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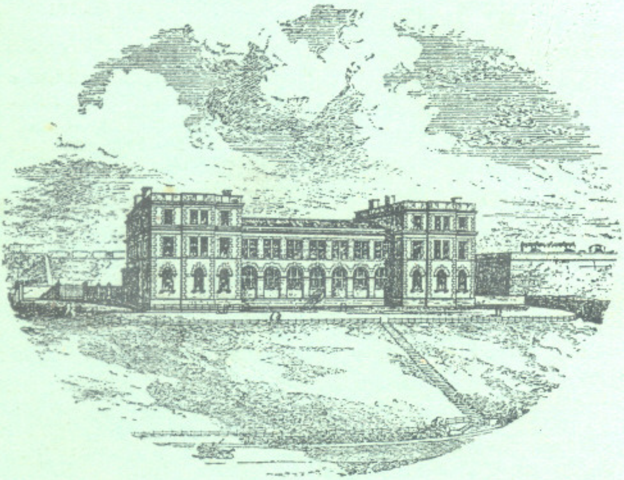
OF THE

MARINE BIOLOGICAL ASSOCIATION

OF

THE UNITED KINGDOM.



THE PLYMOUTH LABORATORY.

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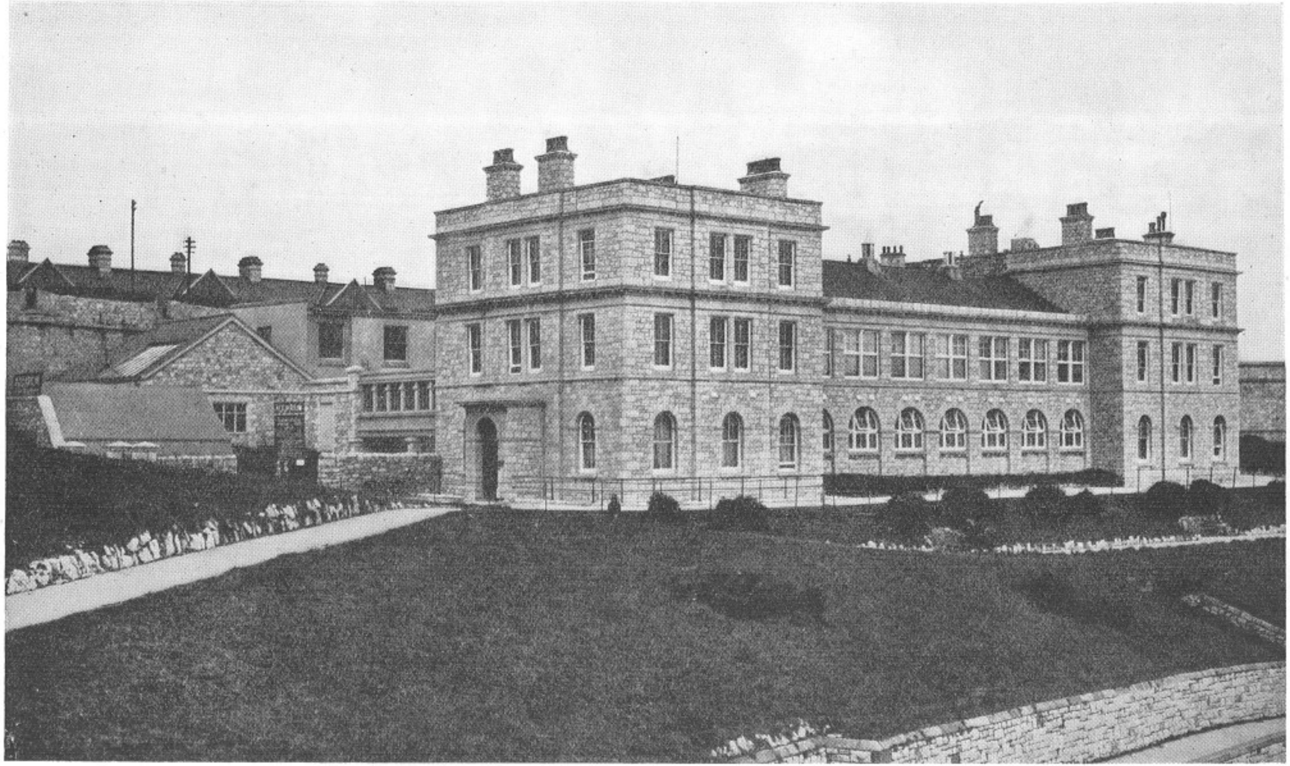


Fig. 1.—The Marine Biological Laboratory, Plymouth.

The Laboratory of the Marine Biological Association at Plymouth.

By

E. J. Allen and H. W. Harvey.

With Figures 1 to 7 and Plans I to VII.

THE Marine Biological Association of the United Kingdom, to whom the Plymouth Laboratory belongs, is a corporate body of subscribing members, interested in scientific investigations concerning the habits and life-histories of food fishes and other marine animals. The Laboratory is managed by a Council elected annually by the members of the Association.

The Association was founded in 1884—when through the energy and initiative of its present President, Sir E. Ray Lankester, a meeting was held in the rooms of the Royal Society of London at which the chair was taken by Professor Huxley, at that time President of the Royal Society. The meeting was attended by many of the leading scientific men of that day, including Sir John Lubbock (afterwards Lord Avebury) and Sir Joseph Hooker, as well as by a number of public men interested in the sea fisheries of the country. The purpose which the founders of the Association had in mind is well expressed in the first resolution adopted by this meeting, which emphasises the necessity for the establishment of one or more laboratories on the British coast, " where accurate researches may be carried on leading to the improvement of zoological and botanical science, and to an increase of our knowledge as regards the food, life, conditions, and habits of British food fishes and molluscs in particular, and the animal and vegetable resources of the sea in general." The policy indicated in this resolution has been consistently followed by the Association throughout its history, and it has endeavoured to aid at the same time science and industry. Research having a direct bearing on the fishing industry has been carried on side by side with research in pure science, and the two have mutually helped and supported each other.

The Laboratory (Fig. 1), situated below the wall of the Citadel, overlooking Plymouth Sound, was opened in June, 1888, with a staff consisting of a Director, a Naturalist, and one scientific assistant. This permanent staff, which is engaged all the year round in research work, has gradually increased until at the present time it numbers thirteen scientific workers. In addition, over thirty working places are available for visiting research workers from British Universities and abroad.

During its early years the Laboratory had to depend largely on the contributions of voluntary subscribers and on grants from the Fishmongers' Company and from scientific societies for its annual income. From the commencement, also, it received an annual grant from the Government, which during the first five years amounted to £500. This grant was then increased to £1000, at which figure it remained for many years. In 1902 the Association was asked by His Majesty's Treasury to undertake the English scientific investigations in connection with the International Council for the Study of the Sea, an organisation to which the British Government had adhered with a view to co-operating with other European Governments in a comprehensive programme of research into the natural history of marketable marine fishes, of their migrations, and of the great fluctuations which occur in their abundance from year to year. These researches included investigations of the water movements, especially of the North Sea and English Channel, of the distribution of plankton, and of the invertebrate fauna upon which the fishes feed. In connection with the work, which continued in the hands of the Association until 1910, an auxiliary laboratory was established at Lowestoft, and the steam trawler *Huxley* became available, largely through the generosity of Dr. G. P. Bidder, for work in the North Sea. During this period and in the following years the Association owed much to Sir Arthur Shipley, who occupied the position of Chairman of the Council.

After the great war Government grants for fishery research were put under the control of the Development Commissioners. The Laboratory at Lowestoft was re-established under the Ministry of Agriculture and Fisheries for the purpose of studying problems having a direct bearing on the commercial fisheries. At the same time a substantially increased grant was made to the Marine Biological Association for the maintenance of the Plymouth Laboratory, so that researches of a more general or fundamental nature concerning life in the sea might be developed upon a larger plan. With the help of this grant the steamer *Salpa* (Fig. 7), a steam-drifter fitted for trawling, was purchased by the Association from the Admiralty for work at Plymouth, and subsequently a motor boat was obtained for use in inshore waters. In order to give adequate facilities for the larger staff and the increasing number of visiting research workers, an addition was made to the Laboratory buildings in 1920, this being made possible by the generosity of a number of friends of the Association, including once more the Fishmongers' Company and various scientific societies. A temporary building was put up in 1922 to provide accommodation for the students attending the Easter course in marine biology, which has been held at the Laboratory for many years, this building being paid for chiefly by subscriptions from past students. About this time also the use of some sheds, and a small cove, which has since been converted into a sea pond for experimental work, was secured for a nominal rental at Pier Cellars, Cawsand Bay.

At the inaugural meeting of the Association attention was drawn by Mr. G. J. Romanes to the wide field of research offered by the physiology of marine organisms. Later the work of Keith Lucas and of Mines, much of which was carried out at Plymouth, showed how valuable were the facilities provided by the Laboratory for such research, and with the advance of this branch of biology during the last two decades the attention of a growing number of physiologists has turned to the possibility of attacking many fundamental problems by experiments upon the tissues of simple marine animals, a method of attack which seems likely to assist in the interpretation of results hitherto confined chiefly to land vertebrates. The opening of this field of enquiry was followed by the realisation of the wide possibilities of Comparative Physiology in the study of animals of diverse evolutionary descent. No environment yields more representatives of the different animal groups than the sea.

The constant supply of marine animals almost daily by the steamer and motor boat or from the Aquarium, made the Plymouth Laboratory particularly suitable for such research, and the numbers of visitors from the staffs of various Universities working during the Easter and summer vacations severely taxed the accommodation provided by the existing buildings. Through the generosity of numerous benefactors, many of them former workers in the Laboratory, of the Fishmongers' Company, and of the International Education Board a sufficient sum was collected to erect a new wing. This was completed in 1926 and contains seven private laboratories for visiting research workers, a physiological and a chemical laboratory, and cellars for galvanometer or constant temperature work.

The Laboratory as a whole, therefore, now offers facilities for all kinds of biological research, and these facilities have been utilized by numerous investigators from both British and Foreign Universities. The international character of the work has recently shown a marked increase, and the personal contacts with research workers from abroad is a great stimulus to the Association's scientific staff.

An idea of the volume and wide scope of the investigations may be gained by referring to the long list of published original contributions to science, which have emanated from the Laboratory (*Journ. Mar. Biol. Assoc.*, XV, 3, p. 753). In addition to those who have worked at some particular problem and published the results of their investigations, there is a constant and increasing stream of visitors from all countries, who come for short visits to discuss matters appertaining to their own researches or to follow the various investigations in progress. This is a feature of the activities of the Association of no little benefit, for it not only aids the co-ordination of research, but brings those working in the Laboratory into close touch with progress taking place elsewhere.

A further activity of the Association is the supply of specimens of marine animals and plants to biologists in this and other countries, both for research and for teaching purposes. Expeditions and individual naturalists are also supplied with nets, dredges, and apparatus constructed and tested under the supervision of the staff.

The Buildings and Equipment.

(See Figs. 2–5 and Plans I–VII.)

The original building contains a general laboratory (Fig. 2) with cubicles and a series of small aquaria for the use of the staff or visitors engaged

Fig. 2.—The General Biological Laboratory.

in zoological investigations ; an aquarium on the ground floor which is open to the general public ; an extensive library of biological publications, including the leading physiological and biochemical journals (Fig. 3) ; a residence for the Director ; four or five small laboratories ; an office ; and living-quarters for the engineer-caretaker. The general arrangement is shown in Plans I–VII. It is connected with the Allen Building and new wing by a bridge. The Allen Building, 34 ft. by 24 ft., is divided into two laboratories by a temporary partition. In it are housed a type collection of the local marine fauna and flora and apparatus for obtaining photographic records of specimens, etc. A photographic dark room is attached.

FIG. 3.—THE LIBRARY.

In the new wing, the chemical laboratory is well equipped with apparatus of general utility, including ovens, analytical balances, tube and muffle furnaces. There is a large and varied stock of chemicals. The physiological laboratory (Fig. 4) is equipped with kymographic and respiration apparatus, spectroscopes, small electric motors, and temperature baths. Gas, water, and compressed air are led to these and to the seven private laboratories, and alternating electric current, at 210 volts, can be taken from numerous points. In addition, direct current up to 100 volts may be supplied when required from a dynamo situated in the cellars of the main building. A supply of ice, liquid air, and of compressed oxygen can be obtained at short notice in the town. On the ground floor provision is made for the reception of dredging and other material brought in by the boats, and a constant supply of sea-water is provided by means of a motor pump from one of the reservoirs (Fig. 5).

The building (Plan I), in which a course of marine biology is held for a month during the Easter vacation, is fitted with gas, water, and electric light, accommodates eighteen to twenty students engaged in microscopic and faunistic work, or about twelve post-graduate students engaged in general physiological technique, for whom a class is held at the end of the summer vacation.

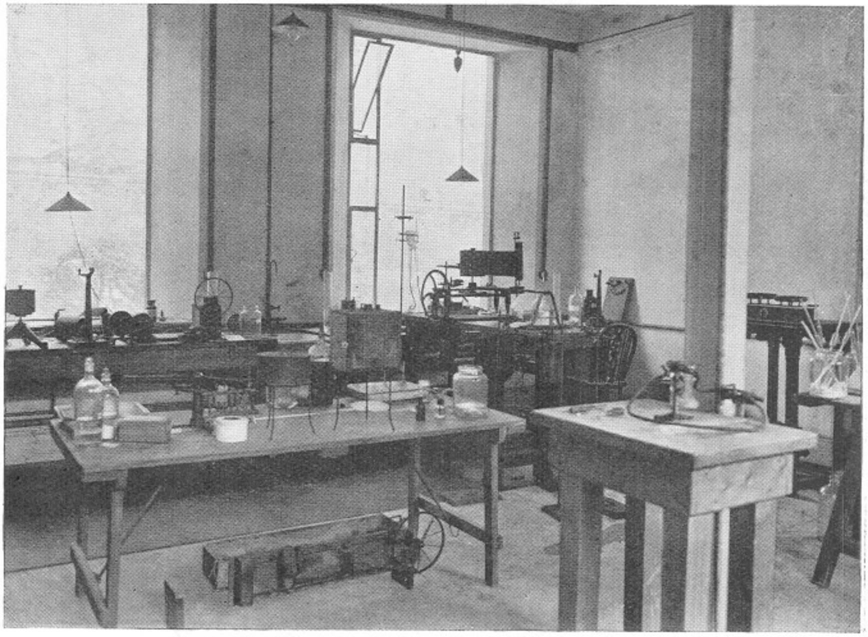


FIG. 4.—THE PHYSIOLOGICAL LABORATORY.

THE AQUARIUM AND SEA-WATER TANKS (Fig. 6).

The Aquarium or tank room, measuring $70 \times 34\frac{1}{2}$ ft., and situated on the ground floor of the main building, is open to the public at a small charge and to fishermen and to parties of school children free of charge. It contains a representative collection of the commoner fishes and invertebrate animals found in the south-western area of the English Channel, and a small collection of fresh-water fishes (Fig. 6).

The tanks are built of slate, with glass fronts fitted against cast-iron frames. On the south side are nine tanks, 4 ft. wide and 4 ft. deep, one being 15 ft. long, two 10 ft., and the remaining six 5 ft. long. On the north side are three tanks each 5 ft. deep, one being 30 ft. 6 ins. long $\times$ 9 ft. wide, one 15 ft. 6 in. long $\times$ 9 ft. wide, and one 15 ft. long $\times$ 5 ft. wide. In the centre are a row of five glass-fronted "table tanks," 1 ft. 9 ins.

deep × 2 ft. 3 ins. wide, and 9 ft. 9 ins. long, several of them being divided into two by transverse partitions. The height of these tanks is 4 ft. above ground level, so their contents can be examined from above as well as through the glass front. In addition to these fixed tanks a number of small wooden aquaria have been added, and a collection of preserved specimens of general interest is displayed on the east and west walls.

A guide book has been prepared, and is on sale at 1/– per copy, giving a simple account of the life-history and habits of most of the sea creatures living in the Aquarium.

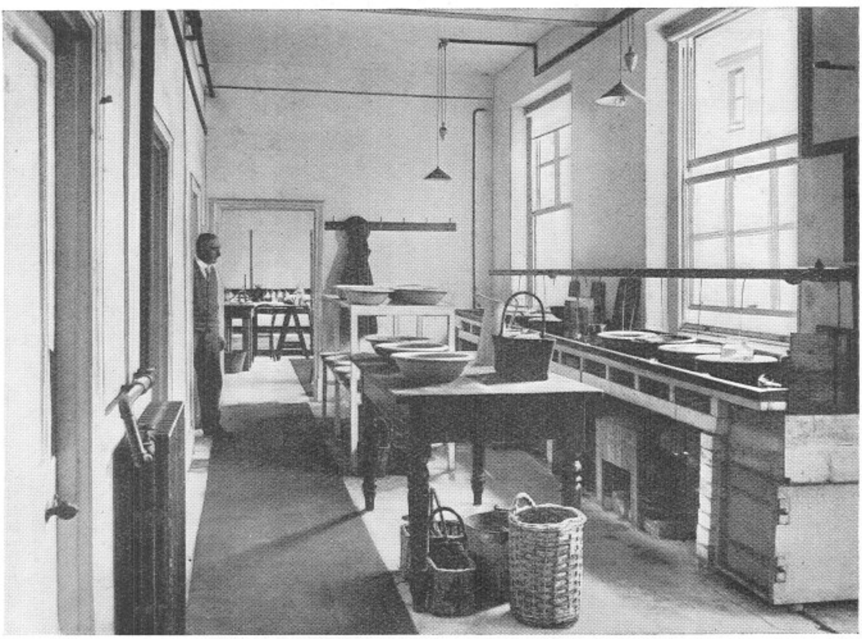


FIG. 5.—RECEPTION OF MATERIAL AND SEA-WATER CIRCULATION.

