A Contribution to Our Knowledge of the Life-Histories of the Dogfishes Landed at Plymouth.

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With Figures 1–19 in the Text.

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INTRODUCTION.

In view of the fact that dogfishes are now of undoubted importance as marketable food fishes, it is necessary that the life-history of each of the species concerned should receive closer attention than hitherto. The present publication is the result of an endeavour to gain a personal working knowledge of the general life-history of the species which are landed at Plymouth. In carrying out a scheme of work of this kind it is certain that many of the observations made will have already been carried out previously by other workers, but, nevertheless, the results obtained are of value, not only in regard to the degree of confirmation which they afford, but also in the building up of an account of the life-history under the local conditions. In some instances, too, it will be seen that the actual numeric results in themselves are of little statistical value, but they yield very interesting suggestions which may be confirmed or disproved by a repetition of the experiments on a larger scale. I express my thanks to the fish-buyers at Plymouth fish-market, particularly Mr. J. Vanstone, for their kindness in allowing me to handle their fish before dispatch, and for their assistance in obtaining a regular supply of material for many months.

SPECIES WHICH OCCUR.

Five species of dogfish are landed at Plymouth :—

Specific Name (according to the classification by Regan (10) and (11)).	Local Name.
Squalus acanthias	Spur-dog.
Scyliorhinus canicula . . .	Rough-dog.
Scyliorhinus stellaris . . .	Nursehound.
Mustelus vulgaris } *Galeus canis* } . . .	Sweet William.*

* No distinction is made locally between these two species.

Of these the Spur-dog is by far the most important, and during the winter months in particular, catches are landed by all classes of fishing craft. They are sold by public auction in lots, usually of one or two hundred, according to the size of the fish and the numbers available, and after being gutted, skinned and beheaded are dispatched by rail under the commercial name of Flake. A varying number of skins, according to demand, are forwarded with the fish for disposal to commercial dealers.

The Rough-dog is landed fairly regularly throughout the year, chiefly by the sailing trawlers, but the catches can hardly be considered of economic importance. They are sold for local consumption.

The Nursehound also occurs fairly regularly, but only in very small numbers, and, like the rough-dog, is sold for local food purposes. The skins are of some commercial value, provided they are of a certain size and undamaged.

Sweet Williams are irregular in occurrence. Of the two species thus designated *Mustelus vulgaris* is the more common, and on several occasions upwards of one hundred have been observed in one day's landings, but generally the species is represented by a solitary specimen here and there among the heaps of the other species. The second species, *Galeus canis*, is rarely seen, and during the winter of 1919–1920 only five specimens were obtainable for examination. The professional gutters are careful to pick out Sweet Williams from the other dogfish, explaining that the offensive smell affects the flesh of the spur-dog. They are, however, purchased locally for food.

SQUALUS ACANTHIAS (Spur-dog).

Maximum Size of Adult.

The fact that the female of this species normally grows to a longer length than the male receives confirmation in the size of the largest female and male fish as yet observed at Plymouth, viz. 110 cm. and 83 cm. respectively.

Sexual Maturity.

The sexes differ also in regard to the length at which they become sexually mature. In the male, the attainment of maturity is indicated externally by a distinct increase in the length and size of the claspers. The smallest male so far observed, in which the claspers were thus enlarged, measured 59 cm. in length. There is no corresponding external expression of sexual maturity in the female, so that it is necessary to direct attention to the internal reproductive organs. The presence of embryos in the uterus is, of course, a clear indication of maturity, and the smallest female in this condition had a length of 72·8 cm., but this information is not sufficient. In the next section of the present publication it will be demonstrated that in the ovaries of a female carrying a brood of embryos in the uteri, a set of eggs is developing whose rate of growth is proportional to that of the embryos, so that when the latter are born, the ovarian eggs will be in a condition ready to enter the oviducts. In other words, an ovarian egg, in order to reach its full size, requires a period of time equal to that which is necessary for the complete develop-

ment of a uterine embryo. There seems no reason to assume that the initial set of ovarian eggs in a young female will develop at a different rate, so that it may be concluded that a female before becoming mature undergoes an extended adolescent period during which her first set of eggs are developing in the ovaries. During the month of February, 1921, a number of female fishes from 68 cm. to 98 cm. in length were measured and the condition of the ovaries and uteri in each examined. The specimens under 70 cm. in length were quite immature, and no conspicuous eggs were present in the ovaries. Adolescent fishes, in which a set of eggs were developing in the ovaries, but the uteri were empty and undeveloped, varied in length from 71 cm. to 81 cm. Mature fishes with embryos in the uteri were of lengths from 74 cm. to 98 cm. :—

Type of fish.	Number of specimens in the following size-groups (cm.)					
	71–74	75–79	80–84	85–89	90–94	95–99
Adolescent .	7	12	1	—	—	—
Mature . .	1	3	13	14	6	2

The Mature Female.

On December 12th, 1913, sixty-three female fishes were measured, and the number of the uterine embryos and the obviously developing eggs in each was determined together with their size. In the first place it was found that in any one parent the embryos were of the same general size, and, similarly, the developing ovarian eggs. (*Vide* Smitt, 13, page 1162, and Borcea, 1, page 205.) Secondly, it was observed that the size of the ovarian eggs was related to the size of the corresponding embryos, in that the larger eggs were associated with the larger embryos:—

Diam. of Ovarian Egg in cm.	Number of Embryos in the following 2 cm. groups.					
	9·0–10·9	11·0–12·9	13·0–14·9	16·0–17·9	23·0–24·9	27·0–28·9
1·0–1·9	2	49	13	—	—	—
2·0–2·9	1	9	19	5	—	—
3·0–3·9	—	—	—	—	4	—
4·0–4·9	—	—	—	—	—	6

During the month of February, 1921, a similar set of observations was made in order to ascertain the size of the ovarian eggs which would be associated with newly formed embryos, and, as was expected, the ovarian eggs were always quite small. These results justify the conclusion that in a pregnant female, during the time that a brood of embryos are developing in the uteri, a fresh batch of ovarian eggs are increasing proportionately in size, so that, eventually, when the embryos are born, there is a set of fully developed eggs in the ovaries ready to pass into the oviducts.

As a general rule the mature ova, after leaving the ovaries, occupy both oviducts, but fishes have frequently been obtained in which only one oviduct was occupied. One particular female was in the interesting condition of having an egg-capsule* containing four tiny embryos in one uterus, while the other was empty, and at the same time with a single fully developed egg still remaining in the ovary.

The determination of the sex of the embryos removed from the uteri of pregnant females has shown that males and females are equally represented and may occur together in the same uterus. Of a total of 2720 embryos collected from the fish-market at various times, 1377 were males and 1343 were females.

It is not as simple as would be imagined to obtain precise information on the number of embryos which may be carried by a pregnant female. Some interesting data have been derived by directing attention to the following :—

(1) The number of free embryos in the uteri of fishes landed on the quay.
(2) The number of embryos present in egg-capsules.
(3) The number of maturing eggs in the ovaries.

(1) The number of free embryos in the uteri of fishes landed on the quay will only yield approximate results unless there is good evidence to show that during the course of capture, or after, none of the embryos have been pressed out of the mother. The following are the results of the counting of the number of embryos in each of seventy-four females obtained from the fish-market :—

Number of Embryos per fish.	1	2	3	4	5	6	11
Number of fishes .	7	16	25	15	3	7	1

It will be noticed that there is an absence of fishes containing from seven to ten embryos. It is suggested that this may be due to the artificial pressing-out already referred to above.

(2) A total of 384 egg-capsules, collected at various times from March, 1920, onwards, from the fish-market, has been examined in regard to the number of enclosed embryos, and the following are the results obtained :—

Number of Embryos per Capsule.	1	2	3	4	5
Number of capsules .	65	223	85	10	1

* The term "*egg-capsule*" is used throughout the text as a convenient name for the horny capsule enclosing one or more impregnated eggs in which the earlier developmental stages are undergone. An excellent coloured drawing of an egg-capsule containing six embryos is given by Ed. Graeffe in Arbeit. Zool. Institut. Univ. Wien and Zool. Stat., Triest, 1888, Bd. VII, Heft III, Taf. XXIX, Fig. 1.

It is generally found that a female carries two egg-capsules, one in each uterus, although it is not uncommon for only one to occur. In many instances, also, the two capsules in the one parent contain the same number of embryos, but this is by no means a constant feature. The above results thus indicate that the total number of embryos which may be carried by a pregnant female varies from one to ten, but with a maximum frequency of from three to five.

(3) The number of maturing eggs in the ovaries of each of seventy-four fish of varying lengths was as follows :—

Number of Ovarian Eggs.	1	2	3	4	5	6	7	8
Number of fishes	4	7	28	15	9	4	6	1

These results indicate that the potential brood of young developing in the ovaries of a pregnant female may vary in number from one to eight, with a maximum frequency of three.

Thus, the combined results of the three separate sets of observations, 1, 2 and 3, indicate that if the length of the parent fish be ignored the number of embryos per fish may vary from one to eleven, and is most frequently from three to four. Some observations conducted in February, 1921, however, tend to confirm the view that the number of embryos increases with the length of the parent fish :—

Length of Parent Fish (cm.).	Number of Fishes.								Number of Egg-Capsules.						Number of Fishes.						
	No. of Ovarian Eggs.								No. of Embryos.						No. of Free Uterine Embryos.						
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	1	2	3	4	5	6	11
70–74	–	–	3	2	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
75–79	–	2	4	3	2	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–
80–84	–	1	–	1	3	2	2	–	2	3	1	–	–	–	–	2	1	4	–	–	–
85–89	–	–	1	1	1	1	2	–	–	6	4	–	–	–	1	3	3	–	–	–	–
90–94	–	–	–	–	–	–	1	1	–	–	3	1	1	–	–	–	1	1	–	–	–
95–99	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	1

The number of fishes examined is too small for these results to be of conclusive value, but they suggest that the number of ovarian eggs, the number of embryos per egg-capsule, and the number of free uterine embryos increase with the length of the parent fish.

The Egg-Capsule. (See Footnote on page 472.)

It is well known that the embryos in each uterus of a female are enclosed within a common horny capsule during the earlier stages of development. It is difficult to state definitely the period of development

at which the capsule breaks and the embryos become free in the uterus, nor is the ultimate fate of the remains of the ruptured capsule clearly understood. Kerr (6, page 478) states that as development goes on (embryo of 7–8 cm.) the thin horny shell of the capsule becomes still thinner, breaks up, and disappears. Unruptured egg-capsules have been taken during the present series of observations enclosing embryos up to a length of 7 cm., but it seems possible that under natural conditions the capsule may remain unbroken for a longer period. On November 23rd, 1920, a female embryo of 13·5 cm., when extracted from the uterus, was found to be encased almost completely by the slightly torn shell of the capsule, and it is quite feasible that the rupturing of the latter was a post-mortem injury. On December 2nd, 1920, the remains of the capsule were present in a uterus containing three fully grown embryos of 28–29 cm., so that the capsular remains may rest in the uterus until the embryos are ready for birth.

