854.

is every indication so far that there is tendency for all *Patella vulgata* to become male at the first sexual maturity.

A selection of females in preference to males could produce a preponderance of females among the older limpets, but there is no evidence nor indication of any such kind of selection known in the case of *Patella*.

The existence of a small proportion of tiny females as well as very large males is somewhat incompatible with complete protandry, but in *Crepidula fornicata*, in which species all young individuals develop a penis

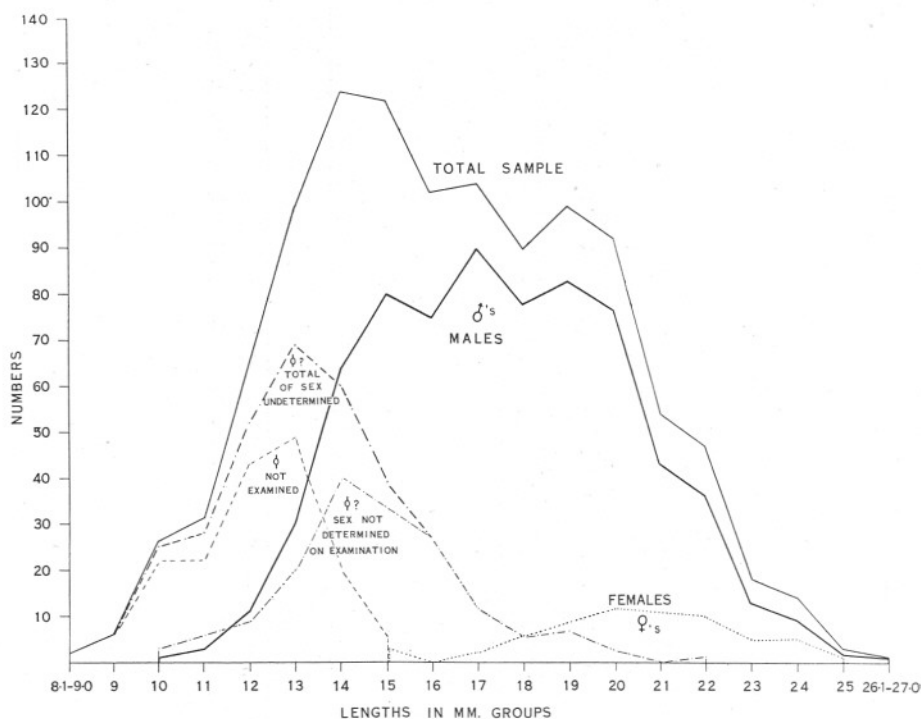


FIG. 2.—Analysis for sex and length (in mm. groups) of a sample of 1097 *Patella vulgata* (less than one inch in length) collected at random at Plymouth, October 31, 1919 (see Sample 1, Table I, p. 854).

and pass through at least a transient male gonad phase, there may occur both tiny females and large males. In this case the tiny (dwarf) females have passed the male stage rapidly from the absence of opportunity to function as males, and the large males have maintained their initial sex from continued opportunity to function as males (see Orton, *Nature*, 110, p. 213, 1922). There is, however, as yet no indication that the conditions which control sex in *Crepidula fornicata* can be applied in the case of *Patella vulgata*. It is, however, not unreasonable to infer that a

small proportion of *Patella* may pass through a hypothetical male phase unusually quickly and attain a female phase at a relatively small size. The large males, on the other hand, are inexplicable on a hypothesis of complete protandry in the present state of knowledge. The difficulty of accounting for these males would be removed if it could be shown that two kinds of males exist, one pure and one a protandric hermaphrodite. In this event it might reasonably be expected that an investigation of the chromosome constitution of the males would disclose two types and afford virtual proof of the hypothesis. In *Patella* sex may be controlled by special, but as yet unknown, metabolic conditions in a manner which is comparable with that governing sex in *Crepidula* (mainly contiguity of females to males), and in this connexion the possibility of the occurrence of spat in late autumn as well as in spring may be noted.

The occurrence of hermaphrodite individuals of *Patella vulgata* is recorded by Gemmill (loc. cit., 1896), who found three individuals with an ovo-testis among a sample of only 250 specimens at Millport, Scotland, and by Pelseneer (Mém. Acad. Roy. Belgiq., VIII, 11, 1926), who found one among 2750 individuals examined. In my investigations at Plymouth I have never seen hermaphrodites of the type described by Gemmill, although 10% of a sample may consist of males with a brown and white mottled gonad—similar in colour to that described as occurring in Gemmill's hermaphrodites—containing cells suspiciously like young ova. Such individuals may very well be in process of changing from male to female. In the female, and usually also in the male, the gonad is discharged completely during the spawning season, and afterwards passes into a neuter condition. Therefore, since secondary sexual characters are absent, there is no simple clue—as in *Crepidula* or *Calyptraea* which retain a rudimentary penis—to a preceding sex-condition, assuming that a change of sex does occur. Therefore, in order to follow possible sex-changes in *Patella*, it is necessary to examine populations from season to season, and to investigate closely by microscopic sections those classes of individuals which experience shows may be in the process of changing sex. Ainsworth Davis and Fleure (*L.M.B.C. Memoir*, X, *Patella*, p. 60, 1903) state that hermaphroditism may be more common in *Patella* than is supposed.