Twelve glass-fronted tanks, 1 ft. 6 ins. deep, 2 ft. 3 ins. wide, and 4 ft. 8 ins. long, are installed in the general laboratory above the tank room, and also a shallow wooden table tank, 8 ft. by 5 ft. 6 ins. and 8 ins. deep.

In the yard behind the Aquarium there is a brick-work tank lined with asphalte, 18 ft. × 3 ft. × 1 ft. 10 ins. deep, in which animals are kept as a reserve from which to replenish specimens in the Aquarium, or for use by workers in the Laboratory. Since the opening of the Aquarium of the Zoological Society in London a large number of marine animals have been collected and acclimatised to life under aquarium conditions in the Plymouth tanks and then despatched to Regent's Park.

A wooden table, 24 ft. long, coated with asphalte, is also placed in this yard ; on it glass or other vessels containing living animals can be kept under a continuous flow of sea-water from a launder situated above the table.

Both outside tanks and table are protected from rain by galvanised iron roofing, and are not subjected to direct sunshine.

Most of the tanks are aerated for about 20 hours daily from a compressed air supply at 5 lbs. per square inch pressure, which is led to the bottom of each tank and issues through a porcelain or cane nozzle, the air being thus delivered in streams of minute bubbles.

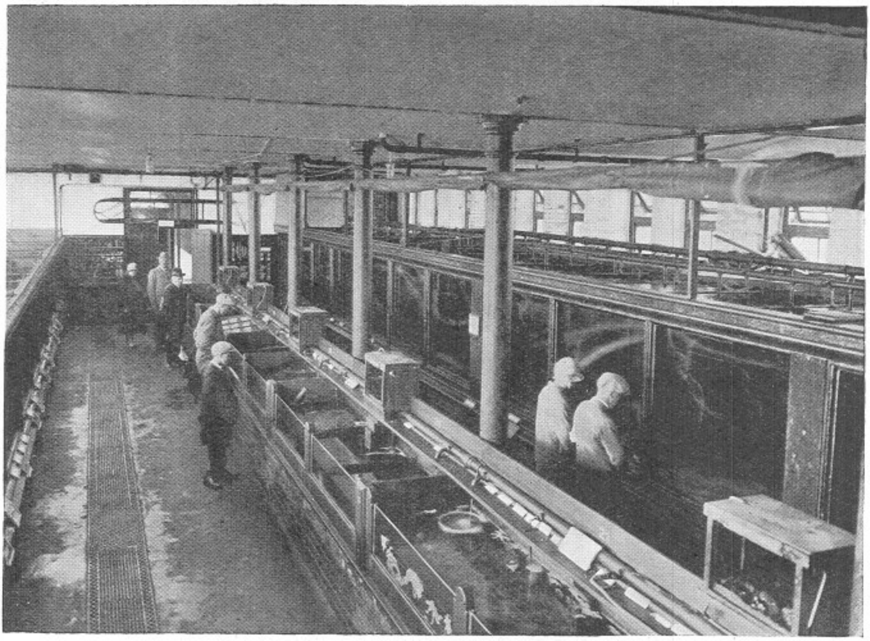


FIG. 6.—THE AQUARIUM.

THE SUPPLY AND CIRCULATION OF SEA-WATER TO THE AQUARIUM TANKS.

Behind the main building and below ground level are two concrete reservoirs, asphalte lined, 37 ft. 6 in. long, 21 ft. 6 ins. wide, 11 ft. deep, and each capable of holding 55,000 gallons of water. These are filled with sea-water from a well, built in the rocks on the shore below the Laboratory, which has a depth of about 14 ft. at high tide. A Shone's Ejector in the bottom of the well is supplied with compressed air which forces the water up to the reservoir through a 4-in. cast-iron pipe enamelled inside. The ejector was installed in 1887 and is still working.

These reservoirs are entirely cleaned out and refilled at comparatively long intervals ; losses are made up and a proportion of the water replaced by pumping in fresh sea-water at high tides during the summer, when conditions are most favourable. An increase in salinity up to 37 parts per thousand is not found to be detrimental to the animals in the tanks.

The water in one reservoir is pumped to the Aquarium tanks for about 20 hours daily for one week, through a system of vulcanite pipes supplied with nozzles several inches above the level of water in the tanks. It is forced through these nozzles in jets which carry air in fine bubbles deep into the tanks. The water overflowing is carried by culverts back to the reservoir.

At the expiration of a week the circulation is changed over to the other reservoir. In the resting reservoir particles of suspended matter in the water fall to the bottom. The hydrogen ion concentration of the circulating water is kept close to that in the open sea by addition of two pounds of lime to each reservoir every second week. For forty years this circulation has never failed for long enough to cause the death of fish in the Aquarium, although for nearly thirty years it was maintained by original " Otto " gas engines, capricious in their behaviour and exacting much attention.

For the last five years two alternative methods of circulation have been used. (1) By a cast-iron 2-in. centrifugal pump driven directly by a 3-h.p. electric motor. This is designed to deliver 2,500 gallons per hour against a head of 35 feet. The motor also drives, through gearing, a rotary air compressor delivering 7 cubic feet of free air per minute at a pressure of 5 lbs. to the square inch. (2) By one of a pair of cast-iron 2-in. centrifugal pumps driven from shafting by a 5-h.p. gas engine. A small air compressor is also driven from the same shafting, and an independent air compressor driven by its own electric motor has recently been fixed.

The compressed air supply to the Shone's Ejector, pumping water from the sea into the reservoirs, is obtained by an air compressor driven from the 5-h.p. gas engine. This can be added to by compressed air from a compressor built in one unit with a 4 h.p. " Otto " gas engine installed forty years ago and still functioning.

The Ship and Motor Boat.

The s.s. *Salpa* (Fig. 7) is a wooden steam drifter 88 ft. long, 19·9 ft. beam drawing 10·5 ft. aft and 5 ft. forward, built in 1918 and capable of a speed of 9½ knots. She is equipped with a steam winch for trawling and a small deckhouse laboratory. A 60-ft. otter trawl is carried, together with various small trawls, dredges, and plankton nets. During most of the year the ship works daily from Plymouth, longer cruises being made from time to time.

The motor boat *Gammarus*, 25 ft. long and 8 ft. beam, drawing 2 ft. 9 ins. and propelled by two 3-h.p. Kelvin engines, works daily in and around Plymouth Sound.

Provision for Visitors and Students Working in the Laboratory.

The accommodation provided for visitors includes cubicles, separate rooms, or bench space with adequate fittings for biochemical and physiological work, the use of all ordinary glassware, chemicals, and apparatus of a general nature. The Association undertakes, as far as possible, to supply the animals or plants or water samples required for any investigation, or such facilities for obtaining them as may be at the command of the Laboratory.

Microscopes are not usually provided. Intending visitors are advised to write to the Director stating the nature of the investigations which they propose to carry out and the apparatus which they will require. Every effort is made to provide any special apparatus which is needed, and to collect the animals wanted for research.

The Laboratory is open for research during the entire year, including holidays, and workers are provided with a key so that they may work at night when they desire to do so. The fishermen are engaged in the collection of material daily, except on Sundays and for three or four days at Christmas and Easter. The services of a laboratory assistant are available if necessary.

The facilities are primarily intended for visitors who are engaged in their own research or wish to collaborate with members of the staff who are investigating some particular problem of biological science. Every effort is made by the staff to give information and assistance.

With regard to the admission of research workers from the Dominions, from foreign Universities, and members of Government departments who desire to make use of this Laboratory, the Council of the Association are usually willing to remit all charges, welcoming such visitors as guests. Research workers from this country may be nominated in many cases to occupy working space in the Laboratory free of charge; Founders and Governors of the Association have the privilege of making such nominations. Accommodation may also be rented at 50 guineas per year, 5 guineas per month, or thirty shillings per week. Particulars regarding nominations, copies of the regulations and lists of recommended lodgings in the vicinity are supplied on application to the Director.

A course of study in marine biology is held during the Easter vacation

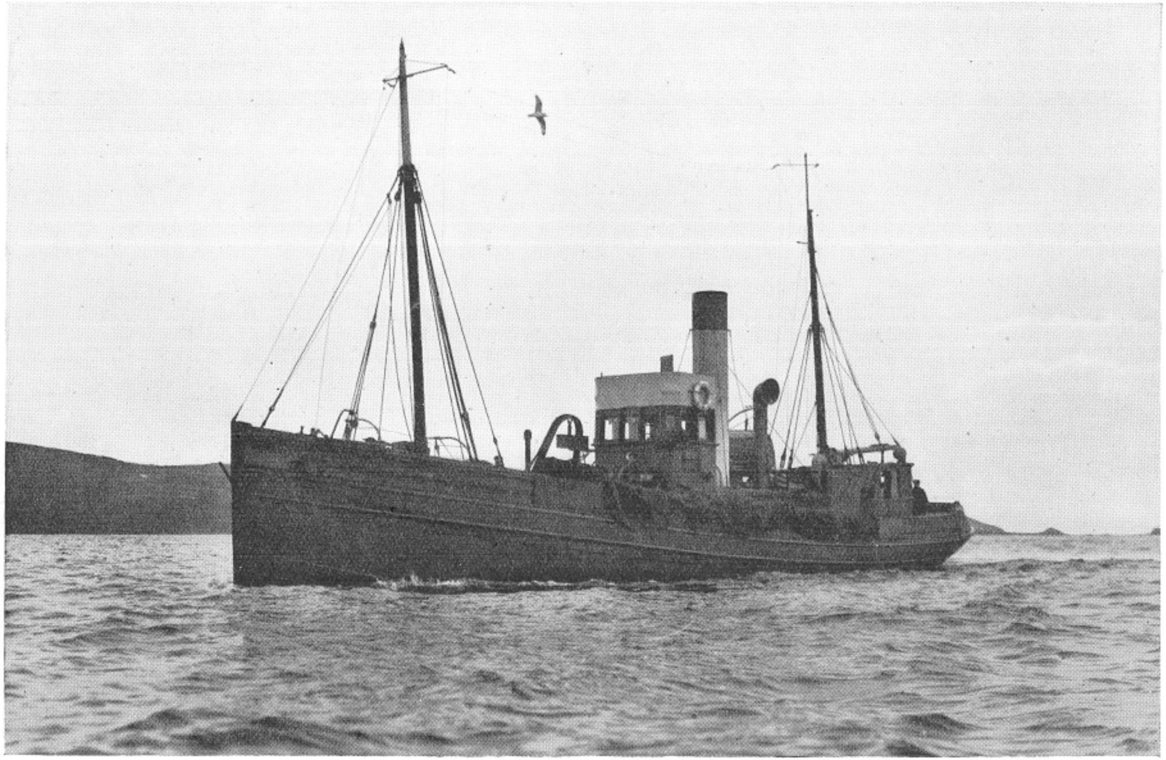
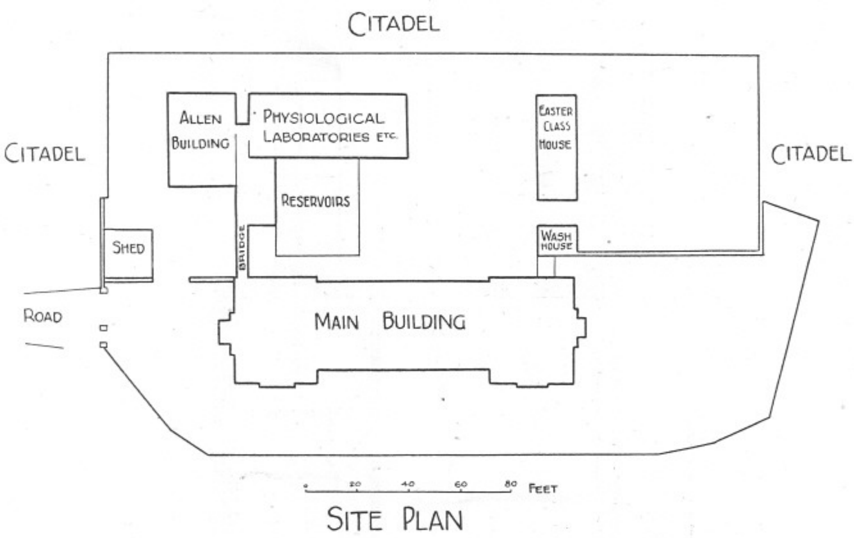


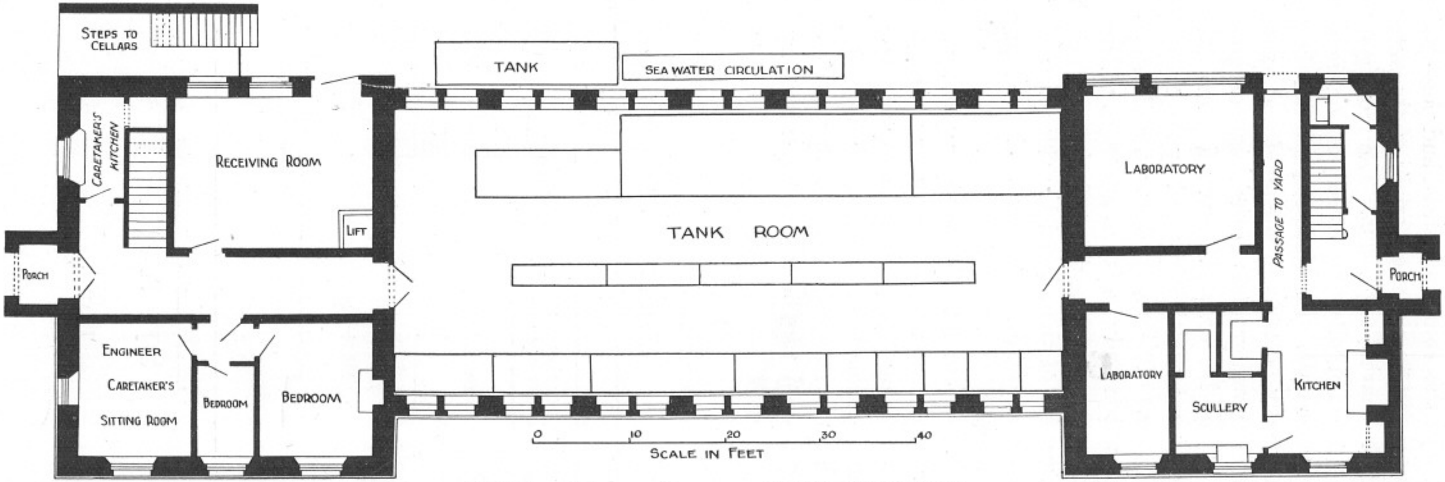
Fig. 7.—The "Salpa."

of the Universities. In this course advanced and post-graduate students are given the opportunity for practical study of the structure and life-histories and habits of marine organisms. The more general aspects of marine biology are studied in collecting expeditions on the shore and in the s.s. *Salpa* and the motor boat. The characteristics of the shore fauna on sandy, muddy, and rocky bottoms in sheltered and exposed places are demonstrated on well-known grounds in the neighbourhood. The varied geological nature of the Devon and Cornwall shore line supports an extensive and varied fauna, which is exposed by the considerable rise and fall of the tide. The use of tow-nets, dredges, and trawls employed in investigating the plankton and the fauna and flora of the sea bottom is explained and demonstrated. A special study is made of the chief larval stages of different groups of the animal kingdom, and simple artificial fertilisations are made to obtain those stages of development which are rarely taken in the nets.

Another course is held in late summer for post-graduate students commencing research in comparative physiology, who wish to explore the possibilities of attacking various outstanding problems by means of experiments on marine animals, and for zoologists who desire to become conversant with physiological methods and apparatus and the possibilities of their application to problems concerning physiological processes.