There is a large amount of variation in the size of egg-capsules. During the months of January and February, 1921, the volume, as a convenient expression of size, of each of 148 newly formed capsules taken from fishes of varying lengths, was determined by the method of displacement. The results obtained, which are summarized below, will convey a fair idea of the general range in volume of egg-capsules derived from fishes irrespective of length :—

Number of Embryos per capsule (n).	Number of Capsules.	Range in Volume in ccm. (R).	Average Volume in ccm. (Vn).	$\left(\frac{Vn}{n}\right)$
1	27	29–68	45·7	45·7
2	86	40–125	91·4	45·7
3	32	65–196	136·9	45·6
4	2	165–210	187·5	46·9
5	1	200	200·0	40·0

The successive values of the ratio $\left(\frac{Vn}{n}\right)$ show that, on average, the volume of an egg-capsule is approximately proportional to the number of embryos it contains, but the corresponding values of the range in volume (R) indicate equally clearly that this relation is merely an average probability which by no means applies to individual capsules. Thus, it will be seen that a capsule containing a single embryo may exceed in volume one containing two or even three embryos. These individual differences in volume are of considerable significance, for they are undoubtedly due to differences in the quantity of yolk associated with the enclosed embryos. It would be expected, therefore, that the embryos in the larger capsules, having a larger available supply of yolk, would be able to grow to a correspondingly larger size before birth, and, assuming

that the rate of embryonic growth is independent of the quantity of yolk, they would remain for the longer time in the uterus (see page 477).

While watching the gutters at work on the quay, the impression was gained that the egg-capsules extracted from the smaller fishes were of a smaller size, and in consequence of this a number of ungutted females were purchased in February, 1921, and measured, and the volume of the egg-capsules, when present, was determined. Unfortunately, the percentage of specimens containing egg-capsules in the total of sixty fish opened was not large, but the results do not conflict with the above impression :—

Number of Fishes.	Length of Fish (cm.).	Egg-Capsules.		
		No. of Embryos.	Range in Volume (ccm.).	Average Volume (ccm.).
4	70–79	2	45–75	62·2
5	80–89	,,	81–115	94·8
1	90–99	,,	90	90·0
—	70–79	3	—	—
4	80–89	,,	116–130	126·5
3	90–99	,,	124–170	156·5

In the first place it is seen that the four specimens from 70 cm. to 79 cm. in length contained capsules which were all considerably under average size. The resultant embryos would, therefore, according to expectation, be below average size at birth. It has already been shown on previous pages, also, that the number of embryos may be dependent on the size of the parent fish, so that there is a combined indication that fishes from 70 cm. to 79 cm. in length give birth to embryos which are below average size and fewer in number. The adolescent period of a female fish is usually undergone, however, when the length is between 70 cm. and 80 cm., so that it is probable that any fish which is carrying embryos and whose length lies between these two limits, is pregnant for the first time. The above results may thus provide some degree of confirmation to the assertion that the embryos of the initial brood of the pregnant female are smaller and lesser in number than those of the subsequent broods.

In the second place, it will be noticed that the egg-capsules containing three embryos are greater in volume in fishes from 90 cm. to 99 cm. in length than in those from 80 cm. to 89 cm. in length. This may indicate that the largest fishes contain the largest egg-capsules, and will therefore produce the largest embryos.

A repetition of the above observations on a much larger scale would thus yield some exceedingly interesting information.

The Embryo.

The external gill filaments, which are so conspicuous a feature of young Elasmobranch embryos, cease to be visible to the naked eye in this species at a varying length between 10·0 cm. and 14·0 cm. :—

Length of Embryo in cm.	Number of Embryos. Gill filaments visible to naked eye.	Gill filaments invisible to naked eye.
10	29	1
11	33	2
12	42	12
13	14	25
14	3	29

The size at which embryos may be regarded as ready for birth needs careful attention. The sex of embryos may here be ignored, for no difference has yet been observed between the male and female in respect to size at any corresponding stage of embryonic development. It is first necessary to determine the condition by which an embryo may be assumed to be ready for birth. It does not appear feasible that the young of this species will be born with any more than a mere external remnant of the yolk-sac. The newly hatched embryos of both the rough-dog and the nursehound usually have a tiny pin-head remnant still unabsorbed, as is also the case in the young of Raia sp., so that this condition has been accepted as the determining factor as to whether or no an embryo of the spur-dog is ready for birth. It has been shown on previous pages that the amount of yolk associated with embryos varies considerably, and that, in consequence, it would be expected that there would be a corresponding variation in the size at birth. From May 8th, 1920, onwards, notes were kept in regard to the degree of absorption of the yolk-sac in embryos from 23 cm. in length upwards, and the results obtained may be summarised thus :—

Month.	NUMBER OF EMBRYOS. Conspicuous Yolk-sac present. Length of Embryo in cm. 23	24	25	26	27	28	29	30	Tiny remnant of Yolk-sac present. Length of Embryo in cm. 23	24	25	26	27	28	29	30	Umbilical Scar healed, or in process of healing. Length of Embryo in cm. 23	24	25	26	27	28	29	30	31
May, 1920	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
June ,,	12	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
July ,,	33	20	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aug. ,,	15	40	25	18	7	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Sept. ,,	8	21	16	7	2	1	1	–	3	4	14	5	4	1	2	–	–	2	2	–	2	4	–	–	–	–	–
Oct. ,,	–	1	2	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nov. ,,	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2	4	3	6	5	11	1	–	–	–
Dec. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	10	19	16	2	–	–

From May until the end of August the great majority of the embryos had a conspicuous bag-like yolk-sac (Fig. 1 is a drawing of a specimen of 25 cm. in length taken during this period). It was quite inconceivable to me that any of these could possibly be able to carry on a separate existence. There were, however, three specimens of 25 cm. in length during August in which the yolk-sac was reduced to the pin-head size, and thus complied with the arbitrary condition of readiness for birth. Towards the end of September there was a noticeable change, and many of the embryos from 23 cm. upwards had the reduced yolk-sac, while in others from 24 cm. the yolk-sac was not only completely absorbed, but the umbilical scar was actually healed or in process of healing. It was rather surprising to learn that so many embryos may remain in the uterus after the complete absorption of the yolk-sac.

Thus, then, these results indicate that it is not until the end of August that any embryo is in a condition ready for birth, but from September onwards specimens from 23 cm. to 31 cm. inclusive (the largest measuring 31·1 cm. in length and weighing 83 grammes) satisfy the conditions for birth. It may be remembered that when dealing with the variation in the volume of egg-capsules from different fishes (page 475), it was suggested that the embryos from the largest capsules would remain for the longest time in the uterus. It is interesting, therefore, to notice that the largest embryos in the above observations occurred most frequently in December, thus providing some measure of confirmation to this suggestion.

For purposes of comparison, the records of investigators in other districts may be given :—

Recorded by.	Locality.	Size at birth in cm.
Borcea (1)	Roscoff	23–25
Le Danois (2)	La Manche occidentale	25
Lo Bianco (7)	Naples	20–24
Smitt (13)	Scandinavia	22–25

The late embryos possess a fairly constantly occurring scheme of round spots of light colour arranged symmetrically in regard to the long axis of the body (see Figs. 1 and 2) :—

(1) A pair of spots, one on either side of the commencement of the first dorsal fin (Fig. 1 and 2, *1*).

(2) A pair of spots, one on either side of the middle line at the level of the hinder end of the first dorsal fin (Figs. 1 and 2, *2*).

(3) A pair of spots, one on either side of the commencement of the second dorsal fin (Figs. 1 and 2, *3*).

(4) One spot on either side of the body immediately above and just behind the insertion of the pectoral fin (Figs. 1 and 2, *4*).

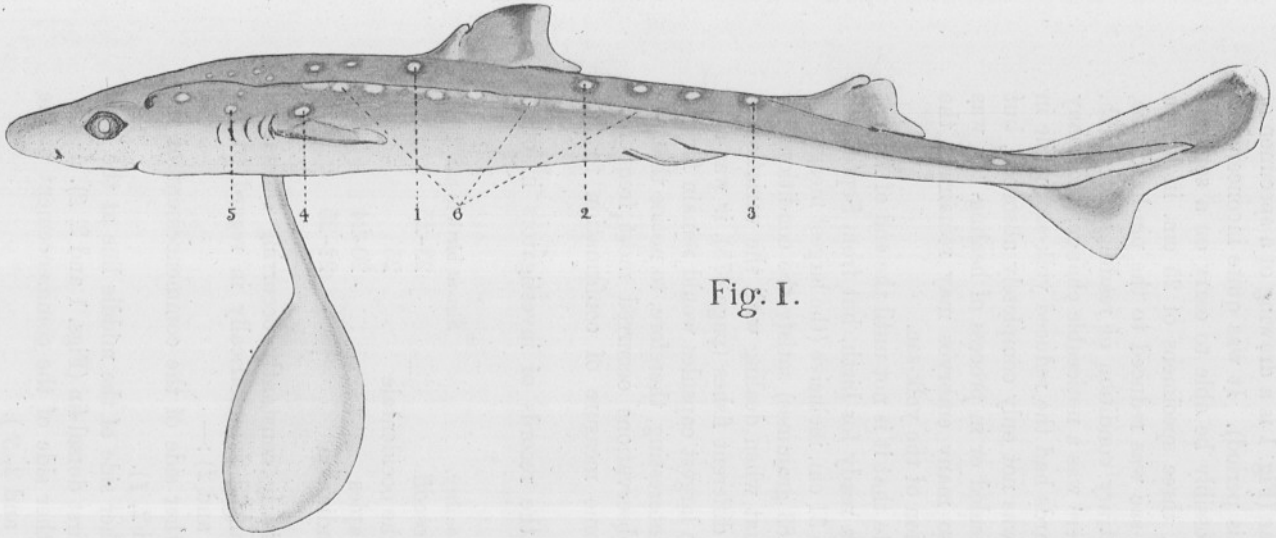


Fig. 1.

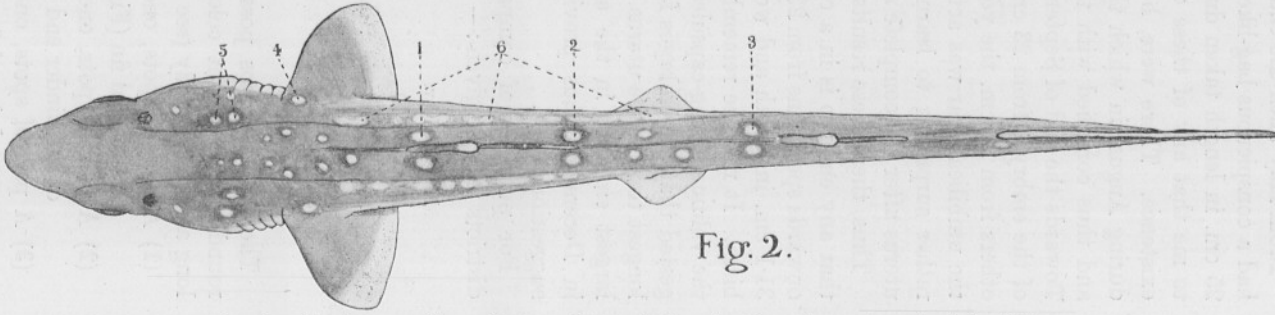


Fig. 2.