BREEDING AND SHELL-GROWTH.

In discussing the breeding period of *Patella vulgata* in Scotland, Russell (*Proc. Zool. Soc.*, 1909, p. 236) concluded that this period extended from July to December or January. Gemmill considered *Patella* to be ripe in the same locality from the beginning of November to the first fortnight in January. On the Devon and Cornish coasts this limpet exhibits full

female gonads in a large proportion of the population from about August–September to about February–March, and spent gonads from about March to August. The period during which full gonads occur varies in different seasons. I have made successful artificial fertilisations during the period 1912–1914 and 1919–1925 at different times during September–October and especially in January and February, and occasionally in March. Although ripe females occur in September, it is not known that natural spawning occurs at this time of the year. Natural spawning does, however, occur in January–February, as larvæ have been taken in the tow-nets at this period. It is probable, therefore, that a certain amount of spawning may occur in the Plymouth locality at any time from August to March, with a maximum at about January–February. These considerations may be of importance in relation to sex-phenomena. Tiny individuals, 2 to 8 mm. long, were observed to be common on the shore in many places in June 1914, 1919, and slightly larger in July in many years (see *Journ. M.B.A.*, XV, 3, p. 868); the same spat attain a range of 11 to 26 mm. by about the following December. In January and February, 1920, a few spat, 2 to 3 mm. long, occurred on the rocks below Plymouth Hoe and in Rum Bay, Plymouth Sound, and were in all probability derived from an early spawning during the preceding autumn. In March, 1920, Prof. Oshima reared *Patella* through metamorphosis to young spat at Plymouth from artificial fertilisations.

Shell-growth in *Patella* is general in spring and early summer in Devon and Cornwall, but critical observations on growth have not yet been made during successive seasons. In 1913 a few individuals, which were marked and measured at intervals of a few weeks, were found to grow regularly from February to June, but ceased to grow, or slowed down considerably in growth, during July and early August, and began to grow again towards the end of August (see *Journ. M.B.A.*, XV, 3, p. 870). In Scotland Russell (1909, loc. cit.) found that the first-year group grew rapidly in June, July, and August, but slowed down gradually from September to December. In the second-year group he found little growth from January to March, a slow increase during the summer, and cessation again after October. Russell's records, however, indicate both in the second-year, and especially in a few individuals of later-year groups, a slowing down of growth also in midsummer. Thus the course of seasonal shell-growth in *Patella* is not yet understood. It is not improbable that two shell-growing-seasons respectively in the spring and autumn may be general in individuals more than one year old, but extensive field and laboratory observations, combined if possible with work on marked individuals, will be necessary to produce satisfactory data. It is clear, however, that the studies of growth and sex in this mollusc cannot reasonably be divorced.

SEXUAL MATURITY AND SHELL-SHAPE.

It has been noted that changes in shell-shape occur in *Patella* round about a length of 25 mm. (Russell, 1909, loc. cit.) and at 25 to 35 mm. at Plymouth (Orton, Part III unpublished). Russell correlates the change at 25 mm. in Scottish limpets with the attainment of the first sexual maturity, but the change in shape in southern coast limpets at about 25 to 35 mm. is coincident with the change-over in sex-proportions (see Fig. 1, p. 852) and calls for further investigation. As the rate of growth is probably greater in southern districts, and in any case varies—when stated in terms of length of shell—in different habitats, it is not unlikely that the underlying cause of change in shell-shape is the same in both localities.

THE COLOUR OF THE GONAD.

The ripe female gonad of limpets at Plymouth (*see also* Pelseneer, loc. cit., 1926) occurs in two well-marked and different colours, i.e. brown and olive-green, with, however, a small proportion of gonads of an intermediate colour. The brown colour is the commoner at Plymouth. Gemmill (loc. cit., 1896) refers to the colour of the gonad of limpets in Scotland as being olive-green. An effort was made in the Plymouth district to find out whether the colour might be due to a difference in food; brown and green gonads were found, however, in closely approximated groups of individuals at many different tidal levels, and in many different localities with one exception. It was found that green-coloured gonads were rare at the Great Western Wharf in September, 1920, there being only 3 in 120 females at sizes round about 25 mm. The outstanding difference in the flora at the G.W.W., as compared with other localities, is the virtual absence of red sea-weeds. Enteromorpha and diatoms are common, and *Ulva* and *Fucoids* are not uncommon at the G.W.W. and red sea-weeds are seldom found. It is possible, therefore, that the brown colour of the female gonad may be due to the absence of red sea-weeds in the diet.