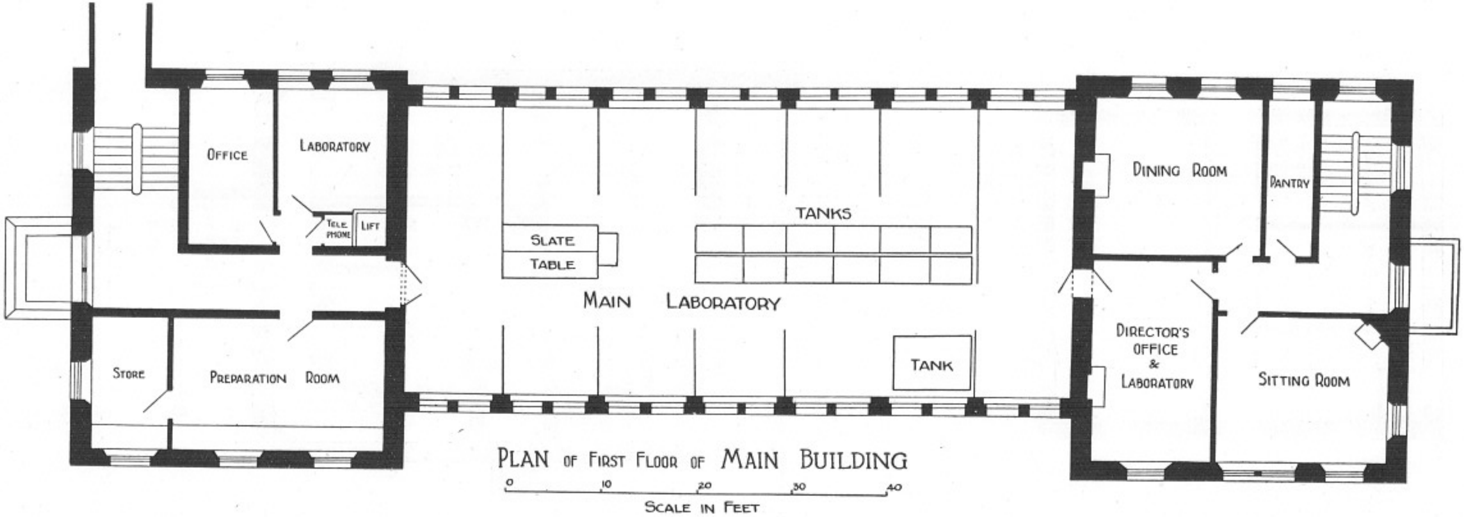


PLAN I.

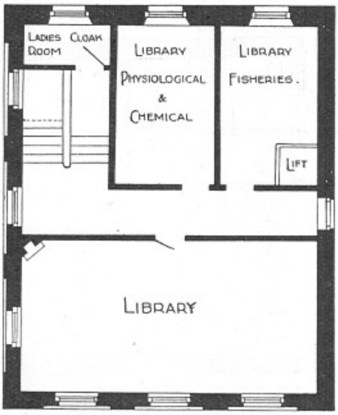


PLAN OF GROUND FLOOR OF MAIN BUILDING

PLAN II.


Office
Laboratory
Tele phone
Lift
Store
Preparation Room
Slate
Table
Tanks
Main Laboratory
Tank
Dining Room
Pantry
Director's Office & Laboratory
Sitting Room
Plan of First Floor of Main Building
0
10
20
30
40
Scale in Feet

Plan III.

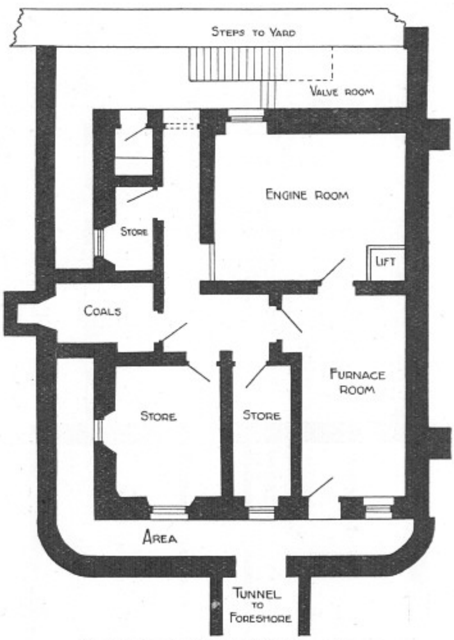


Second floor of West Wing of Main Building

0 10 20

Scale in feet

Plan IV.

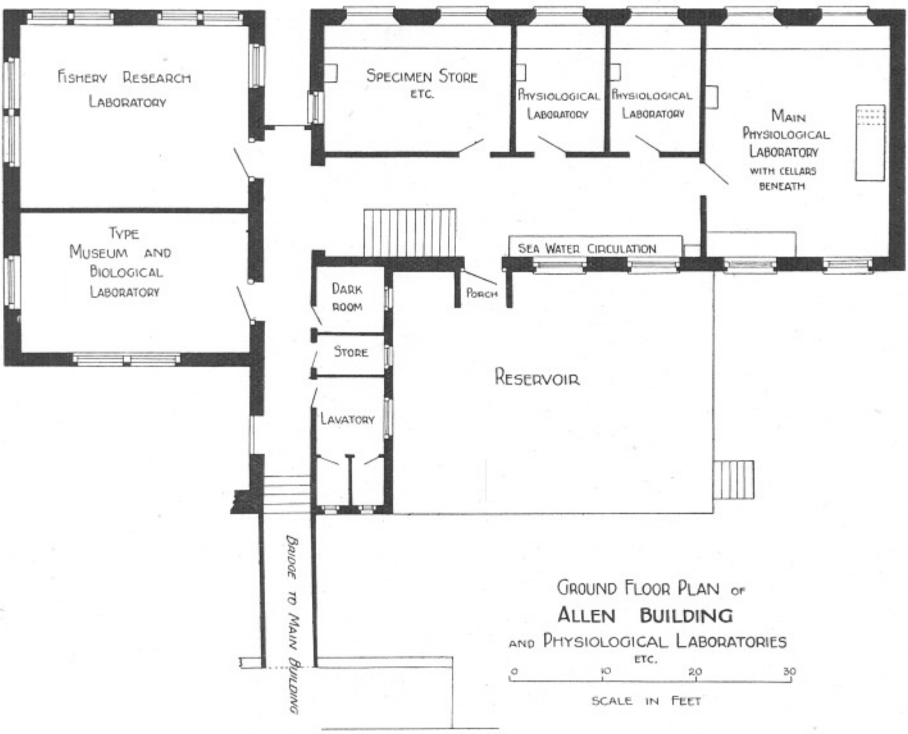


Basement of West Wing of Main Building

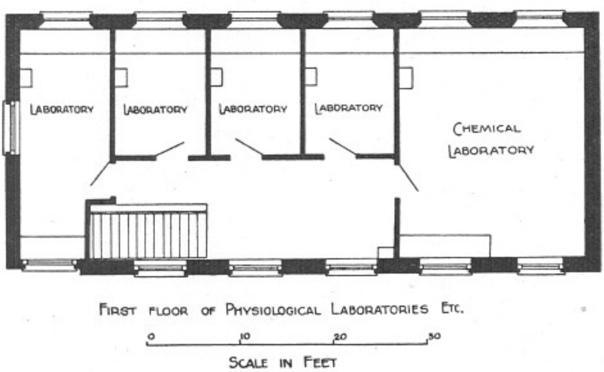
0 10 20

Scale in Feet

Plan V.



Plan VI.



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In attempting to distinguish between economic and more purely scientific publications considerable difficulty has been experienced; indeed, such a distinction is in reality impossible, since all researches bearing on the distribution and habits of marine life of any kind have a more or less direct bearing on fishery problems. All papers dealing with the distribution, habits, and young stages of fishes have been included in the economic division, whether the fishes are themselves marketable or not.

An author's index has been inserted at the beginning from which can be obtained the section and reference number of any paper; the pages on which the sections occur can be found from the Table of Contents.

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LX. MICROSCOPIC TECHNIQUE.

1. Note on a Method of Obtaining Long Working Distances with Low Power Objectives. By D. P. Wilson. Journ. Roy. Micr. Soc., xlvii. 1927, p. 335.

The Vertical Distribution of Marine Macroplankton. VIII. Further Observations on the Diurnal Behaviour of the Pelagic Young of Teleostean Fishes in the Plymouth Area.

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With 6 Figures in the Text.

On June 3rd–4th, 1926, a further series of observations was taken to study the diurnal behaviour of the post-larvæ of teleostean fishes. Collections were made in exactly the same way as on previous occasions (**3**) at a position about 2 miles east of the Eddystone Lighthouse. The net used was the 2-metre stramin ring-trawl, and the duration of each haul was ten minutes. The Admiralty depth-recording instrument was used and tracings of the path of the net through the water on each occasion are given in Fig. 1. The complete log giving details for each haul is set out in Table I; all times are Greenwich mean; and Table II gives the average depths for each haul obtained from the depth-recorder tracings.

General Results.

Larger catches of post-larval fish were taken than on the two previous dates when collections of this type were made, viz. July 15th to 16th, 1924, and June 17th to 19th, 1925. The results bear out the general conclusions arrived at for the previous collections.

The diurnal movements undertaken by most of the species of young fish would appear to be very slight. While a small proportion of each species tends to move into the upper layers near the surface at night, the greater part show little change from their usual daytime distribution and are still found in the deeper layers.

TABLE I.

Date : June 3rd–4th, 1926. Position : 2 miles east of Eddystone. Ship : s.s. *Salpa*.
Gear : 2 metre ring-trawl.

	Depth.	Time net entered water.	Fishing time.	Time net left water.	Length of warp out.	Remarks.
1st Series	VI	$2.18\frac{1}{2}$ p.m.	2.20–2.30 p.m.	$2.32\frac{1}{2}$ p.m.	60 fathoms.	
Sky almost cloudless :	V	$2.40\frac{1}{2}$,,	$2.41\frac{1}{2}$–$2.51\frac{1}{2}$,,	2.53 ,,	45 ,,	
bright sun ; atmo-	IV	3.2 ,,	$3.2\frac{1}{2}$–$3.12\frac{1}{2}$,,	3.14 ,,	35 ,,	
sphere very clear ;	III	$3.24\frac{1}{2}$,,	3.25–3.35 ,,	3.36 ,,	20 ,,	
fresh W.N.W. wind ;	II	$3.43\frac{1}{2}$,,	3.44–3.54 ,,	$3.54\frac{1}{2}$,,	10 ,,	
sea surface, choppy.	Surface	—	4.1–4.11 ,,	—	—	4.20 p.m. Secchi disc, 10 m.
2nd Series	VI	7.23 p.m.	7.24–7.34 p.m.	$7.36\frac{1}{2}$ p.m.	60 fathoms.	7.20 p.m. Secchi disc, 8 m.
Sky cloudless ; atmo-	V	$7.46\frac{3}{4}$,,	$7.47\frac{3}{4}$–$8.57\frac{3}{4}$,,	8 ,,	45 ,,	
sphere very clear ;	IV	$8.8\frac{3}{4}$,,	$8.9\frac{1}{2}$–$8.19\frac{1}{2}$,,	$8.20\frac{1}{2}$,,	35 ,,	
sea choppy ; sun-	III	$8.27\frac{1}{2}$,,	8.28–8.38 ,,	8.39 ,,	20 ,,	
set 8.20 p.m.	II	—	8.46–8.56 ,,	—	10 ,,	9 p.m. becoming hard to read.
	Surface	—	$9.3\frac{1}{2}$–$9.13\frac{1}{2}$,,	—	—	9.10 p.m. deck-lights on.
3rd Series	VI	$10.26\frac{1}{2}$ p.m.	10.28–10.38 p.m.	10.41 p.m.	60 fathoms	
Cloudless ; no moon ;	V	$10.50\frac{1}{2}$,,	$10.51\frac{1}{2}$–$11.1\frac{1}{2}$,,	11.3 ,,	45 ,,	
bright starlight ;	IV	11.12 ,,	$11.13\frac{1}{2}$–$11.23\frac{1}{2}$,,	$11.24\frac{1}{2}$,,	35 ,,	
wind dropped ; sea	III	11.36 ,,	$11.36\frac{1}{2}$–$11.46\frac{1}{2}$,,	11.47 ,,	20 ,,	
nearly flat calm by	II	12.00 a.m.	$12.00\frac{1}{2}$–$12.10\frac{1}{2}$ a.m.	—	10 ,,	
end of series	Surface	—	12.21–12.31 ,,	—	—	
4th Series	VI	$2.21\frac{1}{2}$ a.m.	2.24–2.34 a.m.	$2.36\frac{1}{2}$ a.m.	60 fathoms	2.30 a.m. dawn light in sky and
Cloudless ; no wind ;	V	2.46 ,,	2.47–2.57 ,,	2.59 ,,	45 ,,	$\frac{1}{4}$ moon a little above horizon.
glass calm ; sun	IV	3.8 ,,	$3.8\frac{1}{2}$–$3.18\frac{1}{2}$,,	3.20 ,,	35 ,,	3.10 a.m. lightening quickly.
rose 4.17 a.m.	III	$3.28\frac{1}{2}$,,	3.29–3.39 ,,	3.40 ,,	20 ,,	3.30 a.m. deck-lights out.
	II	$3.48\frac{1}{2}$,,	3.49–3.59 ,,	$3.59\frac{1}{2}$,,	10 ,,	
	Surface	—	$4.7\frac{1}{2}$–$4.17\frac{1}{2}$,,	—	—	
5th Series	VI	$7.27\frac{1}{2}$ a.m.	7.29–7.39 a.m.	7.41 a.m.	60 fathoms	
Cloudless ; bright sun ;	V	$7.51\frac{1}{2}$,,	$7.52\frac{1}{2}$–$8.2\frac{1}{2}$,,	8.4 ,,	45 ,,	
atmosphere clear ;	IV	8.16 ,,	8.17–8.27 ,,	8.28 ,,	35 ,,	
flat calm	III	8.38 ,,	$8.38\frac{1}{2}$–$8.48\frac{1}{2}$,,	$8.49\frac{1}{2}$,,	20 ,,	
	II	$8.58\frac{3}{4}$,,	8.59–9.9 ,,	—	10 ,,	
	Surface	—	9.19–9.29 ,,	—	—	9.30 a.m. Secchi disc, 10 m.

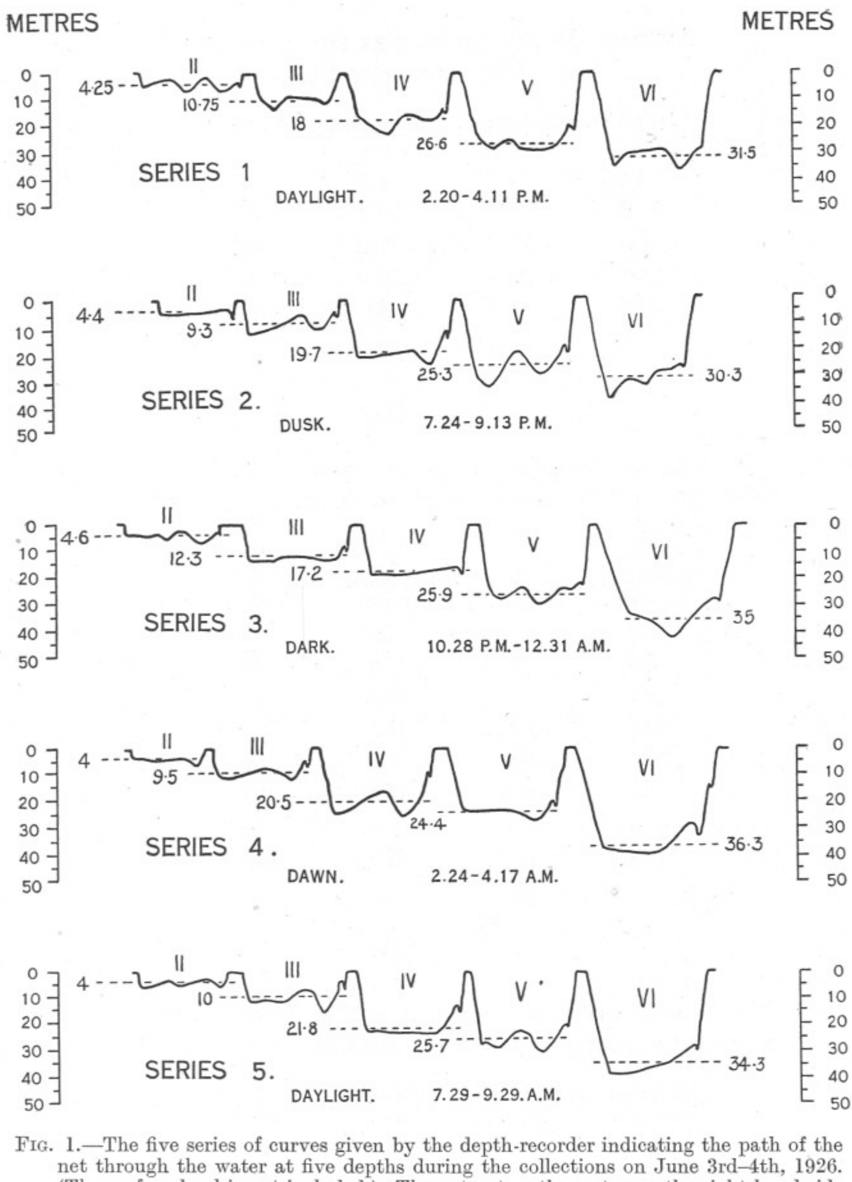

FIG. 1.—The five series of curves given by the depth-recorder indicating the path of the net through the water at five depths during the collections on June 3rd–4th, 1926. (The surface haul is not included.) The net enters the water on the right-hand side of each curve. The dotted lines indicate the calculated "average depths."