Fig. 1.—*Squalus acanthias.* Embryo 25 cm. in length, taken from uterus in July, 1920.
Fig. 2.—*Squalus acanthias.* Same specimen as in Fig. (1) viewed from above.

(5) One or more spots on the gill region on either side (Figs. 1 and 2, *5*).
(6) A more or less continuous row of irregularly circular or oval-shaped spots roughly united to form a light line along either side of the body from the pectorals backwards along the lateral line (Figs. 1 and 2, *6*).

Pairs 1, 2 and 3 are interesting in their origin. In an embryo of 8 cm. in length, instead of the two distinct spots there is a single transverse light-coloured bar. As development proceeds, this bar gradually becomes constructed in the middle, thus producing the pair of spots. The rows (6) along the lateral line arise as a continuous line of light colour, and subsequently break up into the spotted condition.

The fins are typically pigmented. The pectorals and dorsals are brownish black in colour except for the white posterior edge, but the pelvics are uniformly white. The caudal fin is edged with white except for the very deep black tip of the dorsal lobe. This black tip of the dorsal lobe of the caudal and an equally prominent blackened area on the uppermost edge of the first dorsal are the most densely pigmented areas in the embryo. The spines of the dorsal fin conform to the coloration of the fins, except that their protective caps are white.

Examined microscopically, the black pigment appears to be arranged in three layers, one above the other. The most deeply seated layer is composed of fairly large stellate chromatophores. Immediately above this there is a layer of coarse black blotches or dots. The uppermost layer is the least noticeable, and consists of stellate chromatophores which are fewer in number and more widely scattered than those of either of the layers beneath. The light spotted effect is produced partly by a scarceness of black pigment in certain areas, and partly by the presence of greyish white pigment.

The scales of the embryo do not present any unusual feature. They are uniform in character, and although in the largest embryos they are contained each in a finger-like pouch of the skin which projects from the general surface, they do not actually penetrate the latter. The tips of the spines of the dorsal fins are covered by fleshy caps. The scales may be pigmented on their posterior face in a finely granular to stellate manner.

The Breeding Season and the Time Occupied by Embryonic Development.

The information which is at present available in the literature upon these two important subjects is rather indefinite. Some investigators have contended that this species breeds throughout the year (*vide* Lo

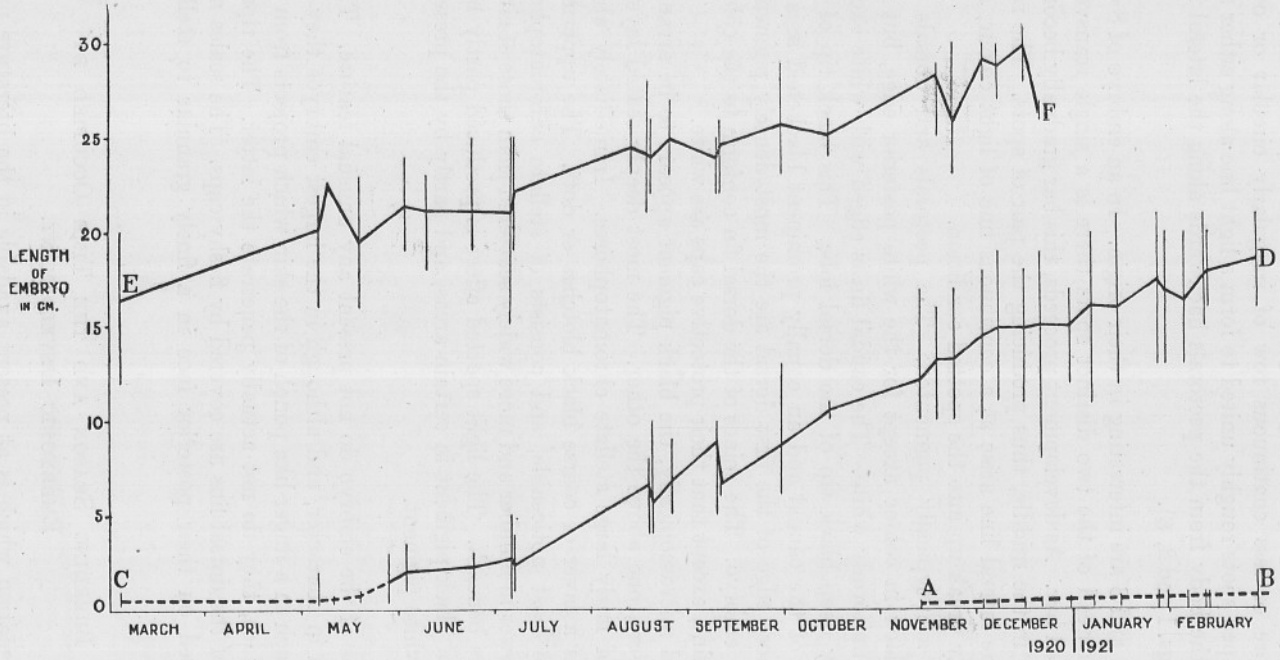


FIG. 3.—*Squalus acanthias.* Graphic representation of the results summarised in Table (A). The range in size of the embryos on any particular day is shown by a thin vertical line. The thickened curves indicate the average length of the embryos on successive days. Average values of less than 1 cm. are represented by the broken lines

Bianco, 7, p. 538, in regard to the Mediterranean, and Day, quoting Mr. Dunn, 3, p. 317, for the English Channel). Le Danois (2, p. 134) states that the fishes of "La Manche occidentale" give birth to their young towards the end of winter. Borcea (1, p. 205) believes that at Roscoff the month of April is the chief time at which embryos in a condition ready for birth are found in the uteri of the females. He gives the range in size of the uterine embryos for different periods during the year, and concludes that embryonic development requires nearly one year to complete. Day (3, p. 317) was of the opinion that the British fishes breed throughout the summer and autumn, but he also quoted the view of Mr. Dunn already referred to above. Yarrell (15, p. 402) expressed the view that the young are born at various periods from June to November, while Garstang (4, p. 229) has recorded the breeding season at Plymouth as from January to March. Smitt (13, p. 1161) has given some interesting information :—

> "Aristotle stated that on the coast of Greece this fish copulates in August, and brings forth its young from May till August. The case is apparently as a rule the same in Scandinavian waters. Ekström concluded from his observations in Bohüslan that the breeding is performed in shoals during August or September in rather deep water. According to many corroborative statements the young are born most plentifully at the end of April and the beginning of May, and afterwards, in less number, throughout the summer."

Since the beginning of March, 1920, embryos and egg-capsules have been collected continuously from the Plymouth fish-market in an endeavour to obtain the range of variation in size of the embryos during the successive months of the year. In the case of unruptured egg-capsules, the number of enclosed embryos was ignored, so that in the summarised results one unbroken capsule simply represents one embryo of a particular size. The results obtained are summarised in the accompanying Table A, and shown in graphic form in Fig. 3.

It will be observed that, on any one day, the embryos are separable into two or three distinct size-groups, according to the time of the year. In addition, the mean values for the corresponding size-groups of successive samples conform to fairly regular curves. It may therefore be concluded that the breeding season of this species has definable limits.

If we accept the twelve months from March, 1920, until February, 1921, both inclusive, as an average year, then the average growth of an embryo may be expressed by a composite curve constructed by linking together the separate elements AB, CD, and EF, of Fig. 3. This curve would be at its lowest point in November, and require a period of about twenty-

five months to reach its maximum in the month of December. Embryos measuring less than 1 cm. in length would occur from November until the beginning of July, but in view of the relatively large average length from late May until July, it seems probable that newly formed embryos would only be met with from November until the middle of May. Again, on page 477 it was shown that embryos in a condition ready for birth occur only from the end of August until the end of December. These two results when applied to our composite curve enable us to conclude quite reasonably that an embryo commencing its growth in November may be ready for birth in the month of August after a lapse of twenty-one months, having attained a length of 25 cm. On the other hand, it may be that at this length the embryo has not yet absorbed sufficient yolk to make a separate existence possible, and in consequence it may continue in the uterus, not only until all the yolk is absorbed, but until the umbilical scar is completely healed, with a resultant increase of length to an observed maximum of 31 cm.

It may be useful to give a summary of the range in size of embryos for each month from March, 1920, until February, 1921 :—

Month.	Range in size of Embryos in cm. Size-group I.	Size-group II.	Size-group III.
March, 1920	>1– 1	12–20	—
April ,,	No observations		
May ,,	>1– 3	16–23	—
June ,,	>1– 3	18–25	—
July ,,	>1– 5	15–25	—
August ,,	4–10	21–28	—
September ,,	5–13	22–29	—
October ,,	10–11	24–26	—
November ,,	10–17	23–30	>1
December ,,	8–19	26–31	>1
January, 1921	11–21	—	>1–1
February ,,	13–21	—	>1–2

The Constitution of the Shoals.

Some general observations on this interesting question were commenced in October, 1919, when the daily landings, irrespective of the method of capture, showed a very great predominance of females, the majority of which were of large size, and in a gravid condition. From November 4th to November 19th, of a total of 885 fish picked up at random from the quay 810 were females and only 75 were males. Towards the end of November, however, it became noticeable that fish of a smaller size were being landed in increasing numbers, while the proportion of

TABLE A.