An additional observation on this subject was made at New Train Bay, Trevone, N. Cornwall, September 14th, 1928, when the percentage of green gonads among limpets living in pools was compared with that among individuals living alongside the pools. In this investigation all the individuals were taken from a small area of about 5×3 metres of sloping rock below and near high water, neap-tide level. In the sample from pools only those individuals living in pools lined by the Corallineous calcareous algæ, *Lithothamnion* or its allies, were regarded as true pool-living forms. This calcareous alga cannot apparently exist out of water, and thus affords a criterion of the minimum level of water in a pool.

From such pools it was found that among 66 ripening females 51 individuals (77%) had green gonads and eggs, while among 94 ripening females from the adjacent dry barnacled rocks 63 individuals had a brown gonad with brown eggs, while only 16 individuals, or 17%, had a green gonad with green eggs. Thus in the pools 77% of the females had green gonads while the adjacent rocks gave only 17%. The calcareous alga in the pools is an ally of the common red seaweeds, and it may be assumed that it is eaten by most of the limpets living on "homes" in the pools, but rarely by those living outside the pools. Other red seaweeds were absent at the time from the area investigated. This observation therefore agrees with the previous ones in indicating that the occurrence of any red alga in the food may produce a green coloration in the eggs, while absence of red algae leaves the eggs brown. Limpets from pools, however, generally have shells of a type which is referred to the doubtful species *Patella athletica*; the shells from the pools in New Train Bay were of this type which, although regarded by the writer as a physiological type of *P. vulgata*, complicates the biology of the common limpet by its uncertain systematic position.

A genetic and potential sex difference between the green and brown eggs is not impossible, although rendered unlikely by the occurrence of intermediate colours, but in any event, it is an interesting fact that fertilised brown-coloured ova of *Patella* begin development with a different heritage from those coloured green.

The occurrence of green gonads at high-water mark on the north side of Mewstone Is. cliffs is associated with the presence of a remarkable matted encrusting red seaweed, probably *Callithamnion Rothii* (see Harvey, *Phycologia Britannica*, Plate 120B).

Spent gonads are either brick-red or chocolate coloured, and in this state sex cannot be determined. The ripe male gonad is creamy white. In some spent males a brown coloration is found, sometimes in the form of mottling on the surface of the gonad; in this type occur cells, 20 to 50 μ in diameter when fresh, which may be very young ova. These individuals, which resemble Gemmill's hermaphrodites, may therefore be suspected of being in a state of sex-change.

CONCLUSIONS.

The differences observed among the sex-proportions at different sizes in numerically large samples, which can be regarded as providing comparable and significant material, along with the observations on hermaphroditism herein collected together, lead to the conclusions (1) that *Patella* is not an ordinary dioecious species, (2) that most, if not all, individuals are male at the first sexual maturity, (3) that change of sex

from male to female may occur at an age of one year and at any time afterwards, (4) that the occurrence of old males indicates the possibility of the existence of two kinds of males, one pure and one protandric. The extended breeding period at Plymouth renders it a difficult matter to collect at random (i.e. without selection) 1000 individuals at about the time of attainment of first sexual maturity when approximately 100% should *ex hypothesi* be male. Such a sample may be obtained in the future, and would afford a critical test—along with microscopical examination of the gonads of suspected sex-changing individuals—of the apparent protandry in *Patella vulgata*.

SUMMARY.

An introductory study of sex in *Patella vulgata* is recorded. The sex-proportions in samples of 1000 or more individuals of *Patella vulgata* show a striking difference in the different size-groups as follows:—

	Lengths.	Age.	Sex percentages.		
			Male.	Indeterminate.	Female.
Small	8-25 mm.	6 to 18 months	70.8	24.8	4.4
Medium	20-35 mm.	1 to 2 years	52.8	0.9	46.4
„	30-45 mm.	1 to 3 „	43.2	0.5	56.5
Large	45-70 mm.	2 to <3 „	34.7	1.3	64.2

The small individuals were examined before the height of the breeding season, and there is a probability that many or most of the indeterminate individuals would become male. Hermaphrodite individuals have been observed previously, and in certain samples 10% of the males contain doubtful young ova in the gonad. It is therefore concluded that *Patella vulgata* is apparently a protandric hermaphrodite, but that the evidence is not yet sufficiently good to prove protandry.

It is suggested that possibly two kinds of male, which may be recognisable by chromosome constitution, may occur, one being pure male and one protandric, and also that sex-change may be controlled by as yet unknown metabolic conditions.

The breeding period is discussed; it may extend from August to March at Plymouth in different seasons, and spawning may occur within this period. A maximum of spawning appears to occur about January-February. The conditions controlling breeding and spawning in *Patella* are unknown, and as the course of seasonal shell-growth is unknown, although shell-growth is general at the end of the breeding season, it is suggested that research on the subjects in the future should be combined.

About the time of the first sexual maturity of females and of the change

in sex-proportion a change in shell-shape occurs. The colour of the gonad is discussed ; it is either brown or olive-green in most ripe females in the Plymouth district in most localities : in one locality scarcity of olive-green gonad is correlated with absence of red weeds, while in pools lined with a calcareous red alga there is a predominance of green gonads. The ripe male gonad is creamy white and mottled brown in suspected hermaphrodites.