Table II.

Average Depth in Metres for each Haul on June 3rd–4th, 1926.

	1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
Surface	—	—	—	—	—
II	4·25	4·4	4·6	4	4
III	10·75	9·3	12·3	9·5	10
IV	18	19·7	17·2	20·5	21·8
V	26·6	25·3	25·9	24·4	25·7
VI	31·5	30·3	35	36·3	34·3

Table III.

Total Numbers of Post-larvæ caught in each Haul on June 3rd–4th, 1926, exclusive of those of Clupea sp., Gobius sp., and Callionymus sp.

	1st Series. Daylight.	2nd Series. Dusk.	3rd Series. Dark.	4th Series. Dawn.	5th Series. Daylight.
Surface	9	39	59	3	45
II	14	94	123	39	98
III	84	99	181	97	140
IV	217	220	182	125	174
V	235	128	252	92	177
VI	161	200	182	62	74
Total	720	780	979	418	708

Table IV.

Total Numbers of different Species of Fish Post-larvæ occurring in the Collections made on June 3rd–4th. 1926.

	1st Series. Daylight.	2nd Series. Dusk.	3rd Series. Dark.	4th Series. Dawn.	5th Series. Daylight.
Surface	6	5	15	5	8
II	11	13	20	16	19
III	17	18	19	22	15
IV	19	20	17	21	16
V	21	20	21	24	18
VI	22	21	20	21	19

The Clupeids, however, form a notable exception to this rule, showing a very marked increase in numbers at night. On this occasion they consisted of a mixture of Sprats and Pilchards, and they repeated almost exactly the behaviour shown by the young pilchards in the previous years (**3**). The only other species that showed a similar increase at night were the Gobies.

Table III shows the number of post-larvæ taken at each depth of all species, exclusive of those of the Clupeids and the Gobies and also of Callionymus sp., which occurred in such numbers as to outweigh all other fish. This table shows very clearly that while there was a general increase in numbers at the surface and in the upper layers down to about 10 metres at night, there was little change in the deeper hauls from that of the daytime. It shows also that in daylight on June 4th (Series 5) there were again nearly as many fish in the surface layers as at night ; this was, no doubt, due to the presence of immense swarms of Calanus which must have decreased the light intensity to a considerable degree.

Table IV gives the total number of different species taken at each depth, and it can be seen that while the majority live in the deeper layers in the daytime, nearly all the species have been involved in the slight upward extension at night. In this respect also the results obtained in the previous years are substantially confirmed.

The general inference to be drawn from these few observations is that except in the case of Clupeids, Gobies, and possibly Callionymus (**3**, p. 408), it is probably safe to base conclusions of seasonal or horizontal distribution, of those species which have been here caught in significant numbers, from collections made either by day or by night with oblique hauls. This applies only to those species whose normal daytime distribution is well above the bottom, so that the complete range of their vertical distribution would be covered by an oblique haul. There is no evidence that the numbers taken at night would be so very much larger than day catches as to show differences greater than those occasioned by local unevenness in horizontal distribution. It must be admitted, however, that these conclusions are based on observations for four nights only, and more observations are certainly desirable, especially in May.

It is interesting to notice that very many of those species, that normally live in the deeper layers in the daytime, when caught near the surface at dawn and daylight on June 4th were very much mutilated. This has been noticed on previous occasions and suggests that during the great mixing up of plankton organisms at night extensive feeding is taking place and dead or dying postlarval fishes are left behind in the upper layers when those that have escaped have retired to greater depths.

In the following pages each species is dealt with in detail. The actual numbers of all species caught are given in Table X, page 850, at the end of the paper. Throughout the expressions "Daylight," "Dusk," "Dark," and "Dawn" have been used to cover the various periods at which collections were made; the actual times, however, are given in the various figures and tables.

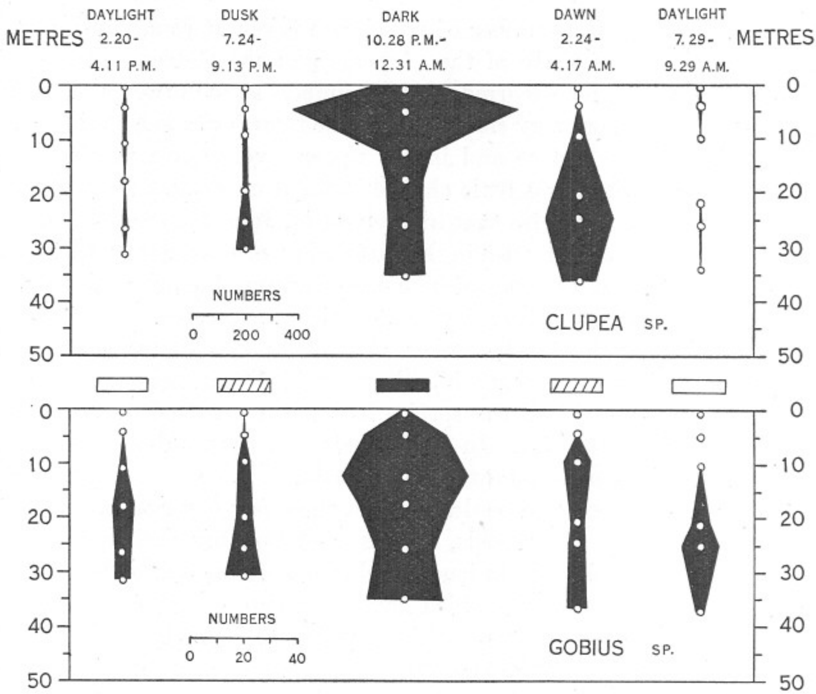

FIG. 2.—The vertical distribution of Clupea sp. (*C. sprattus* and *S. pilchardus*) and Gobius sp. post-larvæ, at the times shown, on June 3rd–4th, 1926. The white spots and black circles indicate the "average depths" at which hauls were taken. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively.

CLUPEIDÆ.

CLUPEA SPRATTUS L. AND SARDINA PILCHARDUS (Walb.).

The Clupeid post-larvæ consisted of a mixture of *Clupea sprattus* and *Sardina pilchardus*, all under 24 mm. in length and mostly between 10 and 20 mm. Fig. 2, which gives the vertical distribution of these post-larvæ together, shows that hardly any Clupeids were caught in the day-time on June 3rd at the depths sampled down to 31 metres, 15 individuals being the largest catch at any one depth. At dusk there was a slight increase in the layers below 20 metres, 41 and 77 being caught at 25·3 and 30·3 metres respectively. In the dark, however, there had been a very marked increase in numbers at all depths, the greatest catch of 852 specimens being taken at 4·6 metres. At dawn they had left the surface layers, but large numbers were still caught from 20 metres downwards. At daylight the next day the previous daytime distribution was repeated, the largest catch being only 13.

In this behaviour the Sprat and Pilchard have exactly repeated that shown by the pilchard on the three previous nights examined in 1924 and 1925 (**3**, p. 396). On the present occasion, however, definite evidence seems to be afforded that the increase in numbers at night is due to the post-larvæ having moved up from the levels below 35 metres. The dawn distribution appears quite definitely to indicate a downward migration, and also at dusk the beginning of an upward migration is apparent in the deepest hauls.

The results of these four nights are of great importance and appear to show definitely that in June and July any study of the distribution of these post-larvæ must be carried out at night. On the three nights in 1924 and 1925 there were over ten times as many caught in the dark (or at dawn in 1924) as in the daytime, while in 1926 there were over thirty times as many caught at night.

Quite the same results were obtained by Johansen (**2**, p. 12) in Danish waters for the young herring, *Clupea harengus* L., many more both of the winter-spawned and of the autumn-spawned herring being caught at night than in the daytime in April, 1925.

GADIDÆ.

Gadus merlangus L.

A study of Table X, page 850, shows that while in the daylight on both days the majority of whiting post-larvæ occurred below 10 metres, at dusk there were very large catches at the surface and in the layers above 10 metres. In the dark there were very few caught, and the majority of these were again below 10 metres, while at dawn the numbers were rather too low to be significant.

Before, however, we can draw conclusions as to the behaviour of these young whiting, it is necessary to analyse the catches and see what sizes the post-larvæ are. In Table V are given the sizes and total numbers of specimens taken in each haul. It is at once evident that the great increase in numbers in the surface layers at dusk is caused by the presence of specimens of 12 mm. and longer, which were completely absent in the daytime on June 3rd. The very large catches in the daylight on June 4th are also due to post-larvæ of 12 mm. and over. Examination of the plankton samples shows that there is obviously a correlation between the abundance of these larger stages and the presence or absence of *Cyanea capillata*.

TABLE V.

GADUS MERLANGUS.

Length in Millimetres.

	Depth in metres	Cyanea	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	32	33	34	35	36	37	38	39	40	41	42	43	44	45	Total
1st Series	S.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	4·25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	10·75	–	–	1	1	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
	18	–	1	5	3	4	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16
	26·6	–	–	3	4	6	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15
	31·5	–	–	–	4	2	1	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
2nd Series	S.	3	–	–	–	1	–	–	2	2	1	2	3	–	3	–	–	1	–	3	4	2	–	1	2	–	2	–	1	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	33
	4·4	2	–	–	–	1	1	3	5	5	3	7	2	6	8	4	6	1	3	3	1	3	4	4	–	–	1	–	2	–	1	–	–	–	–	–	–	1	–	–	–	1	–	1	77
	9·3	1	–	1	–	–	–	–	–	2	4	2	4	4	4	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25
	19·7	–	–	1	9	4	7	4	10	2	2	6	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	48
	25·3	1	1	–	3	5	5	1	1	1	3	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22
	30·3	–	–	1	6	3	4	1	6	1	2	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27
3rd Series	S.	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	4·6	–	–	–	1	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
	12·3	3	–	–	1	2	1	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9
	17·2	–	–	–	–	1	3	1	–	–	2	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
	25·9	1	–	1	1	6	5	1	–	1	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	17
	35	–	–	2	2	3	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
4th Series	S.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	4	–	–	–	–	–	–	–	–	–	–	–	1	–	2	–	–	1	–	1	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8
	9·5	–	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
	20·5	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9
	24·4	–	–	–	–	2	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
	36·3	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
5th Series	S.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	4	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
	10	1	–	1	4	3	3	3	1	2	–	3	2	4	2	3	3	1	4	1	1	3	2	2	1	1	2	–	1	–	3	–	–	3	–	2	–	–	1	–	–	–	1	–	63
	21·8	5	–	3	4	8	12	21	15	5	7	9	7	4	3	3	4	5	1	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1*	115
	25·7	5	–	2	5	4	5	6	8	4	5	1	–	2	1	1	2	–	1	–	–	–	–	–	–	1	1	–	1	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	52
	34·3	–	–	3	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6

*=47 mm.

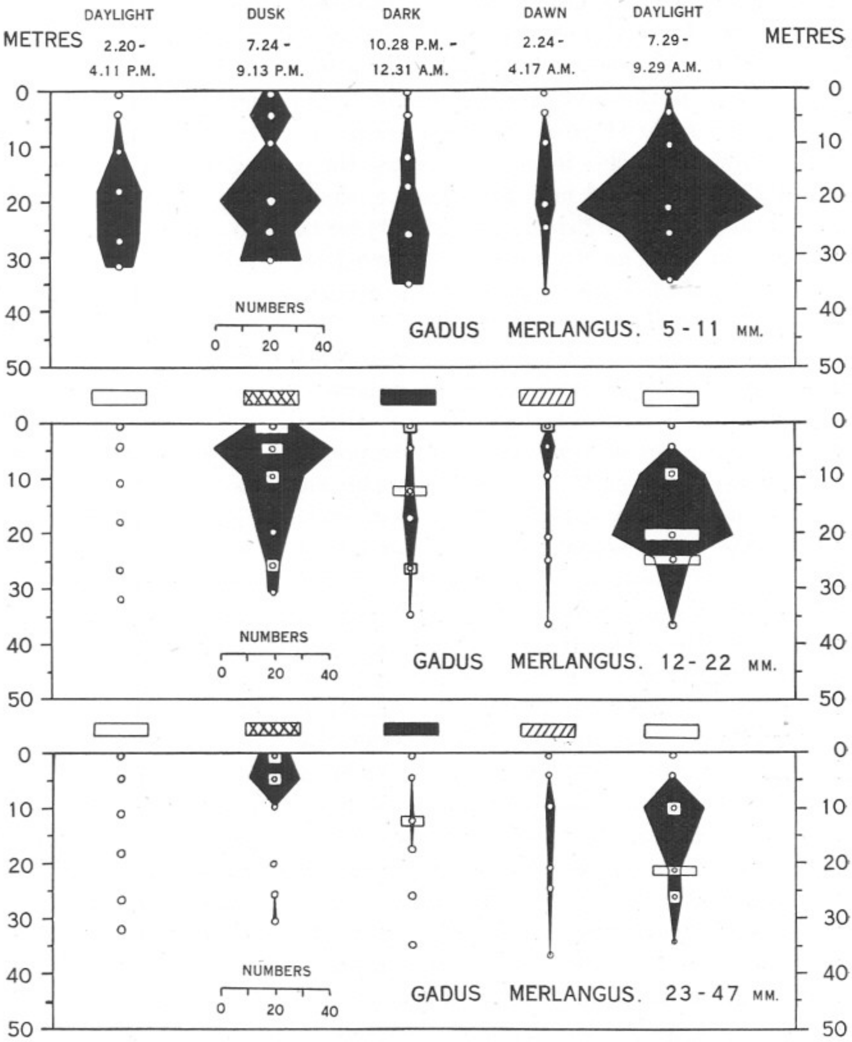

FIG. 3.—The vertical distribution of *Gadus merlangus* of different sizes, viz. 5–11 mm. 12–22 mm., and 23–47 mm., at the times shown, on June 3rd–4th, 1926. The presence of Cyanea is also indicated in the lower two diagrams as white oblong blocks at the depths at which they occurred (for numbers see Table VI). (In haul V of the 5th series the oblong is too small and should be the same size as that immediately above it, corresponding to 3 Cyanea.) The white spots and black circles indicate the "average depths" at which hauls were taken. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively.

Damas (**1**, p. 42) was of the opinion that the association of the young whiting with Cyanea begins after the fish has almost completely metamorphosed at a length of 23 mm. It would seem from Tables V and VI, however, that in these waters the association may begin considerably earlier, since in the daytime specimens of 12 mm. and over only occurred in the catches when Cyanea was also present. In Table VII I have accordingly given the catches in each haul of the three size groups, 4 to 11 mm., 12 to 22 mm., and 23 mm. upwards, i.e. the size quoted by Damas. I have also indicated by single asterisks (*) for the two smaller size groups the hauls in which any Cyanea at all occurred, and by double asterisks (**) in the case of the largest size group the occurrence of large Cyanea, four or more inches in diameter.

This table shows that post-larvæ of the whiting from 4 to 11 mm. in length occurred irrespective of whether there were Cyanea present in the catches. The occurrence of specimens between 12 and 22 mm. however showed quite a close correlation with the presence or absence of Cyanea ; while whiting of over 23 mm. were practically associated only with Cyanea of quite a large size, namely, four or more inches in diameter. In Fig. 3 these same data are shown graphically, and it can be seen very clearly that in the case of specimens less than 12 mm. in length there was little indication of any vertical movement throughout the 24 hours. As regards the two larger size groups there was obviously a migration to the surface at dusk, but this was a movement also undertaken by Cyanea, and the indications are very strong that the whiting have merely followed the Cyanea towards the surface. This behaviour has already been noticed by Damas (**1**, p. 43), who says : " Pendant la longue période où le jeune merlan vit en commensal des méduses, sa distribution bathymétrique est aisée à déterminer. On peut l'observer pendant des journées entières à un niveau plus ou moins élevé et variable avec l'heure du jour. Il suit les méduses dans leur migrations verticales. Celles-ci sont particulièrement marquées par les jours de ciel clair et paraissent dirigées par un phototropisme accentué. Pendant les heures du jour, les méduses et leurs hôtes sont absent de la surface, on a peine à les découvrir à une dizaine de mètres de profondeur. Elles remontent au crépuscule. Après une journée de calme parfait, durant laquelle il n'a été possible de découvrir aucun signe de vie à la surface, on peut assister à la tombée de la nuit à un spectacle qui donne une idée de l'abondance des méduses et en consequence du jeune merlan. Aussi loin que l'œil peut porter, la mer semble frappée par une pluie abondante et silencieuse. Cet effet est dû aux méduses choquant la surface à chaque contraction du disque."

TABLE VI.

NUMBERS AND SIZES (DIAMETER IN INCHES) OF CYANEA CAPILLATA OCCURRING IN THR RING-TRAWL CATCHES ON JUNE 3RD–4TH, 1926.