Date.	Embryos from Unruptured Egg-Capsules.									Embryos from Ruptured Egg-Capsules, or Free in the Uterus.																											Embryos from all Sources.						Date.
	Total No. of Egg-Capsules.	Size of Embryos in cm. groups.								Total No. of Embryos.	Size of Embryos in cm. groups.																											Total No. of Embryos.	Mean Values.					
		>1	1	2	3	4	5	6	7		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		No. of Embryos.	Average Size in cm.	No. of Embryos.	Average Size in cm.	No. of Embryos.	Average Size in cm.	
1920																																										1920
Mar. 4	14	13	1	—	—	—	—	—	—	87	—	—	—	—	—	—	—	—	1	2	6	16	30	12	13	5	2	—	—	—	—	—	—	—	—	—	—	101	14	<1	87	16·3	—	—	Mar. 4
May 5	7	6	—	1	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	3	2	6	2	—	—	—	—	—	—	—	—	22	7	<1	15	20·0	—	—	May 5
,, 8	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	3	—	—	3	22·7	—	—	,, 8
,, 10	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	<1	—	—	—	—	,, 10
,, 18	13	(largest was 1 cm.)					—	—	—	70	—	—	—	—	—	—	—	—	—	—	—	—	1	3	11	23	21	5	5	1	—	—	—	—	—	—	—	83	13	<1	70	19·4	—	—	,, 18
,, 27	21	3	9	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	21	ca 1·5	—	—	—	—	,, 27
June 2	19	—	7	4	8	—	—	—	—	77	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	16	27	21	8	4	—	—	—	—	—	—	96	19	2·0	77	21·4	—	—	June 2
,, 9	—	—	—	—	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	4	5	2	—	—	—	—	—	—	—	15	—	—	15	21·1	—	—	,, 9
,, 23	19	1	2	11	5	—	—	—	—	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	11	18	15	2	2	1	—	—	—	—	—	75	19	ca 2·3	56	21·1	—	—	,, 23
July 5	24	1	2	8	8	4	1	—	—	54	—	—	—	—	—	—	—	—	1	4	1	—	3	9	12	9	9	5	1	—	—	—	—	—	—	—	78	24	2·7	54	21·0	—	—	July 5
,, 6	26	—	4	12	8	2	—	—	—	123	—	—	—	—	—	—	—	—	—	—	—	—	3	11	24	43	24	15	3	—	—	—	—	—	—	—	149	26	2·4	123	22·1	—	—	,, 6
Aug. 13	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	4	—	—	4	24·5	—	—	Aug. 13
,, 18	1	—	—	—	—	1	—	—	—	37	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	3	6	3	10	5	3	4	1	—	—	—	38	3	6·6	35	24·1	—	—	,, 18
,, 19	17	—	—	—	—	5	12	—	—	66	3	5	21	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	1	8	14	8	2	—	—	—	—	83	50	5·6	33	24·0	—	—	,, 19
,, 25	26	—	—	—	—	—	9	15	2	69	—	3	10	6	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	3	15	14	12	3	—	—	—	95	48	6·8	47	24·9	—	—	,, 25
Sept. 9	—	—	—	—	—	—	—	—	—	35	—	3	—	1	—	6	3	—	—	—	—	—	—	—	—	—	—	—	1	3	16	2	—	—	—	—	—	35	13	8·9	22	23·9	—	—	Sept. 9
,, 10	1	—	—	—	—	—	—	1	—	23	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	4	12	3	—	—	—	—	24	2	6·5	22	24·6	—	—	,, 10
,, 29	—	—	—	—	—	—	—	—	—	137	—	—	2	6	29	30	10	3	1	1	—	—	—	—	—	—	—	—	—	6	6	17	9	8	6	3	—	—	137	82	8·7	55	25·7	—	—	,, 29
Oct. 14	—	—	—	—	—	—	—	—	—	11	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	2	2	3	—	—	—	—	—	11	4	10·5	7	25·1	—	—	Oct. 14
Nov. 13	2	2	—	—	—	—	—	—	—	54	—	—	—	—	—	—	1	18	19	8	6	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	56	54	12·1	—	—	2	<1	Nov. 13
,, 18	—	—	—	—	—	—	—	—	—	134	—	—	—	—	—	—	1	8	25	26	32	12	6	—	—	—	—	—	—	—	—	1	3	5	5	10	—	—	134	110	13·2	24	28·3	—	—	,, 18
,, 23	—	—	—	—	—	—	—	—	—	143	—	—	—	—	—	—	3	14	20	45	34	11	—	7	—	—	—	—	—	1	2	3	—	1	—	1	1	—	143	134	13·2	9	25·8	—	—	,, 23
Dec. 2	13	13	—	—	—	—	—	—	—	90	—	—	—	—	—	—	2	1	3	24	15	16	9	4	3	—	—	—	—	—	—	—	—	—	2	7	4	—	103	77	14·5	13	29·2	13	<1	Dec. 2
,, 7	2	2	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—	1	5	8	18	18	16	7	—	1	—	—	—	—	—	—	—	2	7	11	6	—	102	74	14·9	26	28·8	2	<1	,, 7
,, 15	6	6	—	—	—	—	—	—	—	119	—	—	—	—	—	—	—	5	9	7	16	31	23	13	5	—	—	—	—	—	—	—	—	—	1	1	6	2	125	109	14·9	10	29·9	6	<1	,, 15
,, 20	5	5	—	—	—	—	—	—	—	105	—	—	—	—	2	—	—	—	2	8	25	16	26	17	4	1	—	—	—	—	—	—	3	1	—	—	—	110	101	15·1	4	26·3	5	<1	,, 20
,, 31	7	7	—	—	—	—	—	—	—	93	—	—	—	—	—	—	—	—	3	19	15	13	27	16	—	—	—	—	—	—	—	—	—	—	—	—	—	100	93	15·0	—	—	7	<1	,, 31
1921																																										1921
Jan. 6	7	7	—	—	—	—	—	—	—	107	—	—	—	—	—	—	—	1	5	4	5	14	36	16	15	8	3	—	—	—	—	—	—	—	—	—	—	114	107	16·2	—	—	7	<1	Jan. 6
,, 14	4	4	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—	—	2	5	14	13	30	17	9	6	2	2	—	—	—	—	—	—	—	—	—	104	100	16·1	—	—	4	<1	,, 14
,, 27	24	23	1	—	—	—	—	—	—	59	—	—	—	—	—	—	—	—	—	3	2	1	3	16	16	11	5	2	—	—	—	—	—	—	—	—	—	83	59	17·6	—	—	24	<1	,, 27
,, 29	15	14	1	—	—	—	—	—	—	65	—	—	—	—	—	—	—	—	—	2	3	9	9	18	14	4	6	—	—	—	—	—	—	—	—	—	—	80	65	16·9	—	—	15	<1	,, 29
Feb. 5	18	17	1	—	—	—	—	—	—	32	—	—	—	—	—	—	—	—	—	4	5	6	2	5	—	4	6	—	—	—	—	—	—	—	—	—	—	50	32	16·4	—	—	18	<1	Feb. 5
,, 11	13	12	1	—	—	—	—	—	—	32	—	—	—	—	—	—	—	—	—	—	—	4	4	—	15	6	1	2	—	—	—	—	—	—	—	—	—	44	32	17·8	—	—	13	<1	,, 11
,, 12	21	17	4	—	—	—	—	—	—	44	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10	16	9	5	—	—	—	—	—	—	—	—	—	65	44	18·0	—	—	21	<1	,, 12
,, 28	40	35	4	1	—	—	—	—	—	37	—	—	—	—	—	—	—	—	—	—	—	—	1	2	11	18	4	1	—	—	—	—	—	—	—	—	—	77	37	18·7	—	—	40	<1	,, 28

To face page 488.

the conspicuously large fish was diminishing. In consequence of this, attention was directed to the landings of individual boats in order to ascertain the degree of variation in size of the fish in each case. The impression gained was that the fish caught by an individual boat on any one day were of a fairly uniform size, but that the average daily size varied considerably on different occasions. This suggests, first, that the shoals are constituted of fish of a similar size, and second, that during the period of observation shoals of large fish and shoals of small fish were present on the fishing grounds.

As often as possible the proportion of sexes in the fish of individual boat-landings was ascertained, and it soon became evident that the former was closely related to the average size of the fish. For instance, in the largest fish, as shown above, the females were overwhelmingly predominant, but in the smallest fish examined the sexes were approximately equal in numbers.

Observations of this kind have been continued, and a number of the results obtained are tabulated below, from which it is possible to derive a good deal of interesting information in regard to the shoaling habits of this species.

Reference No.	Date.	Details of Sample of Fish Examined.	Total No. of Fishes	No. of Females.	No. of Males.
1	Nov. 4th–19th, 1919	Random samples from landings, irrespective of the method of capture. Majority of the fish over 80 cm. in length.	885	810	75
2	Nov. 25th, 1919	From the catch of s.s. *Condor*. Average size of fish 50–70 cm.	258	51	207
3	Nov. 26th, 1919	A small heap of discarded fish of sizes from 36–50 cm.	56	30	26
4	Jan. 8th, 1920	From s.s. *Condor* which landed about 9000 uniformly medium-sized fish. N.B.—On the same day the local sailing boats had catches of fish of large size showing the predominance of the female element.	284	200	84
5	Jan. 17th, 1920	A small heap of discarded fish of sizes from 40–50 cm.	75	41	34
6	Jan. 21st, 1920	A sample of " drift " fish of average size from 45–50 cm. with which were a very small number of males from 70–73 cm.	290	180	110
7	Feb. 7th, 1920	A sample of fishes of sizes from 50–60 cm.	104	52	52
8	Mar. 10th, 1920	From the catch of s.s. *Trojan* consisting of small fish with an occasional larger ♂ and ♀.	272	142	130
9	July 5th, 1920	From s.s. *Oithona* off Looe, of average size from 50–60 cm.	97	48	49
10	July 29th, 1920	From local smacks off Falmouth, sizes 45–60 cm.	300	150	150
11	Aug. 19th, 1920	From French boat *Resurrection*, about 15 miles E.S.E. of the Start. Average size 80–90 cm.	100	98	2
12	Aug. 25th, 1920	Hook and line fish from a Fowey boat. Average size 80–90 cm.	101	100	1
13	Sept. 23rd, 1920	From local trawler. Average size 45–60 cm.	100	45	55

Before proceeding to the discussion of these results it is necessary to recall to mind several biological facts which have already been dealt with in preceding pages, viz. :—

(1) The adult female normally grows to a longer length than the male.
(2) Sexual maturity in the male is acquired at a length of about 59–60 cm., but in the female at between 70 and 80 cm.
(3) Males and females are born in equal numbers and at the same length.

With these facts in mind one is led to suggest that size and sexual condition are important factors in the constitution of the shoals in this species, the former probably being the more influential one. It seems reasonable to expect that in general it is more advantageous for fishes of the same average size to run together, both from the point of view of ensuring a fair chance of obtaining food, and of adapting the speed and extent of the swimming to the limit of endurance of the majority of the shoal. In shoals of fish of greatly varying sizes it is probable that the small fish would suffer in their chances of obtaining food, and would also have difficulty in maintaining the speed and endurance of the larger and stronger members. On the other hand, when it is remembered that the females in the pregnant condition may carry as many as ten embryos all of the same general size which may be as much as 30 cm. before birth, it is equally logical to expect that they require to move at a more leisurely rate and under conditions favourable to their temporary disability. In this case the factor of size may be of lesser importance. There would therefore appear to be a balance between these two factors of size and sexual condition whereby the shoals of fish are formed to ensure maximum comfort and equal chances of survival for the members of the shoal. The catch of s.s. *Condor* on November 25th, 1919 (Ref. No. 2), however, in which males were greatly predominant, is not explained by the above factors. The occurrence of shoals of males has been recorded by other investigators, e.g. Borcea (1, p. 205), Meyer (9) and Smitt (13, p. 1161), so that there is evidence of the segregation of males, for some part of the year at any rate. At present it is difficult to suggest a reason for this, unless, on reaching maturity, the male, unlike the female, prefers to remain in deeper waters and does not approach the coast (*vide* Borcea, 1, p. 205).

If it be assumed that during the period of investigation the two factors of size and sexual condition were in operation, it would be expected theoretically that shoals of the following constitution would be met with :—

A. Shoals of large fish consisting exclusively of females, the majority in the pregnant condition.

B. Shoals of medium-sized fish exclusively males in the mature condition.

C. Shoals of medium-sized fish of which the majority were immature females.

D Shoals of immature fish in which the males and females were equal in number.