	1st Series. Daylight.	2nd Series. Dusk.	3rd Series. Dark.	4th Series. Dawn.	5th Series. Daylight.
Surface	–	3 (5″; 2″; 2″)	1 ($2\frac{1}{2}$″)	1 ($\frac{3}{4}$″)	–
II	–	2 (4″; 3″)	–	–	–
III	–	1 (3″)	3 (2″; $4\frac{1}{2}$″; 6″)	–	1 (4″)
IV	–	–	–	–	5 (5″; 5″; 4″; 4″; 3″)
V	–	1 (3″)	1 ($1\frac{3}{4}$″)	–	5 ($7\frac{1}{2}$″; $5\frac{1}{2}$″; 4″; 2″; $\frac{1}{2}$″)
VI	–	–	–	–	–

TABLE VII.

DISTRIBUTION OF DIFFERENT SIZE GROUPS OF WHITING AND OCCURRENCE OF CYANEA.

	1st Series. Daylight.	2nd Series. Dusk.	3rd Series. Dark.	4th Series. Dawn.	5th Series. Daylight.
			4–11 mm.		
S.	–	5*	1*	–*	–
II	–	15*	1	–	3
III	4	3*	5*	4	17*
IV	16	37	5	7	68*
V	15	17*	15*	3	34*
VI	10	22	11	1	6
			12–22 mm.		
S.	–	17*	–*	–*	–
II	–	44*	2	5	–
III	–	22*	3*	1	24*
IV	–	11	5	1	43*
V	–	5*	2*	1	13*
VI	–	4	–	–	–
			23–47 mm.		
S.	–	11**	–	–	–
II	–	18**	–	3	–
III	–	–	1**	1	22**
IV	–	–	–	1	4**
V	–	–	–	–	5**
VI	–	1	–	–	–

* Presence of Cyanea.
** Presence of Cyanea 4 or more inches in diameter.

Fig. 3 shows also that there is a slight indication that at night the young whiting may separate from the Cyanea, because although Cyanea were present in some of the catches, the numbers of whiting of 12 mm. or more were very few; also at dawn a few whiting were caught but no Cyanea. This, however, is only a bare indication.

Gadus minutus (O. F. Müll.).

As usual the post-larvæ of this species were scarcely taken at all above a depth of 25 metres in the daytime. At dusk and in the dark there was hardly any change in their vertical distribution, except that in the dark a few were taken in the layers above 20 metres up to 5 metres below the surface (Fig. 4). At dawn the numbers were rather too low to be at all

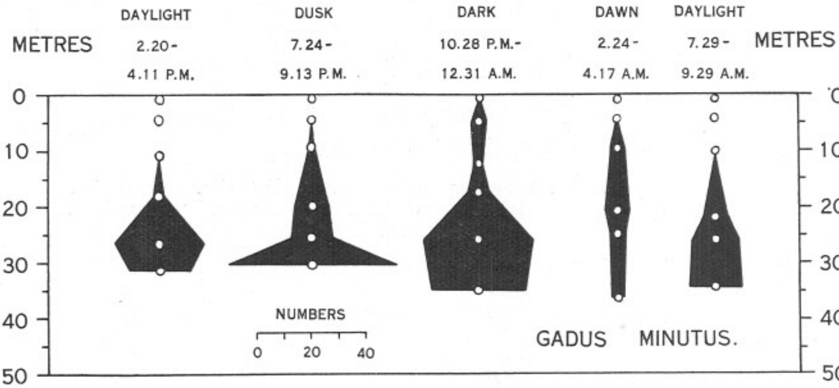

Fig. 4.—The vertical distribution of *Gadus minutus*, at the times shown, on June 3rd–4th, 1926. The white spots and black circles indicate the "average depths" at which hauls were taken.

significant. An examination of the sizes of these post-larvæ showed that in the daytime they were all between 4 and 11 mm. in length. At dusk and in the dark, however, a few appeared in the deeper layers 12 to 15 mm. in length, and one 20 mm. long was caught at 20·5 metres at dawn.

Onos sp.

Post-larval rockling were not very abundant in daylight on June 3rd or at dusk, the few there were being evenly distributed from the surface downwards. At night more were caught, the largest catch of 21 specimens being from the surface itself. Again, very few were taken at dawn, but in the daylight on June 4th another large catch of 28 was taken at the surface itself.

Of the remaining Gadoids, *Gadus pollachius* L., *Gadus luscus* L., *Molva molva* L., and *Merluccius merluccius* L., very few were taken. Of these

G. pollachius and *M. merluccius* post-larvæ only occurred singly, while *G. luscus* and *M. molva* were only caught in the deeper levels.

BOTHIDÆ.

Scophthalmus norvegicus (Günther).

Large numbers of the post-larvæ of this species were captured in each series of hauls. In daylight on June 3rd the majority occurred at depths between about 14 metres and 31·5 metres, the deepest depth sampled (Fig. 5). At dusk there had been a slight upward movement, the greatest catch occurring at 19·7 metres. In the dark there was evidence of an increase in number at all depths and an extension upwards of a few to the surface itself, although the majority still lay below about 10 metres. An examination of Table VIII, which gives the sizes of the post-larvæ caught at each depth, shows that this increase in numbers is due to an influx of individuals of 8 mm. or over. While the total number of specimens from 4–7 mm. inclusive was in the daytime 142 and in the dark 143, those of 8–11 mm. increased in number from 18 in the daylight to 60 in the dark.

At dawn, although there were fewer taken at all depths, the majority occurred between 5 and 25 metres. In the daylight on June 4th there was, however, a marked rise towards the surface, the greatest catch being at 4 metres. It is probable that this rise towards the surface was occasioned by a diminution of light intensity caused by an extremely dense swarm of *Calanus finmarchicus*. Examination of my records (not yet published) showed that Calanus also exhibited this upward movement, and that their numbers were so great that they may well, so to speak, have caused their own shading.

An interesting corroboration of the fact that there appears to be some factor (probably light intensity) which governs all species alike occurs here. Research has shown that there are associations of animals which live at the same depths, and in the upper layers amongst such species as Calanus, Upogebia larvæ, and Turris appear also the post-larval stages of *Scophthalmus norvegicus*, Callionymus sp., and Trigla sp. Fig. 6, page 846, shows that Callionymus sp. exhibited almost the same rise to the surface in the daylight on June 4th as did *S. norvegicus*. This suggests that possibly these young fish may be limited in their upward movements by their speed of swimming. At dusk the light wanes so quickly that they have no time to reach the surface by following their optimum intensity, and in the dark owing to the absence of the light stimulus there is no incentive to move towards the surface and the young fish move about anywhere, most staying at the levels at which they already were. It is very different, however, if the intensity is lowered during the daytime by the persistent presence of a swarm of Calanus. Under such conditions the light is not changing rapidly, but remains constantly low. The fish then have time to pick up their optimum level.

In comparison with the records for previous years *S. norvegicus* has always behaved in the same manner.

Table VIII.

Scophthalmus norvegicus.

	Depth in metres.	Length in millimetres. 4	5	6	7	8	9	10	11	Total numbers of fish.
1st Series	*S.*	–	–	–	–	–	–	–	–	**0**
	4·25	–	–	1	1	–	–	–	–	**2**
	10·75	–	4	5	5	–	–	–	–	**14**
	18	3	12	13	10	4	1	–	–	**43**
	26·6	2	16	16	19	6	–	1	–	**60**
	31·5	6	13	12	5	6	1	–	–	**43**
2nd Series	*S.*	–	–	–	1	–	–	–	–	**1**
	4·4	–	–	3	–	–	–	–	–	**3**
	9·3	–	5	9	4	4	–	–	–	**22**
	19·7	2	4	9	8	14	5	2	–	**44**
	25·3	1	4	10	8	–	–	–	–	**23**
	30·3	1	1	5	9	2	–	1	–	**19**
3rd Series	*S.*	–	–	2	4	–	1	–	–	**7**
	4·6	1	5	4	3	4	–	–	–	**17**
	12·3	1	9	11	11	7	4	2	–	**45**
	17·2	–	3	14	15	18	2	–	1	**53**
	25·9	2	11	10	17	7	3	3	–	**53**
	35	1	6	4	9	7	–	1	–	**28**
4th Series	*S.*	–	1	–	–	–	–	–	–	**1**
	4	–	2	3	–	–	–	–	–	**5**
	9·5	3	10	6	1	–	–	–	–	**20**
	20·5	1	8	5	10	–	1	–	–	**25**
	24·4	–	1	5	2	4	–	–	–	**12**
	36·3	–	–	1	–	–	1	2	–	**4**
5th Series	*S.*	–	3	4	1	–	–	–	–	**8**
	4	3	14	17	7	3	1	–	–	**45**
	10	–	3	9	9	7	4	–	–	**32**
	21·8	1	2	8	2	4	–	–	–	**17**
	25·7	2	8	9	6	5	2	–	–	**32**
	34·3	–	1	3	2	1	–	–	–	**7**

Zeugopterus punctatus (Bloch.).

Only a few post-larvæ of this species were taken, and it can be seen from Table X, page 850, that the majority were always below a depth of 10 metres.

Post-larvæ of Arnoglossus sp., 5–9 mm. in length, only occurred in a few hauls and then nearly always singly.

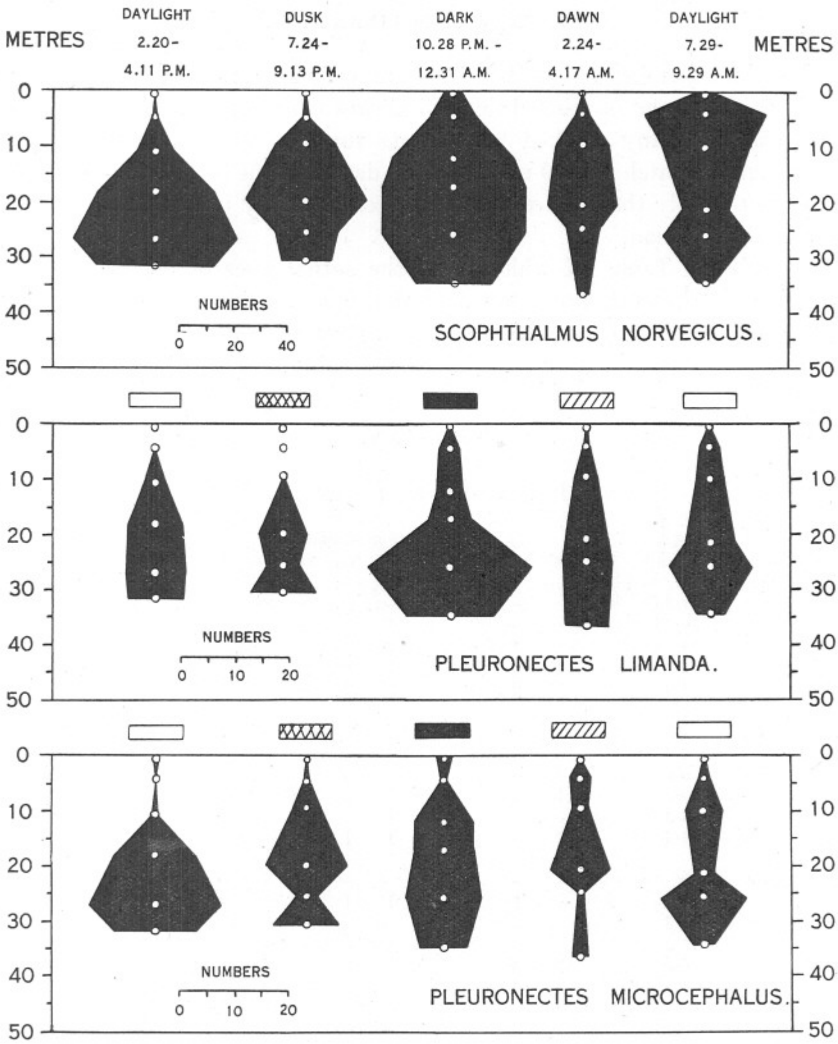

FIG. 5.—The vertical distribution of *Scophthalmus norvegicus*, *Pleuronectes limanda*, and *P. microcephalus*, at the times shown, on June 3rd–4th, 1926. The white spots and black circles indicate the " average depths " at which hauls were taken. The plain, cross-hatched, black, and shaded rectangles represent " daylight," " dusk," " dark," and " dawn " respectively.

PLEURONECTIDÆ.

PLEURONECTES LIMANDA L.

Post-larval stages of the dab were not very abundant. The majority were taken in the daytime below 15 metres (Fig. 5), and there were no indications of any marked movements towards the surface at night. Although the catch at 25·9 metres in the dark was the largest at any time, it is quite likely that this was merely occasioned by unevenness in horizontal distribution.

A study of Table IX which gives the actual sizes of the post-larvæ caught at each depth shows, however, that in the dark there was evidently quite a definite incursion of early bottom stages from 13 to 17 mm. in length.

TABLE IX.

PLEURONECTES LIMANDA.

	Depth in metres.	Length in millimetres.													Total numbers of fish.
		5	6	7	8	9	10	11	12	13	14	15	16	17	
1st Series	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4·25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	10·75	–	–	–	2	1	1	–	–	–	–	–	–	–	**4**
	18	–	–	2	1	2	2	3	–	–	–	–	–	–	**10**
	26·6	–	1	3	3	1	2	–	1	–	–	–	–	–	**11**
	31·5	–	–	2	2	–	2	2	–	2	–	–	–	–	**10**
2nd Series	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4·4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	9·3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	19·7	–	1	1	–	1	3	2	–	–	1	–	–	–	**9**
	25·3	–	–	2	–	1	3	–	–	–	–	–	–	–	**6**
	30·3	–	2	–	2	4	1	1	1	–	1	–	–	–	**12**
3rd Series	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4·6	–	–	1	–	–	1	1	–	1	–	–	–	–	**4**
	12·3	–	–	–	2	–	–	–	–	1	–	1	1	–	**5**
	17·2	–	–	–	2	3	1	–	–	1	–	–	–	1	**8**
	25·9	–	3	5	3	5	7	2	–	2	–	2	–	1	**30**
	35	–	3	5	–	4	1	1	1	–	1	–	–	–	**16**
4th Series	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	–	1	–	–	–	–	–	–	–	–	–	**1**
	9·5	–	–	1	1	2	–	–	–	–	–	–	–	–	**4**
	20·5	–	–	4	2	2	–	–	–	–	–	–	–	–	**8**
	24·4	–	–	3	1	2	1	1	–	–	1	–	–	–	**9**
	36·3	–	–	1	–	1	3	1	–	–	–	1	1	–	**8**
5th Series	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	1	3	–	–	–	–	–	–	–	–	–	**4**
	10	1	–	3	–	–	1	–	–	–	–	–	–	–	**5**
	21·8	–	–	3	2	2	1	–	1	–	–	–	–	–	**9**
	25·7	–	5	3	2	–	2	1	1	–	1	–	–	–	**15**
	34·3	–	–	–	2	–	–	1	1	1	–	–	–	–	**5**

PLEURONECTES MICROCEPHALUS (Don.).

Post-larvæ of this species, between 5 and 14 mm.* in length and almost all between 6 and 11 mm., were in the daytime on June 3rd mainly distributed from about 15 metres downwards (Fig. 5). At dusk there was evidence that they had slightly extended their distribution upwards to about 10 metres, and in the dark they were more or less evenly distributed from 10 metres downwards, but above this level they were almost absent, there being only 3 at the surface and one at 4·6 metres. At dawn the numbers were really too small to be significant, but the largest catch was made at 20·5 metres. In the daylight on June 4th again the numbers were low and the largest catch occurred at 25·7 metres.

The evidence from this and the observations in preceding years, on which far fewer post-larvæ were caught, is that while in the daytime they live mostly below 15 metres, at night they tend to move about at all depths from about 10 metres downwards, but only a few reach actually to the surface or to 5 metres.

Only one post-larva of *Pleuronectes flesus* L. was caught, at 25·3 metres at dusk.

SOLEIDÆ.

SOLEA VARIEGATA (Don.).

Post-larvæ of *S. variegata*, between 4 and 8 mm. in length, were most abundant below 10 metres in the daytime on June 3rd (Fig. 6). At dusk they were slightly higher in the water, being most abundant at about 10 metres. In the dark they were almost evenly distributed from about 10 metres downwards, while a certain number had extended to the surface itself. At dawn the majority were below 10 metres, but the numbers caught were very small. In daylight on June 4th there were indications of a movement towards the surface again as with other species, the numbers were still, however, very low compared with the day before, evidently due to unevenness in horizontal distribution.

At dusk two metamorphosing post-larvæ, of 9 and 10 mm., appeared at 19·7 and 30·3 metres respectively, while in the dark three were taken, one each at 4·6, 12·3, and 25·9 metres. Four early bottom stages also were caught in the dark, two at 25·9 metres and two at 35 metres.

Only two specimens of *Solea vulgaris* (Quenn.) were caught, one at 31·5 metres in daylight on June 3rd and one at 25·3 metres at dusk.

* One metamorphosed specimen, 19 mm. in length, was taken in the deepest haul at dusk.