These theoretical expectations are not inconsistent with the practical observations which have been tabulated above :—

Reference No. of sample of Fish.	Theoretical category of shoal from which derived.
1	A
2	B
3	D
4	C
5	D
6	D
7	D
8	D
9	D
10	D
11	A
12	A
13	D

The Food of the Spur-Dog.

From the beginning of November, 1919, until the end of January, 1920, samples of stomachs were obtained from the fish-market, and their contents examined in the Laboratory. Of the 143 stomachs which contained recognisable food, 137 contained remains of fish, 6 contained crustacean remains, and 3 molluscan remains. Of the 137 containing fish remains, the percentages of various species of fish are given in the following table :—

Species.		Percentage of stomachs in which present.
Clupea sp.	*C. pilchardus*, *C. harengus*	67·2
Scomber scomber		19·0
Gadus sp.	*G. merlangus*, *G. luscus*, *G. minutus*	4·0

Species.	Percentage of stomachs in which present.
Pleuronectes sp.	1·4
Trigla sp. (*T. gurnardus*, *T. cuculus*)	1·4
Callionymus lyra	1·4
Raia sp.	1·4
Species unidentified	10·1

It must be remembered that the time during which these estimations were made coincides with that of the local pelagic fisheries for herring, pilchard and mackerel, so that there was a large available supply of these fishes as food for the dogfishes. The high proportion of the former fishes in the stomachs of the latter may therefore be due to this fact, quite apart from any selective action by the dogfishes. On November 26th, 1919, eighteen stomachs of fish from 36 cm. to 50 cm. in length were obtained, but owing to the stale condition it was not possible to determine the nature of the whole of the stomach contents. Remains of herring, mackerel and callionymus sp. were recognised, however, so that at this small size fish may form part of the diet.

SCYLIORHINUS CANICULA (ROUGH-DOG).

Maximum Size and Sexual Maturity.

Unlike the spur-dog this species exhibits no marked difference between the male and female in regard to the maximum length to which they may grow, and the largest specimens of both sexes measured at Plymouth do not exceed 70 cm. in length. Mr. A. J. Smith of the Plymouth Laboratory, who has had the handling of several thousands of rough-dogs yearly over a long period, has informed me that during the autumn of 1919 he observed some unusually large specimens which he estimated were at least 30 inches in length. Although no actual measurements of these specimens are available, the observation is noteworthy in view of the fact that the fish were sufficiently unusual in size to command attention.

A second difference from the spur-dog is that sexual maturity is in this species acquired at approximately the same length in both male and female, usually from 57 to 60 cm., although one female of 54 cm. was found to be carrying fully developed egg-purses in the oviducts. The claspers of the male do not appreciably lengthen on the attainment of sexual maturity.

The Egg-Purses.

According to Philip White (14, p. 6) the egg-purses of the rough-dog are obtainable by shore-collecting at the lowest spring tides at Careg Dion on the Anglesea side of the Menai Straits, but no such convenient ground has yet been discovered at Plymouth. (Cf. the nursehound on p. 492.) They may be obtained quite easily, however, either from the local trawlers or by actual removal from adult females landed on the quay. The embryos from specimens obtained in the latter way will hatch out quite satisfactorily in aquaria. The egg-purses exhibit a good deal of variation in size, as will be seen from the results tabulated below, of the measurements of fifty-five egg-purses extracted from adult females on August 17th, 1920 :—

	Minimum Length (in cm.).											Maximum Width (in cm.)								
	5·3	5·4	5·5	5·6	5·7	5·8	5·9	6·0	6·1	6·2	6·3	6·4	2·1	2·2	2·3	2·4	2·5	2·6	2·7	2·8	2·9
No. of Egg-purses	3	3	6	2	4	10	8	10	2	3	1	3	3	22	13	12	3	1	–	–	1

	Range of Variation (in cm.).	Average (in cm.).
Minimum length . .	5·3–6·4	5·8
Maximum width . .	2·1–2·9	2·3

The Embryo.

Egg-purses extracted from adult females from time to time have been kept in aquaria, and notes made on the embryos at various stages of development. The external gill-filaments cease to be visible to the naked eye in specimens at between 6 and 7 cm. in length, and the young fish are hatched at between 9 and 10 cm. with a tiny globular remnant of the yolk-sac. When hatched they seem particularly helpless and weakly. Their eyes are closed and they remain practically motionless. If they are induced to swim, they show little powers of equilibrium and easily turn over, continuing to swim with the ventral surface uppermost. These signs of weakness may, of course, be entirely due to the artificial incubation, and may not be the normal feature under natural conditions in the sea.

The consideration of the development of scales, and the scheme of pigmentation of the embryo is deferred to a separate section on page 493 in conjunction with the closely allied species, *S. stellaris*.

The Breeding Season.

There is evidence that the breeding season of this species is a protracted one. In May, 1920, the plan was adopted of keeping a continuous record of the number of females in which fully developed egg-purses were

present in the oviducts, as they arrived at the Laboratory from the quay. The results so far obtained may be summarised monthly, as follows :—

Month.		Total number of females examined.	Total number carrying egg-purses.	Percentage.
May,	1920	80	18	22·5
June	,,	313	74	23·6
July	,,	109	27	24·8
August	,,	5	2	*40*
September	,,	71	7	9·9
October	,,	198	19	9·5
November	,,	143	24	16·8
December	,,	138	24	17·4
January,	1921	147	18	12·3
February	,,	113	22	19·5

Although results for the months of April and March have not yet been obtained, it is definitely known from past experience that egg-purses are deposited in considerable numbers during this time of the year, so that there is the strongest evidence that in the waters off Plymouth the rough-dog may deposit egg-purses in any month. (Cf. Lo Bianco, 7, p. 544, in regard to the fishes at Naples.) The numerical results suggest that egg-deposition takes place principally during the spring and summer, and is least during the autumn.

The Proportion of the Sexes in the Adults.

A fairly regular supply of adult fishes is received at the Plymouth Laboratory throughout the year for disposal chiefly to universities and schools, and while, admittedly, only reasonably large specimens are accepted, yet there is no attempt at sexual selection in the daily consignments from the fish-market. It has already been pointed out that there is no appreciable difference in maximum size between the males and females of this species, so that these daily consignments may be accepted as a rough estimate of the relative frequency of the sexes for the particular day. The numbers of males and females in each sample of fish received have been noted, and the results summarised as in Table B.

These results, when plotted as in Fig. 4, show a curious alternating predominance in the sexes—during the winter the males are the predominant element, whereas in the summer the females are the more numerous. The curves suggest that in late spring and late autumn the sexes will be approximately equal in number. It is difficult to under-

TABLE B.

Date.	Total No. of Samples Examined.		No. of Samples in which ♂ predominant.		No. of Samples in which ♀ predominant.		No. of Samples in which Sexes were equal.		Total No. of Fishes Examined.		Total No. of ♂		Total No. of ♀		Percentage of ♂		Percentage of ♀	
Nov., 1919	13	**19**	8	**14**	5	**5**	—	—	654	**1028**	353	**607**	301	**421**	54	**59**	46	**41**
Dec. ,,	6		6		—		—		374		254		120		68		32	
Jan., 1920	8	**9**	7	**8**	1	**1**	—	—	524	**579**	337	**375**	187	**204**	64	**65**	36	**35**
Feb. ,,	1		1		—		—		55		38		17		69		31	
May ,,	5	**21**	1	**5**	4	**14**	—	**2**	186	**735**	90	**326**	96	**409**	48	**44**	52	**56**
June ,,	16		4		10		2		549		236		313		43		57	
July ,,	5	**6**	—	**1**	5	**5**	—	—	181	**193**	72	**79**	109	**114**	40	**41**	60	**59**
Aug. ,,	1		1		—		—		12		7		5		*58*		*42*	
Sept. ,,	7	**17**	3	**5**	3	**11**	1	**1**	140	**474**	69	**205**	71	**269**	49	**43**	51	**57**
Oct. ,,	10		2		8		—		334		136		198		41		59	
Nov. ,,	8	**18**	4	**13**	4	**4**	—	**1**	260	**629**	117	**348**	143	**281**	45	**55**	55	**45**
Dec. ,,	10		9		—		1		369		231		138		63		37	
Jan. ,,	11	**17**	9	**14**	2	**3**	—	—	352	**730**	205	**461**	147	**269**	58	**63**	42	**37**
Feb. ,,	6		5		1		—		378		256		122		68		32	

stand the significance of these results unless there be a distinct difference in habits in the two sexes.

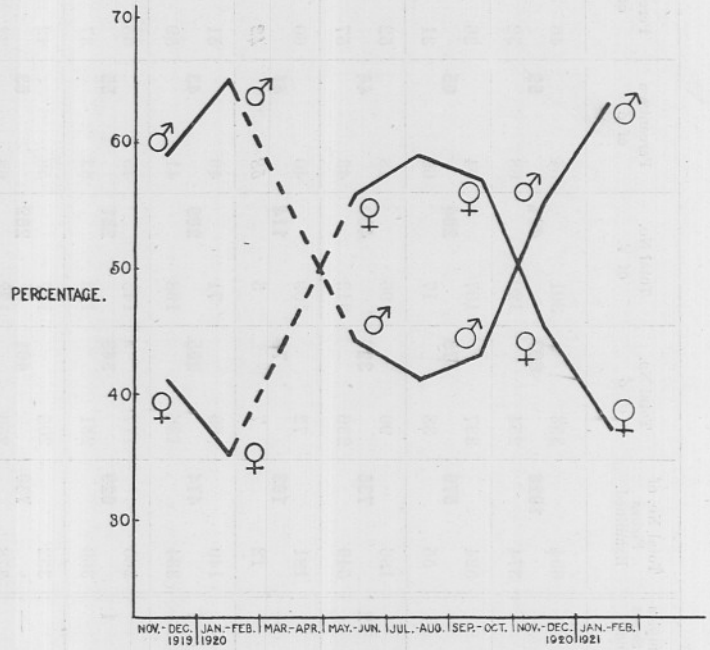


FIG. 4.—*Scyliorhinus canicula*. Graphic representation of the percentage of males and females in the adult fishes received at the Plymouth Laboratory (see Table B).

THE FOOD OF THE ROUGH-DOG.

From November, 1919, until February, 1920, the stomach contents of a total of 146 fish were examined and recorded :—

Stomach Contents.		Number of stomachs in which present.	Percentage.
PISCES		73	50
Clupea sp.	*C. harengus, C. pilchardus and C. sprattus*	20	
Elasmobranch remains	Dogfish and rays	8	
Scomber scomber		6	
Pleuronectes sp.		5	
Gadus sp.	*G. merlangus, G. minutus*	4	
Syngnathus sp.		1	
Gobius sp.		1	
Callionymus sp.		1	
Remains unidentified		32	

Stomach Contents.		Number of stomachs in which present.	Percentage.
CRUSTACEA		131	90
Eupagurus sp.	*E. Bernhardus* *E. prideauxi*	67	
Alpheus sp.		36	
Upogebia sp.	*U. deltura, U. stellata*	24	
Portunus sp.	*P. puber, P. depurator* *P. pusillus, P. holsatus*	19	
Galathea sp.		11	
Nika edulis		9	
Amphipoda		8	
Atelocyclus septemdentatus		7	
Crangon sp.		5	
Gonoplax rhomboides		4	
Palaemon sp.		2	
Ebalia sp.		2	
Inachus sp.		1	
Remains unidentified		6	
MOLLUSCA		35	24
Buccinum undatum		10	
Pecten sp.		7	
Loligo sp.		6	
Cardium sp.		3	
Tritonia sp.		3	
Scaphander lignarius		2	
Mya truncata		2	
Remains unidentified		8	
POLYCHAETA (unclassified)		73	50
ECHINODERMA (Thione sp.)		22	15
GEPHYRAEA (unclassified)		25	17

The presence of the remains of such typically pelagic fish as herring and mackerel in the stomach of an essentially bottom feeder may appear strange. The suggestion is offered that the remains represent fish which have either been dropped from the commercial drift nets, or have been actually picked out from the nets by the dogfish themselves. It is improbable that any free-swimming pelagic fish is likely to be attacked by the rough-dog. The remains of dogfishes and rays were easily

recognisable as the sliced-off spurs and fins of the spur-dog and the offal from rays, which had been removed from the fish-market and dumped into the sea.

SCYLIORHINUS STELLARIS (NURSEHOUND).

It has not been possible to obtain sufficiently large numbers of specimens of this species to derive reliable indications in regard to the adult form, but, on the other hand, whereas the egg-purses of *S. canicula* cannot be obtained by shore-collecting, those of *S. stellaris* have been found during exceptionally favourable spring-tides in rock pools at Wembury Bay. In the months of March and September, specimens have been discovered attached to the base of bunches of *Cystisira* sp. On March 20th, 1920, twenty egg-cases were collected, varying in minimum length from 11·0 to 12·5 cm., and in maximum width from 4·0 to 4·5 cm. (cf. *S. canicula*, p. 487). The developing embryos were separable into two distinct size-groups, twelve being of a length not exceeding 1·2 cm., and the remaining eight of sizes from 9·8 to 16·0 cm. The absence of individuals of lengths between 1·2 cm. and 9·8 cm. recalls the experience in the case of the embryos of the spur-dog, and suggests that the breeding season has definable limits. On September 13th, 1920, only one egg-capsule could be found owing to unfavourable conditions, but it contained an embryo measuring 4·4 cm. in length. It will be noticed that embryos of this size were not found in the previous March, and it may be assumed that this September specimen belonged to the same size-group as the March specimens which did not exceed 1·2 cm. in length.

From an examination of the Laboratory collection of embryos it has been concluded that the external gill-filaments cease to be visible in embryos of about 10 cm. in length, and that hatching occurs when the embryo is about 16 cm. in length, a tiny globular remnant of the yolk-sac being present, as in the rough-dog.

There is a noticeable difference in regard to the sizes at birth of dogfish between the records of investigators in other districts, and those observed at Plymouth, particularly in the case of the nursehound. For instance, Borcea (1, p. 206) states that *Scyllium catulus* (=*Scyliorhinus stellaris*) at Roscoff at the moment of leaving the egg-case has a length of from 10 to 12 cm., as compared with the length of 16 cm. in the case of Plymouth specimens. The sizes recorded by Borcea for the newly born or newly hatched young of *Squalus acanthias*, *S. canicula* and *S. stellaris* are all smaller than those given in the present publication for the Plymouth fish. These differences are very interesting, and may be of significance.

As in the case of *S. canicula* the characters of the embryonic scales and pigmentation are dealt with in a separate section on page 493.

Food of the Nursehound.

It has only been possible to examine the stomach contents of eighteen fish, but the records confirm the belief that this species like the rough-dog is a bottom-feeder :—

Stomach Contents.	No. of stomachs in which present.
PISCES	13
Scyliorhinus canicula	3
Clupeoid remains	3
Callionymus lyra	3
Trigla sp.	2
Gadus sp.	2
Pleuronectes sp.	1
CRUSTACEA	7
Cancer pagurus	5
Eupagurus sp.	2
MOLLUSCA	2
Loligo sp.	1
Moschites cirrosa	1

In three stomachs the more or less complete bodies of small specimens of *S. canicula* were present, suggesting that the nursehounds from which the stomachs were extracted had attacked and eaten the rough-dogs.

The suggestion receives confirmation by the observation in the Aquarium at Plymouth of a nursehound actually devouring a small living rough-dog.

The presence of large specimens of the edible crab in five stomachs may prove to be of commercial importance if it signifies that the nursehound shows a preference for this species of crustacea.

DEVELOPMENT OF SCALES AND PIGMENTATION IN THE YOUNG OF SCYLIORHINUS.

These two subjects may be more conveniently treated in a separate section than as part of the specific descriptions on the preceding pages.

Development of Scales.

The first scales to appear in the embryos of both *S. canicula* and *S. stellaris* are symmetrically arranged in a sequence of transverse pairs forming two longitudinal rows, one on either side of the middle line in a dorso-lateral position. The rows commence anteriorally just in front of and above the level of the insertion of the pectorals, and extend

posteriorally as far as about the middle of the pelvics (see Figs. 5, 6, 8 and 9). The number of scales per row is of specific value (see below, and cf. Mayer, 8, p. 227). The scales themselves develop each in a roughly

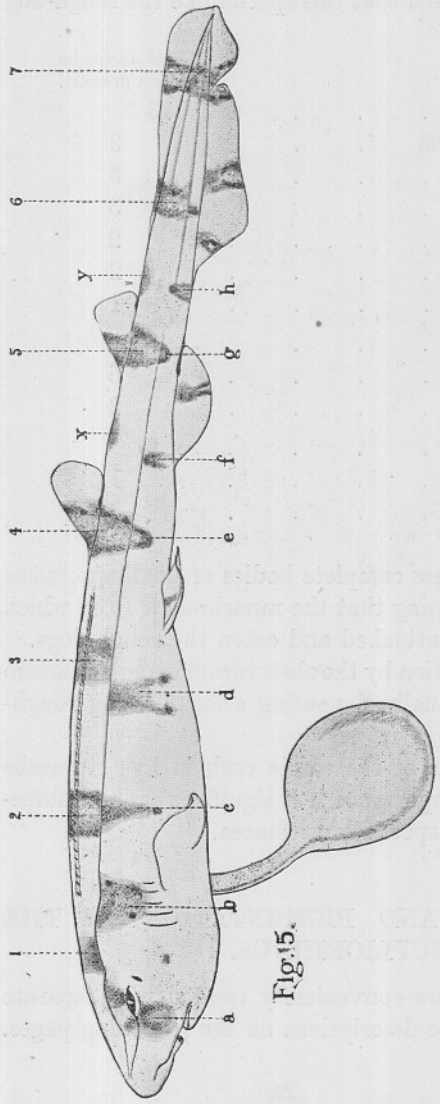


Fig. 15.

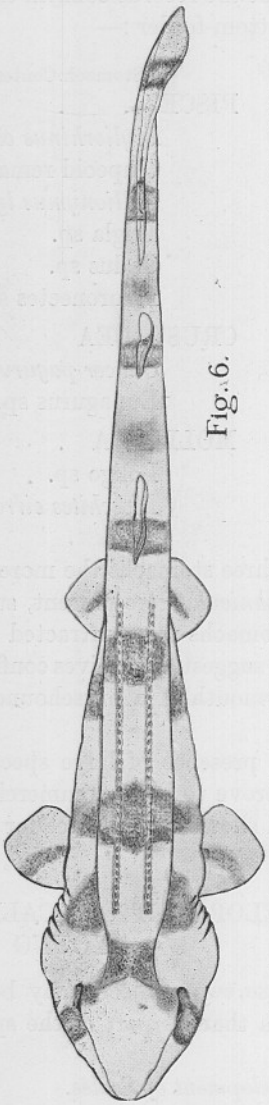


Fig. 6.

FIG. 5.—*S. stellaris*. Embryo 14·8 cm. in length, extracted from an egg-case on March 21st, 1920.
FIG. 6.—*S. stellaris*. Same specimen as in Fig. 5 viewed from above.

oval-shaped "cup" in the dermis (Fig. 7), and they possess a single medium dorso-ventrally flattened cusp with a bluntly rounded apex. The markedly characteristic appearance of these primary scales is retained not only throughout embryonic life, but for some time after the young are hatched. They are always conspicuously larger than the

normal body scales of the embryo, and, unlike the latter, penetrate the skin some considerable time before hatching (Fig. 19). In the young adolescent fish it would seem that they develop into typical body scales of enlarged size (Fig. 14), but they lose their individuality eventually

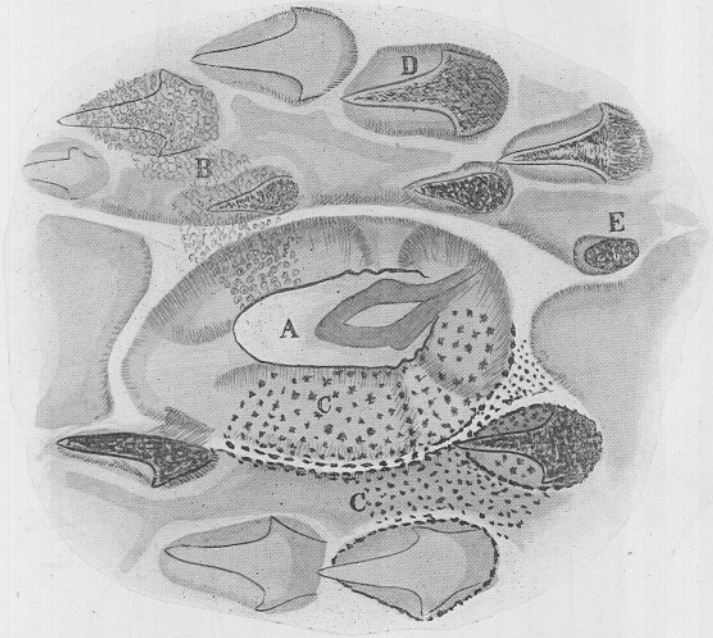


FIG. 7.—*S. stellaris*. Semi-diagrammatic representation of a piece of skin taken from the right side of the body of an embryo of 14·8 cm. in length in the region of the modified primary scales.

A. Modified scale projecting from its dermal "cup."
B. Portion of the epidermis which actually covers the whole, except the cusp of the dorsal modified scale.
C. Black chromatophores which cover the floor of the dermal "cups."
D. A normal body scale developing in its dermal "cup." Note the granular pigmentation.
E. One of the more deeply seated, less developed and heavily pigmented scales.

owing to the presence of equally large and similar scales which have grown up around them.