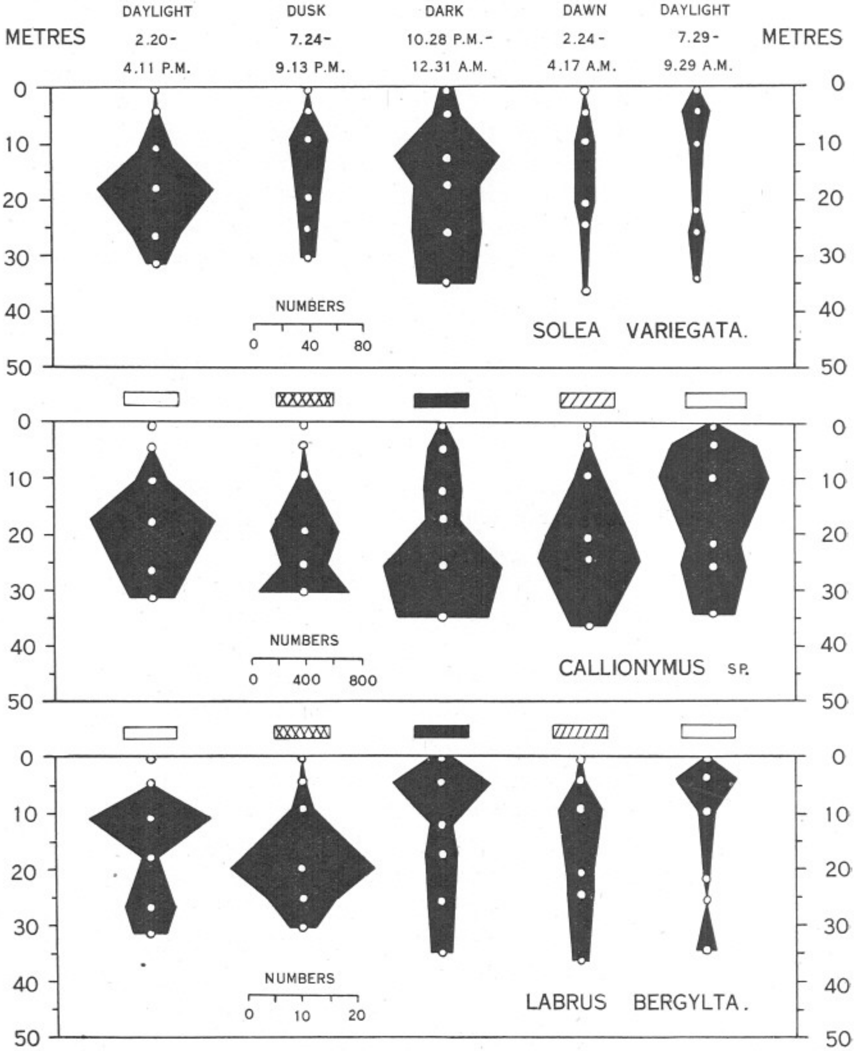

FIG. 6.—The vertical distribution of *Solea variegata*, Callionymus sp., and *Labrus bergylta*, at the times shown, on June 3rd–4th, 1926. The white spots and black circles indicate the " average depths " at which hauls were taken. The plain, cross-hatched, black, and shaded rectangles represent " daylight," " dusk," " dark," and " dawn " respectively.

AMMODYTIDÆ.

AMMODYTES LANCEOLATUS (Lesauv.).

Post-larvæ of *A. lanceolatus*, mostly about 6 to 25 mm. in length, occurred rather unevenly distributed from the surface downwards in daylight on June 3rd. At dusk they were absent above about 10 metres, while in the dark they were again present from the surface downwards. At dawn there were none in the two upper hauls at the surface and at 4 metres, and in the daytime on June 4th only a few were taken, but none actually at the surface itself.

Only very few larvæ of *A. tobianus* were caught.

CALLIONYMIDÆ.

Post-larvæ of Callionymus sp., probably almost all *C. lyra*, were as usual very abundant in the collections. In the daytime the majority lay below 10 metres (Fig. 6), and at dusk there had been little change in the distribution, but slightly fewer were caught. In the dark, although the majority were still below 15 metres, quite a large number had extended up to 5 metres and a few even to the surface itself. By dawn the surface layers had been vacated, and the majority lay again below 10 metres. In daylight on June 4th there had been a considerable upward movement, the same as that shown by the post-larvæ of *S. norvegicus* and commented on in the account of that fish.

As on the previous occasion a few late post-larval and early bottom stages appeared in the deeper layers in the dark.

LABRIDÆ.

Of the post-larval wrasses those of *Labrus bergylta*, 4–7 mm. long, were the most numerous. In the daytime on June 3rd they avoided the actual surface layers and the majority were taken at 10·75 metres (Fig. 6). At dusk they had moved considerably deeper in the water and the largest catch was at 19·7 metres. In the dark there was an upward movement again, most being caught at 4·6 metres. At dawn they were evenly distributed from 4 metres downwards, although fewer were caught. In the daylight on June 4th they had moved once more towards the surface.

Of the other species *Labrus mixtus* were much less abundant, but showed much the same behaviour as *L. bergylta*. But the catches of *Crenilabrus melops* and *Centrolabrus exoletus* were too small to be significant.

SCOMBRIDÆ.

Only very few post-larvæ of *Scomber scomber* were taken.

GOBIIDÆ.

Fig. 2, page 834, shows that there was a marked increase of these post-larvæ at all depths in the dark except at the surface itself. In this respect the results repeat the behaviour shown on the two nights in June, 1925, but differ from that of July, 1924 (**3**, p. 411), when no indication of marked upward movement was shown and the young gobies were already well up in the water in the daytime.

Only very few post-larvæ of *Lebetus scorpioides* (Coll.) were taken, and then only in the deeper layers.

As is usually the case, a few *Crystallogobius nilssoni* appeared in the deeper hauls in the dark, these fish living actually on the bottom in the daytime.

BLENNIIDÆ.

Post-larvæ of *Blennius pholis* (L.) and *B. gattorugine* (L.) both appeared in small numbers in the catches and their distribution was somewhat indiscriminate, with the usual tendency for a preference for the upper layers.

TRIGLIDÆ.

TRIGLA SP.

Post-larval gurnards, mostly between 6 and 11 mm. in length, were taken in the daylight on June 3rd chiefly below 10 metres. At dusk far fewer were caught, but they were still in the same layers. In the dark there had been a definite extension into the upper layers, even to the surface itself, but the numbers taken were rather small. At dawn the majority were again distributed at about 10 metres and lower, but in daylight on June 4th, although the numbers caught were extremely small, there was an indication that they had moved up higher in the water as did Scophthalmus and Callionymus.

COTTIDÆ.

Cottus bubalis post-larvæ were extremely rare and then only occurred singly.

GOBIESOCIDÆ.

Lepadogaster bimaculatus (Penn.).

Although post-larvæ of this species were not very abundant they showed a marked tendency to move into the upper layers in the dark, being deep down in the daylight.

LOPHIIDÆ.

Lophius piscatorius (L.).

Only three specimens of these post-larvæ occurred in the catches.

SUMMARY.

1. Results are given of a further series of collections made with the stramin ring-trawl to determine the diurnal behaviour of post-larval stages of Teleostean fishes in the Plymouth area.

2. The catches were very satisfactory and showed that in no case, except for Clupeids and Gobies, was there any really marked movement of young fish towards the surface. This confirms previous observations.

3. It has been shown on this and previous occasions that Clupeids are many times more abundant in the catches at night than in the daytime, and any study of their seasonal or horizontal distribution would probably have to be carried out at night.

4. For the remaining species, except perhaps Gobies and Callionymus, oblique hauls taken either at day or at night should give a fair picture of seasonal or horizontal distribution. More observations are, however, required.

5. The association of the whiting young with the medusa, *Cyanea capillata*, is discussed.

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TABLE X.—Young Fish Caught, June 3rd–4th, 1926.

	Time.	*Depth in metres.*	Clupea sp.	Gadus merlangus.	G. minutus.	G. pollachius.	G. luscus.	Onos sp.	Molva molva.	Merluccius merluccius.	Arnoglossus sp.	Scophthalmus norvegicus.	Zeugopterus punctatus.	Pleuronectes limanda.	P. microcephalus.	P. flesus.	Solea vulgaris.	S. variegata.	Ammodytes tobianus.	A. lanceolatus.	Callionymus spa.	Labrus bergylta.	L. mixtus.	Crenilabrus melops.	Centrolabrus exoletus.	Scomber scomber.	Gobius sp.	Lebetus scorpioides.	Crystallogobius sp.	Blennius pholis.	B. gattorugine.	Trigla sp.	Cottus bubalis.	Lepadogaster bimaculatus.	Lophius piscatorius.	*Total.*
Daylight June 3rd	4·1 p.m.	*S.*	5	–	–	1	–	3	–	–	–	–	–	–	1	–	–	–	–	4	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**17**
	3.44 ,,	*4·25*	11	–	–	–	–	1	–	–	–	2	–	–	–	–	–	2	–	3	12	–	1	1	–	–	–	–	–	2	1	1	–	–	–	**37**
	3.25 ,,	*10·75*	9	4	–	–	–	2	–	–	1	14	–	4	1	–	–	12	–	12	238	22	2	2	–	–	3	–	–	3	1	4	–	–	–	**334**
	3.2 ,,	*18*	7	16	4	–	2	3	2	–	–	43	5	10	15	–	–	82	–	11	914	3	5	–	–	1	8	–	–	–	1	14	–	–	–	**1146**
	2.41 ,,	*26·6*	15	15	32	–	3	3	6	–	1	60	7	11	24	–	–	34	–	3	542	9	9	1	–	–	6	–	–	–	1	15	–	1	–	**798**
	2.20 ,,	*31·5*	5	10	22	–	2	–	6	1	–	43	5	10	15	–	1	15	1	8	328	6	8	–	–	–	6	1	–	–	–	4	1	2	–	**500**
Dusk	9.3 p.m.	*S.*	8	33	–	–	–	5	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**48**
	8.46 ,,	*4·4*	1	77	–	–	–	1	–	–	1	3	1	–	1	–	–	7	1	–	9	1	–	–	–	–	1	–	–	–	1	–	–	–	–	**105**
	8.28 ,,	*9·3*	10	25	2	–	–	–	–	–	–	22	1	–	5	–	–	28	–	1	66	4	2	1	–	1	4	–	–	1	3	1	–	1	–	**178**
	8.9 ,,	*19·7*	15	48	12	–	2	5	6	–	–	44	9	9	15	–	–	17	–	11	493	26	3	–	–	1	6	–	–	1	–	8	–	3	–	**734**
	7.48 ,,	*25·3*	41	22	15	–	1	1	2	–	–	23	5	6	4	1	–	15	–	5	331	13	4	–	–	–	9	–	–	2	–	3	–	6	–	**509**
	7.24 ,,	*30·3*	77	27	61	–	2	3	4	–	–	19	5	12	12	–	–	12	–	10	655	5	5	–	–	–	13	1	–	3	–	8	1	14	–	**949**
Dark	12.21 a.m.	*S.*	244	1	–	–	–	21	–	–	1	7	–	–	3	–	–	10	1	2	43	4	1	–	–	6	2	–	–	–	–	1	–	–	–	**347**
	12.1 ,,	*4·6*	852	3	6	–	–	2	–	–	2	17	–	4	1	–	–	20	2	29	231	18	6	–	–	1	31	–	–	1	2	5	–	6	–	**1237**
	11.36 p.m.	*12·3*	196	9	3	–	–	1	–	–	–	45	2	5	11	–	–	77	–	8	275	4	1	–	–	–	47	1	1	–	1	7	–	3	–	**697**
	11.13 ,,	*17·2*	147	10	8	–	–	5	–	–	–	53	1	8	11	–	–	48	–	16	242	6	1	–	–	–	35	–	4	–	–	6	–	5	–	**606**
	10.51 ,,	*25·9*	137	17	39	–	3	3	5	–	–	53	5	30	14	–	1	50	–	10	860	5	1	–	–	1	22	–	4	–	–	9	–	2	–	**1271**
	10.28 ,,	*35*	166	11	34	1	–	11	–	–	–	28	2	16	9	–	–	41	–	14	665	4	1	1	–	–	28	1	3	–	–	3	–	1	–	**1040**
Dawn	4.7 a.m.	*S.*	3	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	1	–	**12**
	3.49 ,,	*4*	12	8	–	–	–	–	–	–	1	5	1	1	4	–	–	7	1	–	46	2	2	1	–	–	–	–	–	1	3	3	–	–	–	**98**
	3.29 ,,	*9·5*	50	6	5	–	2	1	1	–	–	20	1	4	3	–	–	13	–	7	197	8	4	3	–	–	10	1	–	8	2	4	–	3	–	**353**
	3.8 ,,	*20·5*	192	9	9	–	3	2	1	–	–	25	2	8	11	–	–	15	–	11	626	5	3	2	–	–	5	1	–	6	–	14	–	3	–	**953**
	2.47 ,,	*24·4*	253	4	6	–	1	1	–	–	1	12	3	9	1	–	–	7	1	17	735	5	5	1	1	1	6	–	–	–	1	11	–	3	2	**1087**
	2.24 ,,	*36·3*	118	1	5	–	1	7	1	–	1	4	1	8	3	–	–	3	1	14	259	3	1	–	–	–	7	–	1	–	–	3	–	5	–	**447**
Daylight June 4th	9.19 a.m.	*S*	3	–	–	–	–	28	–	–	–	8	–	–	–	–	–	3	–	–	75	1	3	–	–	–	–	–	–	1	–	–	–	–	–	**122**
	8.59 ,,	*4*	13	3	–	–	–	2	–	–	1	45	–	4	2	–	–	19	1	7	623	11	2	3	1	–	–	–	–	2	1	4	–	–	1	**745**
	8.38 ,,	*10*	4	63	–	1	–	5	–	–	–	32	2	5	7	–	–	10	–	5	792	3	2	–	–	–	–	–	–	–	–	4	1	–	–	**936**
	8 17 ,,	*21·8*	–	115	9	–	–	–	4	–	–	17	3	9	4	–	–	5	–	3	410	1	–	–	–	–	7	1	–	1	–	1	–	1	–	**591**
	7.52 ,,	*25·7*	5	52	17	–	5	2	5	–	–	32	6	15	16	–	–	12	–	1	475	–	2	–	–	–	14	3	–	–	–	5	–	4	–	**671**
	7.29 ,,	*34·3*	1	6	19	–	1	2	2	–	–	7	1	5	4	–	–	4	–	1	291	4	2	–	–	–	3	2	–	–	–	2	–	2	–	**359**

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

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CONTENTS.

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

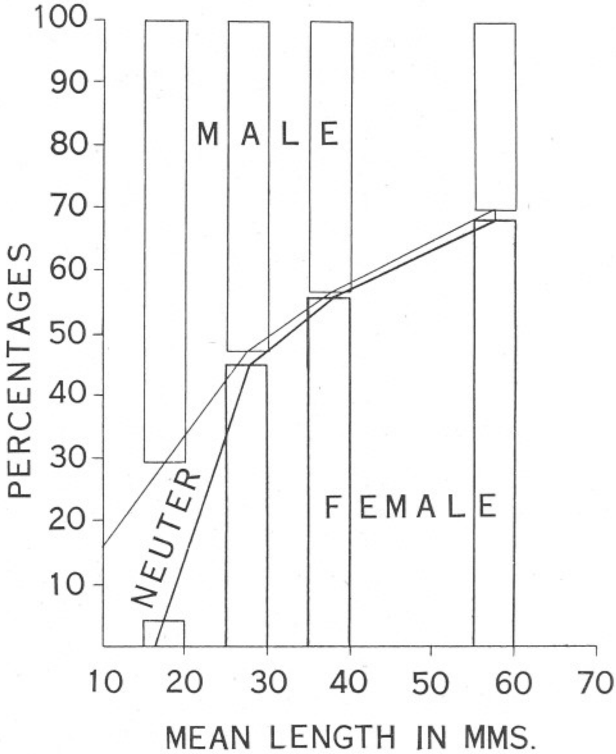

Fig. 1.—Analysis of 5350 individuals of *Patella vulgata* (Plymouth) for length of shell and sex, showing the occurrence of a high proportion of males among small individuals (about one year old), and a high proportion of females amongst larger individuals (mainly three or more years old).

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		1	2	3	1–3	4	5	6	1–4	4–5	5–6
Locality		G.W.W.*	Looe Is.	Hoe	Total	G.W.W.	G.W.W.	Looe Is.	—	—	—
Date in 1919		Oct. 31	Nov. 12	Oct. 31		Nov. 19	Nov. 6	Nov. 12	—	—	—
Length in mm.		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
Age in years†		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 1, 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

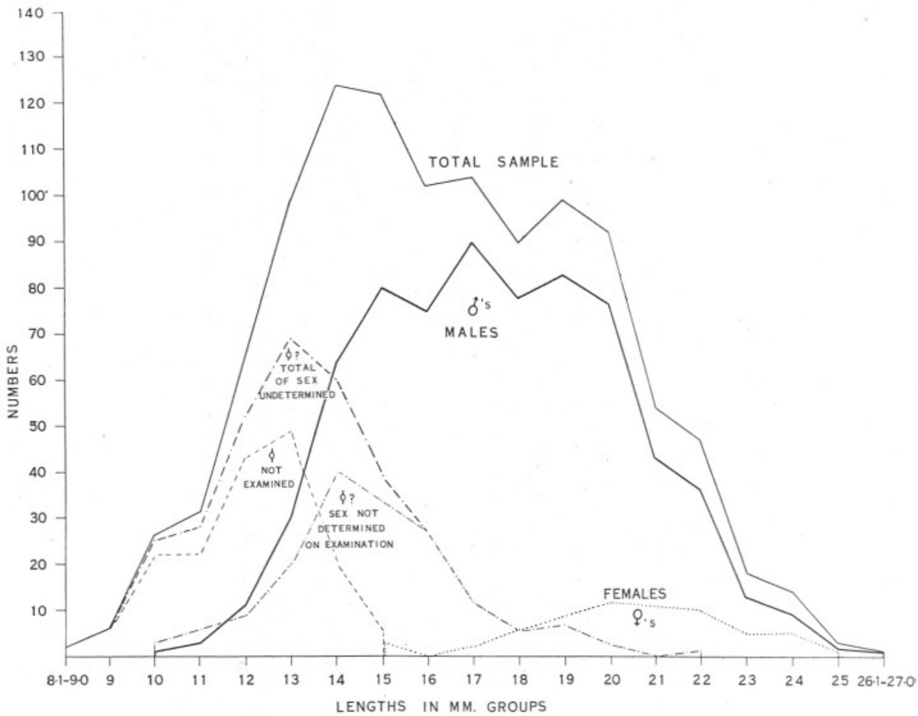

FIG. 2.—Analysis for sex and length (in mm. groups) of a sample of 1097 *Patella vulgata* (less than one inch in length) collected at random at Plymouth, October 31, 1919 (see Sample 1, Table I, p. 854).

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 Calyptræa 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-preportions (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 Corallinaceous 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 algæ 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 developoment 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 Brittanica*, 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 diœcious 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.

Observations on *Patella vulgata*. Part II. Rate of Growth of Shell.

By

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CONTENTS.

INTRODUCTION.

Observations on the rate of growth of *Patella vulgata* have been made over an extended period and are herein collected together. A preliminary notice of some of the results was recorded in the *Journal M.B.A.*, X, p. 319, 1914.

During the course of the building of a new wharf at the Great Western Railway Docks at Plymouth valuable experimental material was obtained gratuitously for general observation on the rate of growth of marine animals. This wharf (referred to later by the abbreviation G.W.W.) was rebuilt in 1911 and 1912 of reinforced cement and is 832 feet long by 60 ft. wide. It was built out into deep water (18 to 24 ft. at low water ordinary springs) to allow cargo vessels to unload alongside, and was erected on a foundation of 269 concrete piles driven into the sea-bottom. The upper ends of the piles were left with about 3 ft. projecting out of the water at L.W. ordinary springs. On the tops of these piles horizontal cement walings were first laid down *in situ* in the form of squares with horizontal and diagonal struts, and later vertical cement piles with diagonal struts were added upon these. The course of the construction was observed in frequent visits to the wharf, and by the courtesy of the Great Western Railway officials, especially Mr. J. A. Denny, the Assistant Divisional Engineer, and the works manager, Mr. Curtis, I was able to obtain detailed records of the dates of completion of construction of every pile or waling of which the structure is composed.

Every portion of this wharf, therefore, provided experimental material for determining the *maximum* age of any marine organisms which might grow thereon after being exposed to the sea. It happened that the year 1911 was an unusually warm one, and unusually favourable for the growth of marine organisms, and the first nine months of the year 1912 were also warmer than the average, so that the growths obtained at this wharf were remarkable. It was soon found that many of the prevalent marine animals attained sexual maturity or full size at an age of only a few months to a few years, so that new generations soon began to overlap the earlier ones. Therefore it became a matter of much importance to define the breeding periods of the different animals obtained in order to evaluate the material collected. The outbreak of the war in 1914 occurred at a critical stage in this work, and postponed publication of many of the results.

Observations on the Rate of Growth of *Patella vulgata*.

During 1912 it was found that limpets settled chiefly on the vertical cement piles, and also on the horizontal ones, but rarely on the cement piles which were driven into the sea bottom and remained projecting about 3 ft. above L.W. ordinary springs, that is, to the level just below L.W. neaps. In a zone 4 ft. above the horizontal walings limpets were common, but rare at heights of 5 to 6 feet, i.e. above the level of H.W. neap tides ; they therefore occurred mainly in a zone 3 to 12 ft. above low-water ordinary spring tides, that is, between L. and H.W. neap tide levels. Early in 1913 collections of Patella were made from various parts of the wharf, and in addition a number of limpets were marked and observations begun on the rate of growth of individuals. Additional material was collected during the year and in 1914. The results of the work are shown in Tables I and II, p. 868 and 870, and in Figs. 1 and 2, p. 866 and 871. In Fig. 1 are plotted the dates at which the cement surfaces (on which limpets were found) were exposed to the sea against the lengths of the limpets at the time of collection or observation. The resulting graphs give the maximum growth-period, but indicate by their angle of slope only the minimum average rate of growth, since larvæ would not actually settle in many cases at the moment the cement was exposed to the sea.

Within a small area the cement walings were constructed at about the same time, so that if far greater latitude of movement be allowed to Patella than is known to occur, the maximum age as determined would not err by more than 2 or 3 weeks if it be assumed that limpets crawled from one part of the wharf to another. The growth of three marked individuals was measured at intervals, mostly of a fortnight, from January 27 to September 1, 1913, and is plotted in Fig. 2, p. 871, as well as by the thicker lines in Fig. 1, p. 866.

The observed rate of growth in the period January to September, 1913, is greater than is indicated by most of the graphs in Fig. 1, i.e. where growth is plotted against the maximum possible period of growth, in spite of the arrest of growth shown in July (see Fig. 2) and the slower growth in February and March. Such a result is, however, to be expected from the fact that the breeding period of Patella at Plymouth extends from August to March, and that spat would only fall over a period from September–October to April–May with a maximum spat fall in the spring (see *Journ. M.B.A.*, XV, 3, p. 857). The settlement of young Patella may therefore be expected to occur from September to May, hence the group of individuals shown at A and B in Fig. 1 are unquestionably limpets derived from early and late falls of spat in the spatting season of 1911–1912. Similarly the groups of records at C and D in Fig. 1 are with little doubt derived from the spatfall of the season 1912–1913. The dotted lines ending at C in Fig. 1 are records of spatfalls whose growth was noted in 1913 (see Table I, Nos. 11 to 19). A few spat obtained on new structures built in the Cattewater in May, 1919, are shown in Fig. 1 as occurring in 1914 for convenience.

These observations show that at the G.W.W., Plymouth, *Patella vulgata* attained a length of at least 30 mm. (see Fig. 1A) in the season 1911–1912 at an age of about one year (reckoning from Sept. to Sept.), and a length of 53 mm. (see Fig. 1A) at an age of not more than two years in the period reckoning from September, 1911, to September, 1913. In December, 1913, the spat of the season, 1912–1913, ranged in size from 11 to 26 mm. (see Fig. 1C) and grew to 37–41 mm. by May, 1914, and 47–49 mm. by September, 1914 (see Fig. 1D). It is important, however, to remember that 1911 was an unusually warm season and that 1912 was warmer than the average during the first nine months of the year. Most of the situations from which Patella were obtained at the G.W.W. were damp and in the shade, and at about half-tide level. All these circumstances are favourable for rapid growth of shell and for increase in length of shell at the expense of height, as will be shown in Part III of the " Observations on Patella." For these reasons I conclude that the growth-rate in length shown by these limpets is high, and that a much lower average rate will occur on the adjacent rocks and reefs in Plymouth Sound. In 1919–1920 10 limpets were measured *in situ* at the G.W.W. (see Table III, p. 872) from July to May, and show a slower growth-rate than in 1911–1912. It was found that small individuals (A and B) grew continuously, though more slowly in September and January than in the remainder of the period. Among larger individuals, i.e. above lengths of 23·0 mm., growth slackened only at the end of August and did not begin again until after February. The number of individuals observed is however small, and the results obtained can only be regarded as indicating the general phenomena of growth.

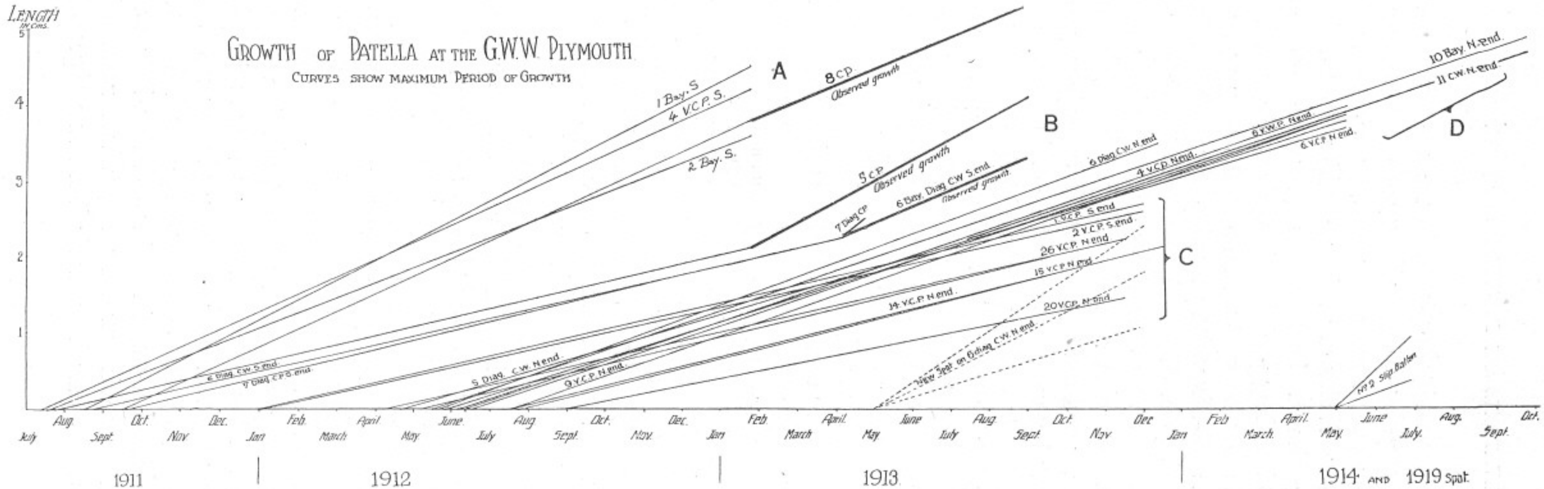

FIG. 1.—GRAPHIC REPRESENTATION OF OBSERVATIONS ON THE RATE OF GROWTH OF *PATELLA VULGATA* BELOW HIGH-WATER NEAPS AT THE GREAT WESTERN RAILWAY WHARF, PLYMOUTH.

The length of the shell at the date of collection or observation is plotted against the date of completion of the structure on which the limpets were found. Thus each graph gives the maximum period of growth, and shows by its slope the minimum mean rate of growth. The thickened lines show the mean rate of growth given by the field observations shown in Table II, p. 870.

In Table I, p. 868, details are given of the greatest possible age of the limpets collected at the G.W.W., and also the probable mean age at the sizes given.

Since spat may fall at any time between September and May, the mean date of the fall of spat may be fixed in January. Field observations in 1913, 1914, and 1919 indicated that the main spatfall occurred about April–May. So that the mean period of growth and probable mean age given in Table I is regarded as likely to be too great in most cases. There is undoubtedly great variation in the size (length) of spat as a result of the drawn-out spawning season—apart from other considerations affecting size—so that it is impossible to dogmatise on the age of any limpet to within a few months. In Scottish limpets Russell (loc. cit., 1909) estimates the lengths at one year old as 20 to 25 mm., at two years 38 mm., about 43 in the third, and 45–48 at the end of the fourth year, whereas it has been shown above that at Plymouth a length of 53 mm. was attained at age certainly not more than two years. Moreover, a glance at A, Fig. 1, p. 866, will show that some limpets spatted in 1911 would in all probability have attained lengths of up to 60 mm.—from the trend of observed and plotted rate of growth—at an age of only two years.

The observations in Scotland and at Plymouth may be compared as follows :—

	Lengths in mm. at 1 year.	2 years.	3 years.	4 years
Scotland, 1908	20–25	38	43	45–48
Plymouth, 1912	26–35	53	—	—
,, 1913	11–27	47–49	—	—

These considerations show in the first place that the limpets spatted at Plymouth in 1911–1912 must be regarded as showing exceptional growth in length, and show in the second place that all the factors regarding shells should be known in order to compare samples from different localities or seasons. It will be shown in a later communication that the relations of length and breadth of the shells given in Table I are similar to those of most limpets growing between H. and L.W. neaps, but the heights and thicknesses are apparently a little less than usual in mid-tide limpets.

An illustration of the variation in the rate of growth of shell in different habitats is afforded by continuous records (see Table IV, p. 872) made on 11 marked shells *in situ* on the rocks in the lower barnacle zone below the Hoe, Plymouth, from July, 1919, to August, 1920. The limpets were all about one inch long and were attached to a rock facing south, and exposed to sun during spring tides. Seven of the shells showed very slight or no growth, and of the others the maximum increase in length was 3·4 mm., and the average 2·6 mm. ; while the average increase in length of all the

TABLE I.

Records of Rate of Growth* of *Patella vulgata* at the Great Western Railway Wharf, Millbay Docks, Plymouth.

(V.=vertical; H.=horizontal; C.P.=cement pile; C.W.=cement waling; W.P.=wooden pile; S.=south; N.=north; h.=height of shell.)

No. of observations.	Site of observation.	No. of individuals.	Maximum period of growth.	Greatest possible age to nearest calendar month.	Probable mean period of growth.	Probable mean age to nearest calendar month.	Maximum size in mm. Length (l) ×	Breadth (b)	Remarks† Measurements in mm.
			1911 1913						
1	1 Inner Bay, S.	6	Sept. 9–Jan. 7	17	Jan., 1912–Jan., 1913	13	46·5	38·0	h=12·5 mm.
2	4 V.C.P., S.	1	July 13–Jan. 25	20	,, ,,	13	43·0	35·0	h=16·0; ripe female.‡
3	2 Bay, S.	3	July 15–Jan. 28	20	,, ,,	13	37·0	31·0	ripe male‡
4	1 Outer Bay, S.	5	Aug. 12–Jan. 25	18·5	,, ,,	13	46·0	39·0	h=14·5; 2 ripe ♀, 1 ripe§ ♂.
5	5 C.P., S.	1	July 22–Jan. 27	20	May, 1912–Jan., 1913	8	21·0	16·0	
6	,,	1	27.1.13–2.9.13	27	—	15	41·0	33·0	observed growth=20 mm., see Fig. 2.
7	8 C.P., S.	1	Sept. 16–Jan. 27	17·5	Jan., 1912–Jan., 1913	13	38·0	32·0	
8	,,	1	27.1.13–2.9.13	25	—	20	53·0	45·0	observed growth=15 mm., see Fig. 2.
9	6 Diag. C.W., S.	1	Sept. 16–April 4	20	May, 1912–April, 1913	12	22·5	17·0	
10	,,	1	4.4.13–2.9.13	25	—	17	33·0	28·5	observed growth=10·5 mm., see Fig. 2.
11	8 C.P., S.	6	Sept. 16–July 18	—	Jan., 1913–July, 1913	3 to 6	14·0	—	1913 spat; 9 to 14 mm.‖
12	6 V.C.P., S.	9	Aug. 19–Sept. 16	—	Jan., 1913–Sept., 1913	5 to 8	21·0	—	,, 12 to 21 mm.‖
			1912 1913						
13	14 V.C.P., N.	4	July 12–Dec. 16	—	Jan., 1913–Dec., 1913	9 to 12	21·0	16·0	,, 10 to 21 mm.
14	15 V.C.P., N.	1	July 27– ,,	—	,, ,,	,,	21·0	15·8	,,
15	26 V.C.P., N.	1	May 4– ,,	—	,, ,,	,,	22·0	16·0	,,

16	20 V.C.P., N.	2	Sept. 30–	Dec. 16	—	May, 1913–Dec., 1913	9	14·5	11·5	1913 spat; 13·5 to 14·5 mm.
17	19 V.C.P., S.	10	Jan. 9–	,,	25	Jan., 1913–Dec., 1913	9 to 12	27·0	20·8	,, from 11 × 8·8.
18	21 V.C.P., S.	3	Jan. 20–	,,	25	,, ,,	9 to 12	26·0	20·5	,, from 24·8 × 17·6.
19	6 Diag. C.W., N.	8	May 20– 1912	Dec. 12 1914	21	May, 1912–Dec., 1913	19	36·0	31·0	also six 1913 spat, 11 to 24 mm.
20	All parts	∞	—	June 9	—	Jan.–June, 1914	3 to 6	10·0	—	∞ 1914, spat up to ca. 10 mm.
21	4 V.C.P., N.	1	June 11–	,,	26	Jan., 1913–June, 1914	18	40·0	33·5	
22	5 Diag. C.W., N.	6+10	May 20–	,,	26·5	,, ,,	18	37·0	—	5 others 34 to 37, and 10 1914 spat to 10 mm.
23	6 V.C.P., N.	13+ ∞	June 21–	,,	25·5	,, ,,	18	39·0	33·5	12 others 30 to 38, and 1914 spat to 10 mm.
24	10 Bay C.W., N.	2	July 19–	,,	24·5	,, ,,	18	41·0	34·0	and one 36 × 29 mm.
25	9 V.C.P., N.	3+ ∞	Aug. 17–	,,	23·5	,, ,,	18	39·0	34·0	and 32 and 38; and ∞ 1914 spat to 10 mm.
26	6 V.W.P., N.	4	July 18–	,,	24·5	,, ,,	18	39·0	32·0	also 38 × 31, 32 × 26, and 30 × 25 mm.
27	10 Bay, N.	20	June 17–	Oct. 23	30	Jan., 1913–Oct., 1914	22	49·0	46·0	
28	11 Bay, N.	35	,, 1919	,, 1919	30	,, ,,	22	47·0	—	
29	No. 2 Slip, Batten	3	Oct. (1918)	June 28	ca. 6	Jan., 1919–June, 1919	2 to 6	9·2	—	1919 spat,‖ 7 to 9·2 mm.
30	No. 2 Sewer-pipe, Batten	1	May	June 28	2	May, 1919–June, 1919	2	3·6	—	a 1919 spat.
31	Cawsand raft	145	July 16	Oct. 1920	—	Jan., 1920–Oct., 1920	6 to 10	13·0	—	1920 spat.