The occurrence of these modified primary scales is not confined to the two species of the Scyliorhinidæ under consideration. I examined recently a number of embryos of different species in the collection at the Natural History Museum, South Kensington, and found that with slight specific modifications similar scales were present in the embryos of *S. ventriosus*, *S. buergeri*, *S. Edwardsii* and *S.* (species ?), and also

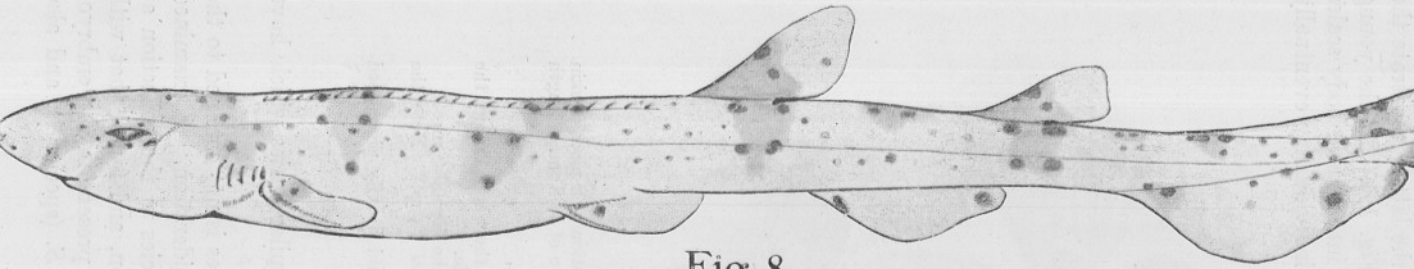


Fig. 8

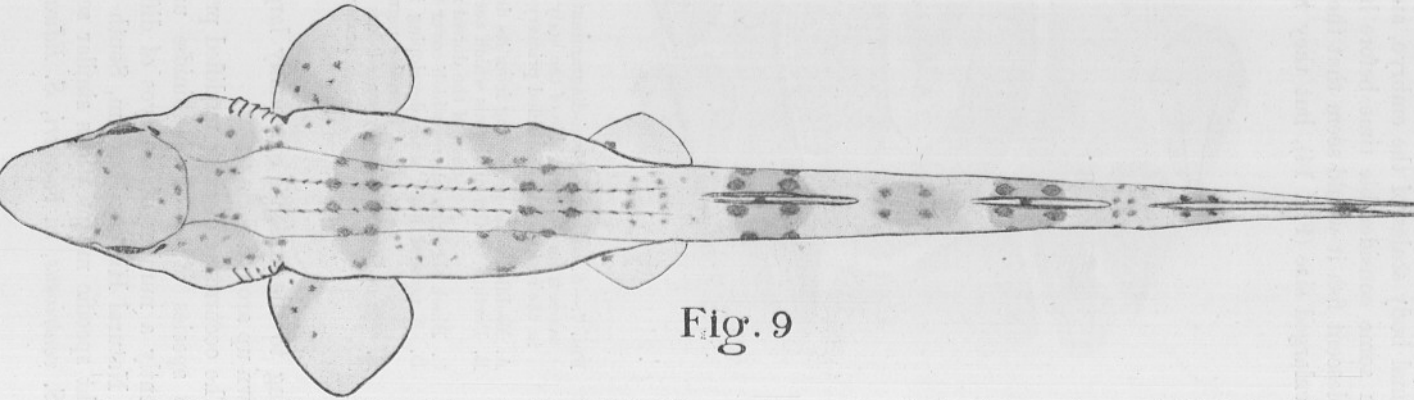


Fig. 9

Fig. 8.—*S. canicula.* Embryos 9·7 cm. in length. March 24th, 1920.

Fig. 9.—*S. canicula.* Same specimen as in Fig. 7 viewed from above

in the young of *Pristiurus melanostomus*. It was of interest to notice that in *S. chilensis* they persist in the adult fish, an exception which is utilised by Regan (11, p. 456) in his classification of the family Scyliorhinidæ. In a young Orectolobid, *Chiloscyllium plagiosum* of about 15 cm. in length, irregular rows of prominent scales were present one on either side of the body, which extended posteriorally to the tail. The young of Chimæra (cf. Günther, 5, p. 403) and embryos of *Callorhynchus antarcticus* also possessed modified scales arranged in a roughly similar system to that seen in Scyliorhinus (cf. Günther, 5, p. 351).

Rynberk (12) has dealt at some length with the general differences between scales from the various parts of the body of the embryos of *S. canicula* and *S. stellaris*, and it will be sufficient to add, in this connection, that the scales constituting the " caudal rasp " are of a larger size and more elongate, almost from the time of their appearance (Figs. 11, 13, 15 and 17).

The degree of development of scales in embryos and young adolescent fish of different lengths has been observed, and may be summarised thus :—

SCYLIORHINUS CANICULA.

Length 4·4 cm.

The dorso-lateral rows of primary scales are visible in their dermal cups, and they are covered by the epidermis. The scales on the body generally have not yet become distinct.

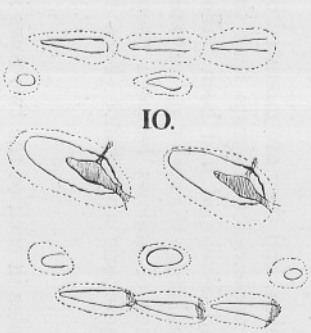
Length 6·5 cm.

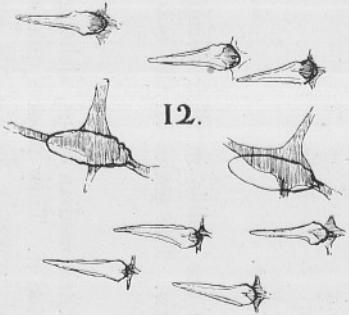
The primary scales are well marked, but their median cusps, although just at the surface, have not as yet penetrated it. They possess quadriradiate bases, and the cusps are directed upwards, backwards and outwards. The normal body scales have now made their appearance, and are seen to be developing in smaller dermal cups. The scales which will eventually form the " caudal rasp " are distinctly larger than the others (Figs. 10 and 11).

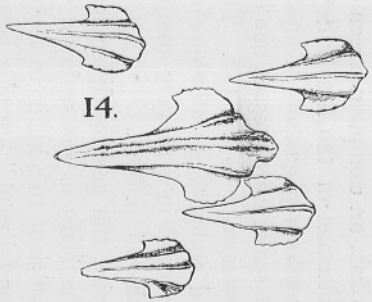
Length 9·5 cm.

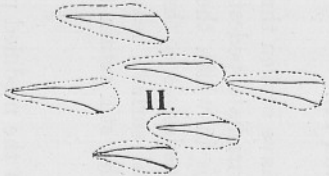
All the scales have broken through the skin, and they are mounted on prominent quadriradiate pedestals. The appearance suggests that the floors of the cups in which the scales had developed had been pulled up to form these pedestals, so that in the final stage the scales are elevated above the general surface, leaving a series of hollows between them. The primary scales still retain their characteristic appearance (Figs. 12 and 13).

The number of the modified primary scales in each of the two rows in 23 embryos of lengths from 6 cm. to 11·3 cm. was determined. In 15









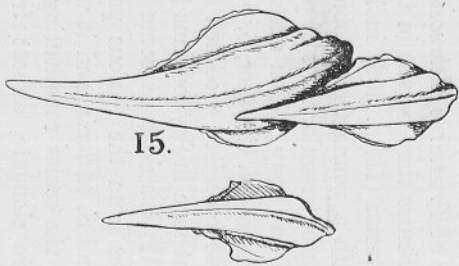


FIG. 10.—*S. canicula.* Embryo of length 6·5 cm. Portion of skin from the region of the modified primary scales on the left side of the body.
FIG. 11.—*S. canicula.* Embryo of length 6·5 cm. Portion of skin from the region of the "caudal rasp."
FIG. 12.—*S. canicula.* Embryo of length 9·7 cm. Piece of skin from the region of the modified primary scales on the left side of the body.
FIG. 13.—*S. canicula.* Embryo of length 9·7 cm. Piece of skin from the region of the "caudal rasp."
FIG. 14.—*S. canicula.* Young adult fish 30·3 cm. in length. Piece of skin from the region of the modified primary scales on the left side of the body. The modified primary scales have assumed the characters of normal scales of large size.
FIG. 15.—*S. canicula.* Young adult fish 30·3 cm. in length. Piece of skin from the "caudal rasp."

specimens both rows had the same number of scales, and in the remaining 8 there was a difference of 1 only. The range in variation in the number of scales per row was from 27 to 32, with a maximum frequency of 31 (cf. Mayer, 8, p. 228, who gave the range as 27–31).

Scyliorhinus stellaris.

Length 14·8 cm.

The modified primary scales are more conspicuous than in *S. canicula*, and the cups in which they are developing have thickened rims which are more or less coalesced in front and behind to form a pronounced ridge on either side of the body (Figs. 5, 6 and 7). The normal body scales are tricuspid, and their elongate medium cusps are contained in projecting pockets of the skin, so that the surface of the body assumes a warty appearance (Fig. 18).

A number of more deeply seated and less developed scales are disposed rather irregularly on either side of the cups in which the modified scales are developing. They are densely pigmented, so that when the embryo is examined by the naked eye they appear as a series of black dots along the longitudinal ridges referred to above (E, Fig. 7).

Length 16·0 cm.

The normal body scales are just at the point of breaking through the skin.

Length 17·3 cm.

All scales have penetrated the skin.

Length 35 cm.

The modified primary scales are still distinct in their rows. Most of them, however, have apparently developed into normal tricuspid scales of enlarged size, although one or two still retain their original character.

Length 36 cm.

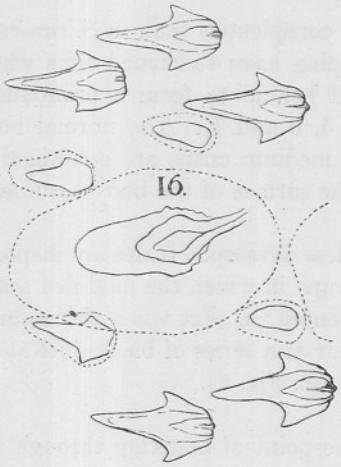
The rows of modified primary scales are barely distinguishable, as they are masked by the presence of equally large and similar tricuspid scales in this part of the body.

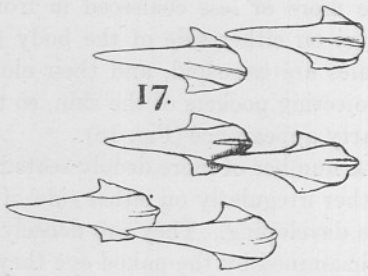
The number of modified primary scales per row in 15 embryos from 9·8 cm. to 22 cm. showed a variation of from 33 to 40, with a maximum frequency of 36 (cf. Mayer, 8, p. 228, who gave the range as 34–38).

Pigmentation.

S. canicula and *S. stellaris* agree very closely in regard to the general scheme of pigmentation in the embryos. In both there are a very distinct series of transverse bands of dark colour. Figure 5, representing an embryo of *S. stellaris* 14·8 cm. in length, may be used conveniently to

indicate the main outlines of the pigment scheme common to both series. The transverse bands are separable into several distinct series according to their position on the body. There is, first, the dorsal series of seven bands which are numbered consecutively from 1 to 7 in Fig. 5; and second, a more lateral series along either side of the body of which the bands have their dorsal boundaries resting on the lateral line (Fig. 5, *a* to *h*). Of the latter, the bands *a*, *b*, *c* and *d* are very regularly and





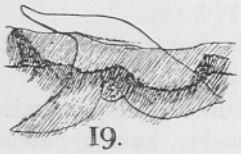


FIG. 16.—*S. stellaris*. Embryo of length 14·8 cm. Piece of skin from the region of the dorsal modified primary scales on the right side of the body.
FIG. 17.—*S. stellaris*. Embryo of length 14·8 cm. Piece of skin from "caudal rasp."
FIG. 18.—*S. stellaris*. Embryo of length 14·8 cm. Section of piece of skin showing the normal body scales covered by the epidermis.
FIG. 19.—*S. stellaris*. Embryo of length 14·8 cm. Section of piece of skin showing the cusp of a modified primary scale projecting through the epidermis.

clearly represented, whereas the others occur sometimes very prominently, but at others less obviously. In addition to the above there are two bands X and Y situated between dorsal bands 4 and 5, and 5 and 6 respectively, which are only feebly represented in *S. stellaris*, but which may be very conspicuous in *S. canicula*.

The pectoral fins are transversely barred, more especially in *S. stellaris*. In the latter species also the pelvic and anal fins are similarly barred, but in *S. canicula*, instead of the bars, there are one or more dots of pigment on the anterior portion of the pelvics, and a single dot at both

the anterior and posterior ends of the anal. The ventral lobe of the caudal fin is marked by three bands in *S. stellaris*, of which the anterior two lie one on either side of the sixth dorsal band. In *S. canicula* the middle one of these three bands does not appear to be represented, although the others are quite distinct.

The microscopic study of cleared and mounted pieces of skin shows the body to be covered with chromatophores of two types. Those of the first type are lemon-yellow in colour and stellate in form, and they are anastomosed to form a lacy network which is spread all over the body beneath the epidermis. In the earlier embryos, when the scales are situated in distinct dermal cups, this yellow pigment is more pronounced between the cups than within the cups themselves, so that a chequered effect is produced. The chromatophores of the second type are brownish black to black in colour, and vary in shape from roughly stellate to irregular masses and dots. They are present practically all over the body immediately beneath the epidermis, and the banded appearance of the embryos is produced by the segregation of chromatophores of this type in certain areas. The detailed structure of the dorsal transverse bands in particular presents some interesting specific features. In *S. stellaris* up to 15 cm. in length they are very distinct and uniform, and their boundaries are sharply differentiated. The abrupt change from banded to non-banded areas of the body is accentuated by the slightly darker edges of the bands in which black spots are beginning to differentiate. In *S. canicula*, at quite a small size, the transverse bands are definitely marked out by two or more of a normal series of four dots which are disposed in a very regular manner, two being at the dorsal end of the band, one anterior and the other posterior, and two at the ventral end of the band arranged anteriorally and posteriorally in a similar way (Figs. 8 and 9). At hatching size in both species a secondary irregular sprinkling of small dark dots is present over the whole of the dorsal and lateral surface, which appears independent of the banded scheme originally laid down. Subsequent to hatching the banded areas are important centres for the development of dark spots which for a considerable time are larger and more pronounced than those arising between the bands.

MUSTELUS VULGARIS (SWEET WILLIAM).

On the few occasions when the number of specimens landed was reasonably large, the proportion of sexes was determined :—

Date.	Total No. of Fishes.	No. of Males.	No. of Females.
Nov. 13th, 1919	55	42	13
,, 14th, 1919	49	41	8
March 4th, 1920	34	22	12

Although the samples were small it may be of significance to note that the male element was conspicuously predominant in each case.

The Embryo.

In the collection of embryos at the Plymouth Laboratory there is a sample of thirty-four embryos of this species which were taken from the uterus in April, 1900. They vary in size from about 19 cm. to 33 cm. inclusive. The smallest specimen in which the yolk-sac is at absorption point measures 29 cm., but one individual of 32·5 cm. still retains a tiny globular remnant. In some of the specimens a similar condition to that observed in the case of *Squalus acanthias* is apparent, namely that the yolk-sac has been completely absorbed, and the umbilical scar is either partially or completely healed.

Food of the Species.

During the period from November, 1919, to February, 1920, the stomach contents of forty-eight fish which had eaten recognisable food were examined and recorded as follows :—

Stomach Contents.		No. of stomachs in which present.	Percentage.
PISCES		2	4·2
CRUSTACEA		48	100·0
Eupagurus sp.	*E. Bernhardus* / *E. prideauxi*	31	
Portunus sp.		29	
Atelocyclus septemdentatus		19	
Galathea sp.		19	
Inachidae	Inachus sp. / Macropodia sp.	7	
Upogebia sp.		6	
Hyas coarcticus		2	
Crangon sp.		1	
Remains unidentified		4	
POLYCHAETA (unclassified)		6	12·5

GALEUS CANIS (SWEET WILLIAM).

Only five specimens of this species have been obtainable, namely, one adult male and four immature fish from 42 to 52 cm. in length. The stomach contents of each consisted exclusively of fish, including remains of Callionymus sp., Gadus sp., and mackerel.

A SUMMARY OF THE MORE IMPORTANT OBSERVATIONS ON THE GENERAL LIFE-HISTORY.

SQUALUS ACANTHIAS (SPUR-DOG).

1. Both the maximum attainable length and that at which sexual maturity is acquired are greater in the female than in the male (cf. *Scyliorhinus canicula*).
2. The female, before becoming sexually mature, undergoes an extended adolescent period during which the initial set of ovarian-eggs are maturing.
3. In a pregnant female the embryos are of the same general size, and similarly the ovarian-eggs.
4. Males and females are equally represented in the embryos and may occur together in the same uterus ; they do not differ in size at any corresponding stage of embryonic development.
5. The number of embryos carried by one fish, if the length of the parent is ignored, is most frequently from 3 to 4 in an observed range from 1 to 11. It may be possible, however, that the number of embryos is dependent on the length of the parent, for the largest number of embryos was found in the largest fish (*vide* 7 below).
6. The remains of the egg-capsule in which the earlier developmental stages are undergone may continue in the uterus until the embryos are ready for birth.
7. In samples of egg-capsules collected at random, the average volume of a capsule is approximately proportional to the number of embryos enclosed, but there is a considerable overlapping in the range of variation in volume for successive number-classes of capsule. The results suggest two possibilities :—
   (*a*) The largest fish contain the largest capsules, and will therefore produce the largest embryos (cf. 5 above).
   (*b*) The embryos in the *initial* brood of a pregnant female are smaller and fewer in number than those of subsequent broods.
8. Newly formed embryos were obtained from November until the middle of May.

   Embryos considered ready for birth occurred from the end of August until the end of December. It was surprising to learn that so many embryos may remain in the uterus after the absorption of the yolk-sac, the umbilical scar either in progress of healing or actually healed.

10. The determination of the average sizes of embryos at frequent intervals during the twelve months from March, 1920, until February, 1921, indicated that a curve of the average growth of an embryo would be at its lowest point in the month of November, and require a period of about twenty-five months to reach its maximum (31 cm.) in the month of December.
11. The combined results of observations 8, 9 and 10 above showed that an embryo commencing its growth in November may be ready for birth in the month of August after a lapse of twenty-one months, having attained a length of about 25 cm., or it may continue in the uterus for a longer period with a resultant increase in length to an observed maximum of 31 cm.
12. The constitution of the shoals of the adult fishes is governed by the factors of size and sexual condition.

Scyliorhinus canicula (Rough-Dog).

1. The maximum attainable size and the length at which sexual maturity is acquired do not differ in the two sexes (cf. *Squalus acanthias*).
2. Egg-purses have not been obtained at Plymouth by shore-collecting (cf. *S. stellaris*).
3. Egg-purses may be deposited in any month of the year, but chiefly during the spring and summer, and in least number during the autumn.
4. There is a curious alternating predominance of sexes in the adults. During the winter the males are the predominant element, whereas in the summer the females are the more numerous.

Scyliorhinus stellaris (Nursehound).

1. Egg-purses have been found at Plymouth by shore-collecting.
2. There is an indication that the breeding season has definable limits, as in the case of the spur-dog.
3. There is a marked difference in regard to the sizes at birth of dog-fishes between the records of investigators in other districts and those observed at Plymouth, particularly in regard to this species.

Mustelus vulgaris (Sweet William).

1. During the period of observation the males were conspicuously predominant in the adult samples. This may indicate a similar condition in this species to that found in the rough-dog.
2. A number of the fully grown embryos extracted from the uterus had the umbilical scar either partially or wholly healed (cf. *Squalus acanthias*).

LITERATURE.

1. *Borcéa, J.* 1905. Recherches sur le système urogénital des elasmobranches. Arch. Zool. Expér., Paris, 1905, sér. 4, t. 4, 199–484.
2. *Danois, E. Le.* 1913. Contribution à l'étude systematique et biologique des poissons de la Manche occidentale. Paris, Masson et Cie.
3. *Day, F.* 1880. The fishes of Great Britain and Ireland, Vol. II.
4. *Garstang, W.* 1893–1895. Notes on the Breeding Seasons of Marine Animals at Plymouth. Journ. M.B.A., N.S., III, p. 229.
5. *Günther, A.* 1870. Catalogue of the fishes of the British Museum. London, Vol. VIII.
6. *Kerr, J. Graham.* 1919. Text-book of Embryology, Vol. II, Vertebrata. Macmillan, London.
7. *Lo Bianco, S.* 1899. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di napoli. Mitth. Zool. Stat., Neapel, 1899, 13, 448–573.
8. *Mayer, P.* 1886. Die unpaaren Flossen der Selachier. Mitth. Zool. Stat. Neapel, 1886, 6, p. 228.
9. *Meyer, F.* 1875. Beitrag zur Anatomie des Urogenital-systems der Selachier und Amphibien. Sitzungber. der naturf. Ges. zu Leipzig.
10. *Regan, C. T.* 1906. A Classification of the Selachian Fishes. Proc. Zool. Soc. London, 1906, II, p. 722.
11. *Regan, C. T.* 1908. A Synopsis of the Sharks of the Family Scyliorhinidæ. Ann. Mag. Nat. Hist., 1908, ser. 8, vol. 1, 453–465.
12. *Rynberk, G. A. van.* 1908. Sur une disposition particulière dans le squelette cutané de quelques sélaciens. Arch. Ital. Biol., 49, 203–212.
13. *Smitt, F. A.* 1893–1895. A History of Scandinavian Fishes, by B. Fries, C. U. Ekström and C. Sundevall. Second edition revised and completed by F. A. Smitt, 1893–1895. Part II.
14. *White, P. J.* 1896. Puffin Island Biological Station. Report for the years 1894–1895, p. 6.
15. *Yarrell, W.* 1836. A History of British Fishes, Vol. II.