* The records of growth are for limpets growing mainly between H. and L W. neaps. The shells are mostly thin and of the low-water type, i.e. flat and broad with length, breadth, and height relationships closely similar to those of the Looe Island mid-tide or low-water limpets, to be described in Part III of the "Observations on Patella."

† Unless otherwise noted the measurements refer to lengths in mm.

‡ Successful artficial fertilisations were made from these ripe individuals.

§ An artificial fertilisation of these individuals gave 10% segmenting eggs and, later, trochospheres.

‖ Spat ranging in length from a few to 10 mm. were observed in June in 1913, 1914, and especially in 1919, when they were found at the G.W.W., rocks below Plymouth Hoe, and Looe Island.

eleven shells for the whole period was only 1·3 mm., and less than 1 mm. for the period July to March in which all survived.

An arrest in shell-growth at lengths of about 25 mm. was observed by Russell (*Proc. Zool. Soc.*, 1909, p. 247), and two instances occur in Table III (D and E). It has been noted that a change in sex-proportion (see *Journ. M.B.A.*, XV, 3, p. 854) begins to show in populations of Patella at about this size, and it is highly probable that the observed arrest in growth is accompanied by profound changes in the gonad.

TABLE II

RATE OF GROWTH OF THREE MARKED *PATELLA VULGATA*, MEASURED* *IN SITU* AT THE GREAT WESTERN RAILWAY WHARF, PLYMOUTH (SEE FIG. 2, p. 871.)

(For explanation of symbols see Table I, p. 868.)

"Home" 1913	5 C.P., S. L	B	8 C.P., S. L	B	6 Diag. C.W., S. L	B
Jan. 27	21·0	16·0	38·0	32·0	—	—
Feb. 21	23·0	18·0	39·0	33·0	—	—
March 12	24·5	20·0	40·0	33·5	—	—
April 4	26·5	21·5	42·0	35·0	22·5	17·0
,, 23	29·0	23·5	43·5	37·5	25·0	19·0
May 23	32·5	26·5	44·5	39·0	27·5	22·5
June 20	36·0	28·0	48·5	42·0	31·5	25·5
July 4	38·0	30·0	50·0	43·0	32·0	25·0
,, 18	37·0	31·0	51·0	43·0	n.m.	—
Aug. 8	38·0	31·5	51·5	44·0	32·0	26·5
Sept. 2	41·0	33·0	53·0	45·0	33·0	28·5
,, 16	lost		lost		33·5	27·0

The shells of these limpets were impregnated by the calcareous lichen *Arthropyrenia foveolata*, as are most Patella and Balanus in this and similar localities, but it seems unlikely that either this or the marking of the shells with a file, and later with anti-fouling paint (which dries rapidly in the sun) can have contributed to more than a fraction, if any, of the observed arrest of growth.

PATELLA SPAT ON AN EXPERIMENTAL RAFT.

On July 16, 1919, a large wooden raft (20×6×2 ft.) was moored in Cawsand Bay for the purpose of carrying out general experiments on rate

* Measured to the nearest 0·5 mm.: errors of 1 mm. may occur by measuring the axis slightly obliquely; see also Tables III and IV.

of growth. On October 9, 1920, a large spatfall of 145 Patella was found on the surface of the raft, which was awash and covered with Enteromorpha. At this time the spat ranged in size (length) from 8 to 13 mm., and were therefore similar in size to the 1913 spat at the G.W.W. (see Fig. 1, p. 866). The raft was unfortunately destroyed in a gale late in December in the same year, and the lid on which the Patella were attached was lost. It had been hoped to determine the sex in all these individuals, which were known with certainty to have been spatted in the 1919–1920 season and were probably not more than 5 months old.

Seasonal Shell-growth.

The observations on seasonal shell-growth herein recorded are incomplete, and are to be regarded as preliminary investigations. It is now known that in order to establish satisfactorily the facts with regard to

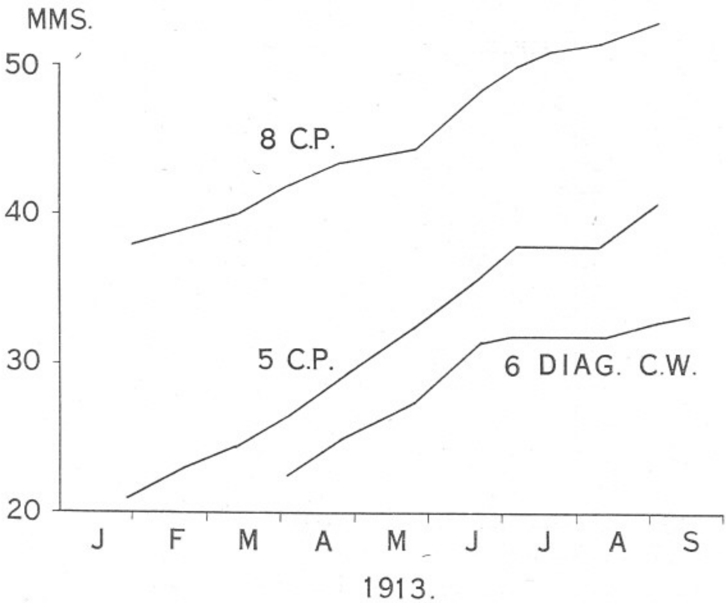

FIG 2.—Observed increase in length of the shell of three *Patella vulgata* at the Great Western Railway Wharf, Plymouth (see Table II, p. 870) showing an arrest of growth at mid summer; from measurements made at intervals of 2 or 4 weeks (Habitat: below H.W. neaps).

seasonal shell-growth, it is desirable to study the material in the field and laboratory fortnightly or monthly during several successive years in different localities.

Shell-growth in young individuals, up to a length of about 25 mm., appears to be almost continuous in the Plymouth district with a tendency

TABLE III.

Rate of Growth of some *Patella vulgata* which were Marked and Measured† *in situ* at the G.W.W. in 1919–1920. (L=length; B=breadth of shell.)

Individual	A.		B		C		D		E		F		G.		H.		I.	J.	
Site of "home."	7 V.C.P., S.		2 D.C.W., S.		7 V.C.P., S.		2 V.C.P., S.		1 V.C.W., S.		1 R.4P., S.		7 V.C.P., S.		8 C.P., S.		1 V.C.P., S.	11 V.C.P., S.	
1919–1920	L.	B.	L.	B.	L.	B.	L.	B.	L.	B.	L.	B.	L.	B.	L.	B.	L.	L.	B.
July 1 . .	11·0	8·0	13·0	9·5	23·5	18·0	24·0	19·0	24·0	20·0	26·0	20·0	28·5	23·0	—	—	33·0	37·0	31·5
,, 25 . .	13·0	9·0	16·0	12·0	23·0	19·0	26·0	21·0	24·5	21·0	29·0	22·5	30·5	24·0	—	—	33·5	38·0	31·5
Increase .	*2·0*	*1·0*	*3·0*	*2·5*	nil	*1·0*	*2·0*	*2·0*	*0·5*	*1·0*	*3·0*	*2·5*	*2·0*	*1·0*	—	—	*0·5*	*1·0*	nil
Aug. 25* . .	15·0	11·0	17·2	14·0	26·0	21·0	27·0	21·5	25·0	21·5	31·5	24·5	32·0	25·5	—	—	35·5	39·4	32·8
Increase .	*2·0*	*2·0*	*1·2*	*2·0*	*2·5*	*3·0*	nil	nil	*0·5*	*0·5*	*2·5*	*2·0*	*1·5*	*1·5*	—	—	*1·5*	*1·0*	*0·5*
Sept. 25* . .	16·0	12·0	18·4	14·2	lost		26·4	21·4	25·2	22·6	lost		lost		28·0	23·4	34·8	39·0	32·0
Increase .	*1·0*	*1·0*	*1·2*	nil	—		nil	nil	nil	*0!5*	—		—		—	—	nil	nil	nil
Oct. 29* . .	18·4	14·0	lost		—		26·6	22·0	25·8	22·6	—		—		28·6	24·4	35·0	39·4	32·2
Increase .	*2·4*	*2·0*	—		—		*0·5*	*1·0*	*0·5*	nil	—		—		*0·6*	*1·0*	nil	nil	nil
Dec. 12* . .	20·6	15·6	—		—		lost		26·2	22·0	—		—		28·6	24·4	35·4	39·4	32·0
Increase .	*2·2*	*1·6*	—		—		—		*0·5*	nil	—		—		nil	nil	nil	nil	nil
Feb. 7 . .	21·5	17·0	—		—		—		lost		—		—		lost		35·0	39·2	32·5
Increase .	*0·9*	*1·4*	—		—		—		—		—		—		—		nil	nil	*0·5*
May 4 . .	lost		—		—		—		—		—		—		—		lost	39·5	33·0
Total increase	**10·5**	**9·0**	**5·4**	**4·7**	**2·5**	**3·0**	**2·6**	**3·0**	**2·2**	**2·0**	**5·5**	**4·5**	**3·5**	**2·5**	nil	nil	**2·0**	**2·5**	**1·5**

TABLE IV.

Measurements† *in situ* of Marked *Patella vulgata* on the Needles, the Hoe, Plymouth, 1919, 1920.

1919–1920	I		II		III		IV		V		VI		VII		VIII		IX		X		XI	
July 3 . .	24·0	19·0	23·0	17·5	24·0	19·5	23·0	19·0	23·0	19·0	25·0	20·0	24·0	20·4	25·0	19·5	26·5	21·0	25·5	20·0	24·0	19·6
Aug. 1* . .	24·0	18·5	23·4	17·6	24·6	19·8	24·4	19·0	23·8	19·6	25·0	21·6	24·4	20·6	24·4	19·6	27·0	21·2	26·4	20·0	25·0	20·0
,, 29* . .	23·8	18·8	23·8	18·2	25·0	20·2	25·0	19·6	24·2	20·0	25·6	21·0	24·6	20·6	24·8	19·6	27·4	21·2	26·0	20·4	25·3	19·8
Oct. 8* . .	23·6	18·4	22·6	18·4	25·0	20·2	24·8	19·6	24·4	19·8	25·0	21·6	24·4	21·0	24·6	19·6	27·2	21·0	26·2	20·2	25·0	19·6
Nov. 24* . .	23·8	19·0	23·6	19·0	25·0	20·0	25·8	19·6	25·0	20·0	25·6	21·0	24·6	21·0	24·8	19·4	26·4	20·8	27·0	20·0	25·4	20·0
Jan. 26 . .	23·8	18·6	24·6	18·0	25·2	20·2	25·0	20·0	24·6	20·2	25·6	21·0	24·2	21·0	24·8	19·8	27·4	20·6	27·2	20·4	25·8	19·4
March 10* . .	24·0	19·0	24·4	18·0	24·8	20·2	25·2	20·0	24·4	19·8	25·6	21·2	24·0	21·0	25·0	19·6	27·2	21·0	27·0	20·6	25·2	20·0
Aug. 5* . .	lost		26·0	20·6	25·6	22·0	26·4	?	25·6	22·0	lost		lost		lost		lost		lost		lost	
Total increase	nil	nil	**3·0**	**3·0**	**1·6**	**2·5**	**3·4**	**1·5**	**2·6**	**3·0**	**0·6**	**1·2**	nil	**0·6**	nil	nil	nil	nil	**1·5**	**0·5**	**1·5**	nil

* Stanley rule divided into 0·2 mm. used with fine dividers. † In mms.

to slower growth at midsummer and in midwinter (see Tables II and III). At lengths of about 25 mm. there is an indication of an arrest of growth in some individuals—apart from seasonal arrest of growth (see Table IV and Table III, C, D, and E). Above lengths of about 30 mm. the growth-period becomes more sharply defined into at least a definite post-breeding spring and early summer phase followed apparently by a resting mid-summer period (see Fig. 2, p. 871), after which growth may or may not occur (see Tables II and III). The extent of the midsummer arrest of growth shown in Fig. 2 is not known, and remains to be investigated. The possibility of two shell-growing periods is indicated, and the problem presented is of importance in interpreting the growth-rings on the shells from any particular locality.

Definite investigations on general seasonal growth during a period of years combined with observations on sex and spawning are now desirable, with a view to defining the relation between breeding and shell-growth on the one hand and the relation of environmental (i.e. habitat and climatic) conditions to both breeding and shell-growth on the other hand.

Variations in Shell-shape and their Primary Cause.

In the course of studies on *Patella vulgata* particular attention has been given to the variations in shell-shape, especially shell-height, and the cause of the variations exhibited. The results of this portion of the work will be given later in Part III of the observations, in which it will be shown that limpets which are covered at neap tides have shells whose dimensions are given by the statement $\frac{L+B}{2(H)}=2{\cdot}55$ to $2{\cdot}81$, for lengths above 35 mm. of about 1000 individuals from different localities; and that limpets occurring above high-water neaps grow shells whose dimensions are given by $\frac{L+B}{2(H)}=1{\cdot}81$ to $2{\cdot}25$ (about 1000 individuals from different localities); where L=length, B=breadth, and H=height of shell. Among high-water shells the lower value for $\frac{L+B,}{2(H)}$ namely 1·81, is given by limpets in dry situations, and the high value by those in damp situations. These facts—along with certain observations—lead to the conclusion that the height of the shell in *Patella vulgata* is governed almost entirely by the sum of the factors which tend to cause the animals to dry up (the desiccation factor), and that therefore wave-action plays only a minor and secondary part in controlling shell-height.

The variations in shell-shape shown by limpets in different habitats is an important matter in relation to studies on rate of growth, and must necessarily be considered in such work.

SUMMARY.

Many common limpets, *Patella vulgata,* settled and grew on the cement piles of a new wharf constructed at Plymouth. Each pile or part of this wharf provided experimental material for the determination of the maximum age of the limpets which grew thereon, as the dates of completion were known. It was found that at an age of about one year limpets grew to lengths of 26 to 35 mm. in 1912, and to at least 11 to 27 mm. in 1913 : and at an age of two years to at least 53 mm. in 1911–1913, and to 47–49 mm. in 1912–1914.

The shells were of the mid-tide-level type, and were low, broad, and rather thin. It is considered that such growth in length is unusual, and is correlated with the habitat and favourable climatic conditions. In the same situation in 1913 marked limpets grew from January 27 to September 2, respectively, 20 mm. (from 21 to 41) and 15 mm. (from 38 to 53), and showed arrest of growth in midsummer.

Other marked limpets showed arrest of growth in the winter period, and many at lengths of about 25 mm. an arrest of growth independent of any season of growth. Seasonal shell-growth is discussed briefly ; a post-breeding shell-growing period is general in spring and early summer, but it is not known whether a midsummer resting-period is general among individuals more than one year old. *Ad hoc* investigations are suggested in combination with work on sex and spawning.

A preliminary notice is given of investigations into the cause of variation in shell-height, wherein it is shown that shell-height is determined probably entirely by the degree of exposure of limpets to desiccation, in such a manner that the drier the habitat the higher the shell is. Limpets submerged at neap tides have a relatively uniformly low shell, those exposed at high-water neaps have a relatively high shell, which is higher in the drier than in the damper situations, apparently irrespective of exposure to wave-action.

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